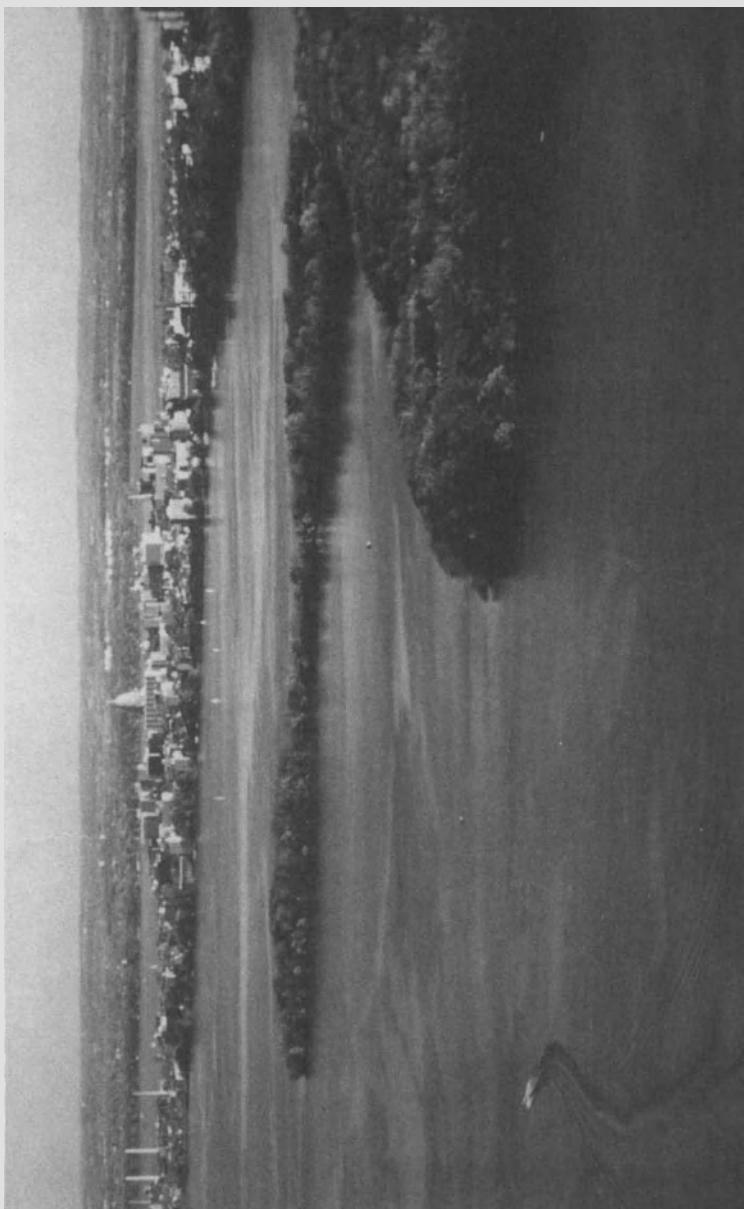


# **Springer Series on Environmental Management**

---

**Robert S. DeSanto, Series Editor**



James F. Kitchell  
Editor

# Food Web Management

A Case Study of Lake Mendota

With 177 Illustrations



Springer-Verlag  
New York Berlin Heidelberg London Paris  
Tokyo Hong Kong Barcelona Budapest

James F. Kitchell  
Center for Limnology  
University of Wisconsin  
Madison, WI 53706  
USA

Frontcover and frontispiece photo © 1992 by David H. Thompson. Used by permission.

*Frontispiece:* An aerial view of Lake Mendota, the capitol isthmus region of downtown Madison and Lake Monona (background). Picnic Point and Second Point (foreground) form the north shore of University Bay.

Library of Congress Cataloging-in-Publication Data  
Food web management: a case study of Lake Mendota / edited by James F. Kitchell.

p. cm.—(Springer series on environmental management)  
Papers presented at Lake Mendota Symposium, held on 20 July 1990 at Madison, Wisconsin.

Includes bibliographical references and index.

ISBN-13: 978-1-4612-8760-5 e-ISBN-13: 978-1-4612-4410-3

DOI: 10.1007/978-1-4612-4410-3

1. Biomanipulation—Wisconsin—Mendota, Lake—Congresses. 2. Food chains (Ecology)—Wisconsin—Mendota, Lake—Congresses. 3. Lake ecology—Wisconsin—Mendota, Lake—Congresses. 4. Water quality—Wisconsin—Mendota, Lake—Congresses. I. Kitchell, James, F.  
II. Lake Mendota Symposium (1990: Madison, Wis.) III. Series.

TD365.5.F66 1992

574.5'26322'09775—dc20

91-36725

Printed on acid-free paper.

© 1992 Springer-Verlag New York Inc.

Softcover reprint of the hardcover 1st edition 1992

All rights reserved. This work may not be translated or copied in whole or in part without the written permission of the publisher (Springer-Verlag New York, Inc., 175 Fifth Avenue, New York, NY 10010, USA), except for brief excerpts in connection with reviews or scholarly analysis. Use in connection with any form of information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed is forbidden.

The use of general descriptive names, trade names, trademarks, etc., in this publication, even if the former are not especially identified, is not to be taken as a sign that such names, as understood by the Trade Marks and Merchandise Marks Act, may accordingly be used freely by anyone.

Permission to photocopy for internal or personal use, or the internal or personal use of specific clients, is granted by Springer-Verlag New York, Inc. for libraries registered with the Copyright Clearance Center (CCC), provided that the base fee of \$0.00 per copy, plus \$0.20 per page is paid directly to CCC, 21 Congress St., Salem, MA 01970, USA. Special requests should be addressed directly to Springer-Verlag New York, 175 Fifth Avenue, New York, NY 10010, USA.

ISBN 0-387-97742-2/1992 \$0.00 + 0.20

Production managed by Bill Imbornoni; manufacturing supervised by Robert Paella.  
Typeset by Best-set Typesetter Ltd., Hong Kong.

9 8 7 6 5 4 3 2 1

## **Series Preface**

This series is dedicated to serving the growing community of scholars and practitioners concerned with the principles and applications of environmental management. Each volume is a thorough treatment of a specific topic of importance for proper management practices. A fundamental objective of these books is to help the reader discern and implement man's stewardship of our environment and the world's renewable resources. For we must strive to understand the relationship between man and nature, act to bring harmony to it, and nurture an environment that is both stable and productive.

These objectives have often eluded us because the pursuit of other individual and societal goals has diverted us from a course of living in balance with the environment. At times, therefore, the environmental manager may have to exert restrictive control, which is usually best applied to man, not nature. Attempts to alter or harness nature have often failed or backfired, as exemplified by the results of imprudent use of herbicides, fertilizers, water, and other agents.

Each book in this series will shed light on the fundamental and applied aspects of environmental management. It is hoped that each will help solve a practical and serious environmental problem.

Robert S. DeSanto  
East Lyme, Connecticut

# Preface

This book is a milestone in an ongoing, collaborative research effort. It is intended to convey a novel and polythetic view of a lake ecosystem which would complement the traditional limnological approach represented in the compilation of Brock (1985). Our approach is different in two major ways: (1) we emphasize food web interactions as the primary object of study and management, and (2) integrating the role of humans in an ecosystem context was a major concern for us. Stated as goals, those two major objectives demand an effective combination of the best of basic research, the most informed of resource management actions, and a holistic view.

The central objective of this program was to assess the potential for food web manipulation as a means for improving water quality in Lake Mendota. That assessment is a continuing process. This volume is a progress report. Critics of the program generally refused to accept that our goal was to explore the possibilities and that this required an ecosystem approach which, of necessity, demands a substantial commitment of time and money. What they considered a foolish and unnecessarily expensive pursuit we viewed as a responsible and courageous undertaking. Readers will judge for themselves, but I am totally convinced that this project is among the most cost-effective of large research efforts.

The second reason for this book was more pragmatic. The first generation of graduate students and postdoctoral researchers involved in the project was moving on to other pursuits; their interests in and capacity for synthesis of project results would logically wane with time away from Madison. In addition, our original design for the project included intensive

work during the period of 1987–89, followed by a lesser tenor (and smaller budget) for the years that followed. A focus point for a collective reporting and summary of accomplishments to date seemed highly desirable. Accordingly, we discussed the means for providing the desired focus and agreed to organize a widely advertised symposium targeted for an audience composed of research scientists, resource managers, and representatives of the several and varied public groups interested in Lake Mendota.

The Lake Mendota Symposium was held on 20 July 1990. It produced a surprisingly large audience that included substantial representation from each of the various sectors of interest. Contributors were asked to prepare manuscripts prior to the Symposium and to resist the temptations of tomorrow by confining their analyses to data collected no more recently than 1989. Those manuscripts are assembled in this volume. As stated above, they represent a progress report from individuals and groups willing to collaborate in accepting the challenge of working on an important set of complex questions.

Two important conclusions can be emphasized here and will become more apparent in the subsequent pages. During the first two years of the study, Mother Nature provided us with a major fish die-off followed by a dry spring. In combination, those events offered a serendipitous view of what was possible when food web interactions were substantially altered and nutrient loading was low. One of our major conclusions is that food web interactions can have remarkable effects on water quality. The summer of 1988 had the greatest water clarity and least objectionable algal blooms reported in any of the written or oral history of Lake Mendota. The summers that preceded and followed it included equally remarkable evidence of the opposite extreme. Clearly, understanding of food web–nutrient loading interactions is a next and necessary research objective.

Our second major conclusion derives from a broader range of lessons. Managing an aquatic food web to allow for interactions with the effects of the top predator—anglers—presents some interesting new challenges. The functional and numerical response of humans that fish must be incorporated in an integrated, realistic, and effective view of water quality management.

In my opinion, Chapters 26 and 27 of this book are of unique and immense importance. They represent our attempts to be accountable to other citizens through the agency mandated to represent their interests. Taxpayers foot the bill for research and rightfully expect to see something practical come of it. In this case, the benefits are those that derive from the ivory tower and become the working tools of resource managers. Some of those tools are analytical, others are conceptual. As Jim Addis puts it in Chapter 2, this is the Wisconsin Idea at work.

I am grateful for the opportunity to help in assembling the components of this effort.

**Reference**

Brock TD (1985) A eutrophic lake: Lake Mendota, Wisconsin. Springer-Verlag, New York

## Acknowledgments

First and foremost I thank the scientists whose work is represented in the pages of this volume. Their creativity, enthusiasm, and cooperation were the essential requisites of this result. As is apparent in the authorship of individual chapters, the leadership and perseverance of Steve Carpenter and Dick Lathrop made exceptional contributions to this effort. Similarly, Brett Johnson, Chris Luecke, and Lars Rudstam deserve special recognition for their role as coordinators of regular meetings and communication among members of the project staff. That kept the program on track; we all profited from their unselfish and effective contribution.

Jim Addis' assertive approach catalyzed this program. His dedication to building strong ties between the University of Wisconsin (UW) and the Wisconsin Department of Natural Resources (WDNR) created both the financial resources and the administrative support that fostered this result and those that follow.

Arthur Hasler regularly offered the benefits of his extensive familiarity with the behavior of Lake Mendota and the holistic view that comes with experience. We genuinely appreciate his encouragement and wise counsel. Linda Holthaus served faultlessly in every administrative aspect of organizing the Lake Mendota Symposium and all that followed in compiling the contributions to this volume. Her remarkable organizational skills brought order from the editor's chaotic desk. John Magnuson, Dave Egger, and Mike Staggs saw to it that money and paper moved with a minimum of resistance through the complex bureaucracies of two large state institutions. We sincerely appreciate that. Phil Emmling, acting on behalf of the Yahara Fishing Club, worked as a liaison between the

research scientists, managers, and anglers. His interest in the program and his candid advice were most valuable.

The major source of financial support to this program derived from the Federal Aid to Sport Fish Restoration Act under Project F-95-P and the WDNR. The Graduate School, UW-Madison, provided essential financial support to help defray the costs of the Lake Mendota Symposium. The Bassett Foundation catalyzed an important and continuing investment in research through their establishment of a professorship for the Madison lakes. Steve Carpenter was added to our faculty as a result. Ancillary funding to some project investigators is acknowledged where appropriate in individual chapters. We also thank Christine Bartels of Springer-Verlag's editorial staff for encouraging the opportunity to compile and synthesize the many aspects of this effort.

James F. Kitchell  
Madison, WI

# Contents

Series Preface	v
Preface	vii
Acknowledgments	xi
Contributors	xvii
<b>1. Introduction: The Rationale and Goals for Food Web Management in Lake Mendota <i>James F. Kitchell</i></b>	1
<b>2. Policy and Practice in UW–WDNR Collaborative Programs <i>James T. Addis</i></b>	7
<b>3. Lake Mendota and the Yahara River Chain <i>Richard C. Lathrop</i></b>	17
<b>4. Paleolimnological Evidence of Food Web Dynamics in Lake Mendota <i>James F. Kitchell and Patricia R. Sanford</i></b>	31
<b>5. Historical Interpretation of Pigment Stratigraphy in Lake Mendota Sediments <i>James P. Hurley, David E. Armstrong, and Andrea L. DuVall</i></b>	49
<b>6. Nutrient Loadings, Lake Nutrients, and Water Clarity <i>Richard C. Lathrop</i></b>	69

<b>7. Phytoplankton and Their Relationship to Nutrients</b> <i>Richard C. Lathrop and Stephen R. Carpenter</i>	97
<b>8. Zooplankton and Their Relationship to Phytoplankton</b> <i>Richard C. Lathrop and Stephen R. Carpenter</i>	127
<b>9. Long-Term Vegetation Trends: A History</b> <i>Stanley A. Nichols, Richard C. Lathrop, and Stephen R. Carpenter</i>	151
<b>10. Benthic Macroinvertebrates</b> <i>Richard C. Lathrop</i>	173
<b>11. Historical Changes in the Fish Community</b> <i>John J. Magnuson and Richard C. Lathrop</i>	193
<b>12. Food Web Structure of Lake Mendota</b> <i>Lars G. Rudstam, Yvonne Allen, Brett M. Johnson, Chris Luecke, John R. Post, and Michael J. Vanni</i>	233
<b>13. Herbivory, Nutrients, and Phytoplankton Dynamics in Lake Mendota, 1987–89</b> <i>Michael J. Vanni, Jo Temte, Yvonne Allen, Richard Dodds, Patricia J. Howard, Peter R. Leavitt, and Chris Luecke</i>	243
<b>14. Interannual Patterns of Planktivory 1987–89: An Analysis of Vertebrate and Invertebrate Planktivores</b> <i>Chris Luecke, Lars G. Rudstam, and Yvonne Allen</i>	275
<b>15. Pelagic Planktivory by Larval Fishes in Lake Mendota</b> <i>John R. Post, Lars G. Rudstam, Denise M. Schael, and Chris Luecke</i>	303
<b>16. Piscivores and Their Prey</b> <i>Brett M. Johnson, Stephen J. Gilbert, R. Scot Stewart, Lars G. Rudstam, Yvonne Allen, Don M. Fago, and David Dreikosen</i>	319
<b>17. The Fishery</b> <i>Brett M. Johnson and Michael D. Staggs</i>	353
<b>18. Modeling in the Lake Mendota Program: An Overview</b> <i>Stephen R. Carpenter</i>	377

Contents	xv
<b>19. Fisheries Management and the Interactive Dynamics of Walleye and Perch Populations</b> <i>John R. Post and Lars G. Rudstam</i>	381
<b>20. Impacts of Variation in Planktivorous Fish on Abundance of Daphnids: A Simulation Model of the Lake Mendota Food Web</b> <i>Chris Luecke, Cynthia C. Lunte, Russell A. Wright, Dale Robertson, and Ann S. McLain</i>	407
<b>21. A Simulation Model of the Interactions Among Nutrients, Phytoplankton, and Zooplankton in Lake Mendota</b> <i>Michael J. Vanni, Stephen R. Carpenter, and Chris Luecke</i>	427
<b>22. Modeling the Lake Mendota Ecosystem: Synthesis and Evaluation of Progress</b> <i>Stephen R. Carpenter, Brett M. Johnson, Chris Luecke, Charles P. Madenjian, John R. Post, Lars G. Rudstam, Michael J. Vanni, Xi He, Yvonne Allen, Richard Dodds, Kathleen McTigue, and Denise M. Schael</i>	451
<b>23. Destabilization of Planktonic Ecosystems and Blooms of Blue-Green Algae</b> <i>Stephen R. Carpenter</i>	461
<b>24. An Analogy for Plankton Interactions</b> <i>Peter R. Leavitt</i>	483
<b>25. Individual-Based Modeling: Application to Walleye Stocking</b> <i>Charles P. Madenjian, Brett M. Johnson, and Stephen R. Carpenter</i>	493
<b>26. Development, Evaluation, and Transfer of New Technology</b> <i>Lars G. Rudstam and Brett M. Johnson</i>	507
<b>27. Benefits on a Larger Scale</b> <i>Michael D. Staggs</i>	525
<b>28. Summary: Accomplishments and New Directions of Food Web Management in Lake Mendota</b> <i>James F. Kitchell and Stephen R. Carpenter</i>	539
<b>Index</b>	545

# Contributors

*James T. Addis*, Division of Resource Management, Wisconsin Department of Natural Resources, Madison, WI 53707, USA

*Yvonne Allen*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA

*David E. Armstrong*, Water Chemistry Program, University of Wisconsin-Madison, Madison, WI 53706, USA

*Stephen R. Carpenter*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA

*Richard Dodds*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA

*David Dreikosen*, Fish Research, Wisconsin Department of Natural Resources, Fitchburg, WI 53711, USA

*Andrea L. DuVall*, Water Chemistry Program, University of Wisconsin-Madison, Madison, WI 53706, USA

*Don M. Fago*, Bureau of Research, Wisconsin Department of Natural Resources, Fitchburg, WI 53711, USA

*Stephen J. Gilbert*, Fisheries Management, Wisconsin Department of Natural Resources, Fitchburg, WI 53713, USA

*Xi He*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA

*Patricia J. Howard*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA

*James P. Hurley*, Bureau of Research, Wisconsin Department of Natural Resources, Fitchburg, WI 53711, USA

*Brett M. Johnson*, Fisheries Management, Wisconsin Department of Natural Resources, Fitchburg, WI 53713, USA

*James F. Kitchell*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA

*Richard C. Lathrop*, Bureau of Research, Wisconsin Department of Natural Resources, Fitchburg, WI 53711, USA

*Peter R. Leavitt*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA (Current address: Department of Zoology, University of Alberta, Edmonton, Alberta, Canada T6G 2E9)

*Chris Luecke*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA (Current address: Department of Fisheries and Wildlife, Utah State University, Logan, UT 84322-5210, USA)

*Cynthia C. Lunte*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA (Current address: Route 1, Loving Creek Ranch, Bellevue, ID, 83313, USA)

*Charles P. Madenjian*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA (Current address: U.S. Fish and Wildlife Service, Sandusky Biological Station, Sandusky, OH 44870, USA)

*John J. Magnuson*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA

*Ann S. McLain*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA

*Kathleen McTigue*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA

*Stanley A. Nichols*, Geological and Natural History Survey, University of Wisconsin-Madison, Madison, WI 53706, USA

*John R. Post*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA (Current address: Department of Biological Sciences, University of Calgary, Calgary, Alberta, Canada T2N 1N4)

*Dale Robertson*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA (Current address: U.S. Geological Survey, Water Resources Division, 6417 Normandy Lane, Madison, WI 53719, USA)

*Lars G. Rudstam*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA

*Patricia R. Sanford*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA

*Denise M. Schael*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA (Current address: Department of Zoology, North Carolina State University, Raleigh, NC 27695-7617, USA)

*Michael D. Staggs*, Bureau of Fisheries Management, Wisconsin Department of Natural Resources, Madison, WI 53707, USA

*R. Scot Stewart*, Fisheries Management, Wisconsin Department of Natural Resources, Fitchburg, WI 53713, USA

*Jo Temte*, Bureau of Water Resource Management, Wisconsin Department of Natural Resources, Madison, WI 53707, USA

*Michael J. Vanni*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA (Current address: Department of Zoology, Miami University, Oxford, OH 45056, USA)

*Russell A. Wright*, Center for Limnology, University of Wisconsin-Madison, Madison, WI 53706, USA

# 1

## Introduction: The Rationale and Goals for Food Web Management in Lake Mendota

**James F. Kitchell**

Lake Mendota is often identified as the “most studied” lake in the world (Brock 1985). Nevertheless, its unpredictable and undesirable behavior—as evidenced in irruptive blooms of noxious blue-green algae, explosive colonization by exotic species, and variable fish populations—continues to fascinate researchers, frustrate managers, and irritate the public. Among the least likely phrases heard in discussions of Lake Mendota is “This has been a typical year.”

Noxious algal blooms are the most commonly perceived water quality problem, and the most parsimonious way to reduce them is to reduce the nutrient load that starts the production process (Schindler 1977, 1981). In the case of Lake Mendota, most of the easily controlled point sources of nutrients were already being regulated or diverted (Brock 1985). Reducing diffuse inputs such as those from agricultural lands or construction activities is more difficult and expensive (Cooke et al. 1986). Although the reversal of cultural eutrophication was underway (Lathrop, Ch. 10) and efforts to accomplish further nutrient reduction continue, the rate of improvement of Lake Mendota’s water quality was a challenge to public patience. Alternative or additional management approaches became of greater interest. As described by Addis (Ch. 2), one of those alternatives was developing in the form of food web manipulation.

The idea of altering food web structure or “biomanipulation” as a means for improving water quality owes much to the work of Joe Shapiro and his associates (Shapiro et al. 1975). Those ideas stem from the early observations of Hrbacek et al. (1961) and Brooks and Dodson (1965), and have a terrestrial analogue in the work of Hairston et al.

(1960). Each of these pioneering studies pointed out that the production and biomass of primary producers reflected the intensity of grazing by herbivore populations, which are controlled by their predators. In lakes, the most important grazers are large zooplankton, which are strongly impacted by predaceous invertebrates and many small fishes (Kerfoot and Sih 1987). Piscivores, in turn, can regulate the zooplanktivorous fishes and, of course, are often the target of active fisheries. Logically, controlling predator-prey interactions that start at the top of the food web is one way to regulate the algae and could be pursued in conjunction with the necessary and continuing efforts to reduce nutrient inputs.

A growing body of theory (Brocksen et al. 1970; Paine 1980; Carpenter et al. 1985; Carpenter and Kitchell 1988) gave encouragement to the prospect that intensive management of predator populations could accelerate the rate of improvement of Lake Mendota's water quality. The tenor of activities related to food web interactions has increased dramatically in the recent past (Carpenter 1988; Oksanen 1991). Reviews by Northcote (1988), McQueen (1990), and Carpenter et al. (1991) and a symposium volume filled with case studies (Gulati et al. 1990) attest to the popularity of the approach and provide a diversity of evidence that it works sometimes and in some places but not every time and in all places (Shapiro 1990; Carpenter and Kitchell 1991; DeMelo et al. 1991).

In a practical sense, manipulating the food web of a large, eutrophic lake requires a significant increase in the populations of large predators (walleye and northern pike) so that certain smaller fishes (cisco and yellow perch) become less abundant. Prey of the smaller fishes', the zooplankton, should then increase in size and abundance to a sufficient extent that grazing on algae reduces the frequency and magnitude of algal blooms. This simple chain of logic requires a number of assumptions about how food webs work. It also requires a management program that will protect the highly desirable large predators from the angling public known to be very effective at reducing fish populations.

The original project design called for a substantial and long-term commitment from the funding agency (Wisconsin Department of Natural Resources, WDNR). That is an atypical expectation in the current context of research funding. We argued that it would take several years to see the effects and that if we were going to do this, we should do it right! Three years of intensive experimental and theoretical work would be followed by a longer period (6 years) of more modest monitoring and a support to the concluding synthesis. That time was dictated by the lags expected for major effects of the stocked cohorts of predators.

We began this effort with a good theoretical foundation, a substantial knowledge of the basic limnology of Lake Mendota, and a willingness to accept the high-risk challenge issued to us by Jim Addis. We were attempting an unproven management approach under the many watchful eyes of an informed, concerned citizenry and within a stone's throw of the Wisconsin State Capitol building. We ventured into this in the spirit of

the adaptive management approach advocated as a way to learn more quickly about the mysteries of large, complex systems (Walters 1986; Walters and Holling 1991) because we believed that waiting for more data was largely a waste of time. At a minimum, we expected that anglers would see some benefits in the availability of large fishes and that we would have a better understanding of this ecosystem. We made a major effort to convey our goals to the various public interest groups and asked their cooperation. We prayed for “average” weather.

As described in the Preface, this volume derived from the Lake Mendota Symposium. It is supplemented with contributions we felt would increase its general value and is organized around three general themes. Chapters 1–11 set the institutional, geographic, and historical context. They include paleolimnological perspectives and the analysis of several unique, long-term data sets. Chapters 12–17 reflect the results of the 3 years of intensive study that began the project. They ascend through the trophic system in a mixture of experimental and empirical approaches. Chapters 18–25 offer a diversity of modeling techniques developed by project staff. In keeping with arguments for a balanced view, they descend from fish population dynamics to the issues of algal blooms. Much of the modeling effort derived from a course taught by Steve Carpenter. Accordingly, we asked him to set the context by providing a brief overview of the modeling papers. As is apparent, no all-inclusive ecosystem model was sought. Instead, models are constructed to scales most appropriate to the questions at hand. The last three chapters offer an accounting of technology transfer, the learning that follows from collaborative ventures, and an attempt to distill the most important results of this effort.

For those that read all or most of this book, it should be readily apparent that we have attempted to avoid imposing a single view on the interpretations of authors. Regular meetings and discussions during the term of the project, preparation for and participation in the Lake Mendota Symposium, plus the round of internal reviews of chapters, have, we believe, established sufficient expectation for the rigor of analyses and the defensibility of conclusions. Authors have advanced their own interpretations of evidence. These differ on some issues and serve as the basis for a healthy, continuing debate.

The accomplishments of this project illustrate directions many scientists feel are essential to the future of limnology and aquatic ecology (Likens 1985; Schindler 1987). Lake Mendota offers a whole-ecosystem test of ideas that have become the focus of intense debate about the relative importance of nutrients and food web interactions as the dominant controls of lake systems (Persson et al. 1988). This dichotomy is often referred to as the “top-down vs. bottom-up” issue (McQueen 1990). Forcing that choice is a dangerous simplification and an unfortunate disservice. What we really need to know about is the nature and importance of interactions when considered at the scale of whole systems. Tests

of mechanisms through reductionism can offer insights but also can lead to confusion (Carpenter and Kitchell 1988; Carpenter et al. 1991). In practice, lakes and fish populations are managed at the whole-system scale. The hard reality is that more experiments must accommodate to that (Kitchell et al. 1988).

A second unique value of this effort is that it explicitly includes the human dimension in an ecosystem context. Limnologists will learn a lot about what fisheries management is and does. Knowing more about managers is a growing necessity for ecological science (Walters and Holling 1991; Lubchenco et al. 1992) and of particular relevance for aquatic ecology (Carpenter and Kitchell 1991). The challenge of global change issues and the growing need for advice at the regional and local scales demand that ecologists accept the responsibility of focusing their efforts on questions that cross the boundaries between research and management (Cullen 1990). Good science and good management are hard to do. Creative science that fosters better management is even more challenging and ever more necessary.

### References

- Brock TD (1985) A eutrophic lake: Lake Mendota, Wisconsin. Springer-Verlag, New York
- Brocksen RW, Davis GE, Warren CE (1970) Analysis of trophic processes on the basis of density-dependent functions. In Steele JH (ed) Marine food chains, Oliver & Boyd, Edinburgh, pp 468–498
- Brooks JL, Dodson SI (1965) Predation, body size, and the composition of plankton. *Science* 150:28–35
- Carpenter SR (ed) (1988) Complex interactions in lake communities. Springer-Verlag, New York
- Carpenter SR, Frost TM, Kitchell JF, Kratz TK, Schindler DW, Shearer J, Sprules WG, Vanni MJ, Zimmerman AP (1991) Patterns of primary production and herbivory in 25 North American lake ecosystems. In Cole M, Findlay S, Lovett G (eds) Comparative analyses of ecosystems: Patterns, mechanisms, and theories, Springer-Verlag, New York
- Carpenter SR, Kitchell JF (1988) Consumer control of lake productivity. *BioScience* 38:764–769
- Carpenter SR, Kitchell JF (1992) Trophic cascade and biomanipulation: Interface of research and management. *Limnol. Oceanogr.* (in press)
- Carpenter SR, Kitchell JF, Hodgson JR (1985) Cascading trophic interactions and lake productivity. *BioScience* 35:634–639
- Cooke GD, Welch EB, Peterson SA, Newroth PR (1986) Lake and reservoir management. Butterworths, Boston
- Cullen P (1990) The turbulent boundary between water science and water management. *Freshwater Biol.* 24:201–209
- DeMelo R, France R, McQueen DJ (1992) Biomanipulation: Hit or myth? *Limnol. Oceanogr.* (in press)
- Gulati RD, Lammens EHRR, Meijer M-L, van Donk E (eds) (1990) Biomanipulation—Tool for water management. Kluwer Academic Publishers, Belgium

- Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. *Am. Nat.* 94:421–425
- Hrbacek J, Dvorakova M, Korinek V, Prochazkova L (1961) Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. *Int. Ver. Theor. Angew. Limnol. Verh.* 14:192–195
- Kerfoot WC, Sih A (eds) (1987) Predation: Direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire
- Kitchell JF, Bartell SM, Carpenter SR, Hall DJ, McQueen DJ, Neill WE, Scavia D, Werner E (1988) Epistemology, experiments, and pragmatism. In Carpenter SR (ed) Complex interactions in lake communities, Springer-Verlag, New York, pp 263–280
- Likens GE (ed) (1985) An ecosystem approach to aquatic ecology. Springer-Verlag, New York
- Lubchenco J, Olson AM, Brubaker LB, Carpenter SR, Holland MM, Hubbell SP, Levin SA, MacMahon JA, Matson PA, Melillo JM, Mooney HA, Peterson CH, Pulliam HR, Real LA, Regal PJ, Risser PJ (1991) The sustainable biosphere initiative: An ecological research agenda for the nineties. *Ecology* 72:371–412
- McQueen DR (1990) Manipulating lake community structure: Where do we go from here? *Freshwater Biol.* 23:613–620
- Northcote TG (1988) The role of fish in the structure and function of freshwater ecosystems: A “top-down” view. *Can. J. Fish. Aquat. Sci.* 45:361–379
- Oksanen L (1991) Trophic levels and trophic dynamics: A consensus emerging? *Trends Ecol. Evol.* 6:58–60
- Paine RT (1980) Food webs, linkage interaction strength, and community infrastructure. *J. Anim. Ecol.* 49:667–685
- Persson L, Andersson G, Hamrin SF, Johansson L (1988) Predator regulation and primary production along the productivity gradient of temperate lake ecosystems. In Carpenter SR (ed) Complex interactions in lake communities, Springer-Verlag, New York, pp 45–68
- Schindler DW (1977) Evolution of phosphorus limitation in lakes. *Science* 195:260–262
- Schindler DW (1981) Studies of eutrophication in lakes and their relevance to the estuarine environment. In Neilson BJ, Cronin LE (eds) Estuaries and nutrients, Humana, Clifton, New Jersey, pp 71–82
- Schindler DW (1987) Detecting ecosystem response to anthropogenic stress. *Can. J. Fish. Aquat. Sci. (suppl.)* 44:6–25
- Shapiro J (1990) Biomanipulation: The next phase—making it stable. In Gulati RD, Lammens EHRR, Meijer M.-L., van Donk E (eds) Biomanipulation—Tool for water management, Kluwer Academic Publishers, Belgium, pp 13–27
- Shapiro J, Lamarra V, Lynch M (1975) Biomanipulation: An ecosystem approach to lake restoration. In Brezonik PL, Fox JL (eds) Proceedings of a symposium on water quality management through biological control, University of Florida, Gainesville, Florida
- Walters C (1986) Adaptive management of renewable resources. Macmillan, New York
- Walters CJ, Holling CS (1991) Large-scale management experiments and learning by doing. *Ecology* 71:2060–2068



**Plate 1.** Setting a gill net as part of the fisheries assessment program. The Wisconsin State Capitol building is a prominent feature of the Madison skyline.

# **2**

## **Policy and Practice in UW–WDNR Collaborative Programs**

**James T. Addis**

### **Introduction**

The Wisconsin Idea, a concept that encourages University of Wisconsin faculty to work with state government to solve significant state problems, creates a special working relationship between the Wisconsin Department of Natural Resources (WDNR) and the University of Wisconsin (UW). It leads administrators to encourage and reward staff for collaborating to solve statewide problems. It accelerates the application of state-of-the-art academic knowledge to solve important statewide problems. This chapter presents an example of the Wisconsin Idea expressed in greater detail through the subsequent pages of this volume.

### **Genesis of the Program**

The Lake Mendota whole-lake manipulation is a collaborative effort between the UW Center for Limnology and the WDNR. My charge is to explain how the project came about, and how the relationship we have developed might benefit other agencies facing similar problems.

During the early 1980s declining walleye populations in Lake Mendota virtually eliminated walleye fishing. Panfish abundance increased, but the fishery was dominated by small fish of little interest to anglers. Nuisance algae blooms and weed-choked shorelines brought calls for action from all segments of the public. Non-point programs funded by local govern-

ments and the WDNR were established to reduce nutrient loading. To partially remedy nuisance problems, local governments sponsored weed harvesting programs. In addition, lake property owners privately funded chemical control of macrophytes and algae.

Chemical control and harvesting are controversial—a controversy typical of the conflicts managers must help resolve. Anglers and environmentalists fear that chemicals will have adverse impacts on fish or their food. Boaters and swimmers, on the other hand, demand clear water and a weed-free shoreline. Anglers recognize the habitat value of littoral vegetation and lobby against its complete removal.

In response to low catch rates, anglers and bait and tackle businesses demanded that the WDNR initiate a walleye stocking program to restore good walleye fishing and formed an association to raise funds and buy fish to stock in the lake. As a result, the WDNR initiated a cooperative project with the Lake Mendota Fishing Association to raise and stock walleye in Lake Mendota. As part of the agreement, the WDNR provides walleye fry and small fingerlings from its hatcheries to the Fishing Association, which raises them to a desirable size for stocking.

In the midst of the controversies and arguments described above, I read the paper by Carpenter et al. (1985). The study described a whole-lake experiment conducted on Peter and Paul Lakes in Vilas County, Wisconsin. The experiment involved stocking largemouth bass and observing the changes in the food web that resulted. The results indicated that stocking predator fish initiated changes in all levels of the food chain. The increased populations of piscivores which feed on planktivorous fish, reduced the abundance of the latter. This reduced the mortality of zooplankton, which increased in abundance, grazed heavily on algae, reduced the abundance of algae, and ultimately produced clearer water.

I was immediately struck that this technique might be transferred to Lake Mendota, where we needed to improve walleye fishing, eliminate a serious blue-green algae problem, and improve the size structure of planktivorous panfish populations. It was especially interesting because Lake Mendota is very eutrophic and unlikely to respond quickly to straightforward non-point pollution control. WDNR researchers had monitored the lake for over 10 years, and a large set of plankton population and water quality data was already available (Lathrop, Ch. 6; Lathrop and Carpenter, Ch. 7 and 8).

A whole lake experiment, however, would be costly, manpower-intensive, and risky. Lake Mendota is over 10,000 acres in size. The WDNR's policy of a stocking limit of 100,000 fingerlings per lake would prevent our obtaining enough fingerlings to make major, rapid changes in the walleye population. Further, WDNR's walleye production capacity was limited to 3.6 million fish, and existing stocking requests far exceeded

this level. The WDNR and other researchers felt that Lake Mendota was too large to conduct a controlled experiment, especially one that would cost hundreds of thousands of dollars each year. We were also concerned that success could result in increased weed growth which would exacerbate an already serious local problem.

Despite the apparent problems, it was also clear that the status quo was not acceptable. The level of walleye stocking that the Lake Mendota Fishing Association cooperative project could provide would only produce palliative results. Because this level was not high enough to assure the adult stock required for natural reproduction, it would only give anglers a taste of how good walleye fishing could be and could produce even more fervent, renewed demands for more stocking. Despite the improved fishing that might result, my reading of the paper by Carpenter et al. led me to conclude that cooperative stocking would not impact the water quality, which was an important issue for both the WDNR and local interest groups.

Furthermore, we were not sure of the impact of increased stocking on the other important fisheries, such as those for smallmouth and largemouth bass. Would the stocking effort produce a mediocre walleye fishery and reduced bass fishing? And not least, would the low level of planned stocking be enough to reduce panfish stocks and improve their growth?

Frankly, I was extremely fascinated with the idea of using fisheries management practices not only to provide good fishing, but also to augment water quality projects. I felt that we had a unique opportunity to impact one of Wisconsin's most renowned lakes right in the shadow of the State Capitol. Was this at all a feasible experiment and where would we get the support and resources to do it?

The UW, especially the Madison Campus Center for Limnology, the Sea Grant Institute, and the WDNR have enjoyed a long history of cooperation. Arthur Hasler pioneered whole-lake studies, promoted an experimental approach throughout his career, and has worked with the WDNR on many cooperative projects. John Magnuson continued these interests, and in recent years our collaboration has been wide-ranging and has included studies of exotic crayfish invasions of small northern Wisconsin lakes, the Great Lakes ecosystem rehabilitation of Green Bay using acoustic assessment techniques to measure forage populations, and studies to quantitatively characterize "winter kill" lake communities.

Over the years the WDNR's working relationship with the UW has ranged from collaborative to competitive. The differing nature of our missions and the work setting of WDNR managers and university faculty and students frequently encourage jealousy or envy, which lead to competition. However, on the whole, I believe we have one of the most

effective state agency–university working relationships in the nation. Thus, to explore my interest in a whole-lake biomanipulation on Lake Mendota, one of my first calls was to John Magnuson and Jim Kitchell at the UW Center for Limnology. Jim was a coauthor of the above-mentioned paper, and John and I had discussed ways of characterizing aquatic communities for many years.

Their immediate response was to point out the difficulty of conducting the experiment on a lake as large and complex as Lake Mendota. We talked about using small northern lakes with less complex cultural influences. I felt strongly about doing something in the southern part of the state. After considerable debate, we decided to cost out a project on Lake Mendota just to see if it was even possible.

### **The Wallop–Breaux Expansion of the Dingel–Johnson Act**

Fortunately, a \$162 million national increase in the Federal Aid for Fisheries Restoration Program (popularly known as the Wallop–Breaux Program) had recently been passed by Congress. This program expanded the mid-1950s Dingel–Johnson Sport Fish Restoration Act, which is funded by a 10% excise tax on sport fishing-related items such as fishing rods, reels, line, lures, and other items.

The Wallop–Breaux program expands the kinds of items taxed and transfers 1.08% of the federal gasoline tax to an Aquatic Resources Trust Fund. All of the excise tax on fishing tackle and a specified part of the motor fuel taxes are then allocated to the Wallop–Breaux account to be used solely for “sport fish restoration.” These funds are apportioned to state fish and wildlife agencies by a formula based on the size of each state in proportion to others and the number of individuals that buy fishing licenses. Additional guidelines which control the expenditure of the fund are:

At least 10% of the funds must be spent on improving motorboat access; States are authorized to spend up to 10% of their apportionment on aquatic educational activities;

Coastal states are required to equitably divide Wallop–Breaux funds between freshwater and marine projects;

Funds may not be used for put-and-take stocking and for public relations or promotional activities.

The program is administered by the U.S. Fish and Wildlife Service, which has a history of flexibility in implementing the requirements of local projects. Discussion held with WDNR Fisheries and Water Resources Management staffs concluded that this project, if feasible,

would represent a model for integrated management of a large lake in an urban area characterized by unmet fishing demand, water quality problems, and heavy boating pressure.

### **Wisconsin Expenditure Strategy for Wallop–Breaux Funds**

Wisconsin receives about \$6 million each year in Wallop–Breaux funds, a \$3.8 million increase over historical averages. Prior to the expansion of the fund, most of our expenditures were for the acquisition of fishery areas and public access, with limited funds directed toward research and habitat restoration. In response to the new monies, we expanded high-visibility programs like the construction of boat ramps with toilet facilities and fish cleaning stations. We have more than doubled the acquisition of lands for fisheries access, generally increased acquisition and protection of critical habitat, and have expanded habitat restoration activities. We also use the fund to support comprehensive planning activities for the fisheries program.

Other uses of Wallop–Breaux funds included a new aquatic ecology education program to support the teaching modules developed for Project Wild, a national program that provides workshops for kindergarten through twelfth-grade teachers and helps them provide their students with an awareness of the need to protect and manage aquatic resources. We also established a new fishing skills program for both teachers and children.

Management-related research has increased by nearly \$1 million. The recognition in the mid-1950s that new and better fisheries management techniques were needed led to the creation of the original Federal Aid for Fish Restoration Program. Despite more than 25 years of progress, there is still a shortage of techniques for resolving fisheries and aquatic resource management problems.

We also decided to use a portion of the new funds as venture capital, to conduct larger-scale studies that address challenging management issues with long-range implications. The studies are aimed at generating new science and management techniques and may change the basic way we do business. In short, these are higher-risk projects with large potential payback.

The key issue was to find a way to expand our knowledge base by managing a whole lake rather than its parts. We all knew that the potential for surprises—which are often seen as failures—increases with the complexity of the system you study. Many of the agency staff were concerned about spending so much money to manipulate a lake that was so difficult to control. We experienced a great deal of resistance from both fisheries managers and fisheries researchers. The central

issue was, Should we spend so much of the new fund on one lake, or would it be wiser to do many small-scale manipulations that could be replicated?

Risk assessment is a highly subjective art, especially in relation to fishery management decisions. In the final analysis, the WDNR faced a serious management problem relating to the low quality of predator fishing opportunities on the Yahara lakes chain. Angling groups were demanding increased fishing opportunities and were looking toward increased stocking of walleyes as a partial solution to their problems.

After considerable discussion and internal debate, we recommended that a whole-lake manipulation project be conducted on Lake Mendota. The purpose of the project was to assess the use of bioacoustic sampling techniques, develop an application of bioenergetics modeling for use in inland lakes, and assess the impact of food web interactions on lake water quality.

We approached top management of the WDNR very directly, outlining the pros and cons of the project. Several factors seemed to support the project. First, it was obvious that to have a major impact on walleye fishing in the southern, urbanized part of the state we needed to manage a larger lake. Most of the literature supports the idea that walleyes do better in bigger waters. Local anglers were already attuned to developing a walleye fishery and were spending thousands of their own dollars to stock the lake. This demonstrated strong public support for a stocking program. Given the size of the lake and past failures to establish walleye with low levels of stocking, we knew that a major stocking project would be needed to produce a naturally reproducing population. It seemed only reasonable to conduct a full-scale assessment of such stocking, to evaluate the stocking success, and to determine the factors influencing the outcome. Equally important was an assessment of stocking impacts on other species of fish and aquatic life in the system.

We also believed that the time had come for inland freshwater fisheries managers to explore multispecies interactions in more depth. Marine biologists were far ahead of us in this regard. Their work indicated that failure to consider interactions could greatly increase the uncertainty of fisheries decisions and increase the risk of management failures.

We argued that given its setting in the state capital (Plate 1) and the likelihood that both walleye fishing and pan fishing would be enhanced, the project made fisheries sense. Because of our proximity to the UW Center for Limnology and access to their expertise in experimentation, bioacoustics, and bioenergetics modeling, we had an excellent opportunity to explore and understand some of the underlying mechanisms that control the system. We also felt, although with less assurance, that we could develop insight into the potential for using top-level predator management to improve water clarity and overall water quality. All this

was to occur in the shadow of the State Capitol, where we needed to gain support for scientific fisheries management.

So we started the project with the idea that it was time to look at ways to manage large, whole-lake systems. There was great local support for enhancing the fishery in Lake Mendota. The cooperative spirit had already been expressed by angling clubs and managers who were embarked on a walleye stocking program. The chapters that follow cover the details of the results of water quality changes (Lathrop, Ch. 6; Vanni et al., Ch. 13 and 21), fishery responses (Johnson and Staggs, Ch. 17), and the transfer of technology (Rudstam and Johnson, Ch. 26; Staggs, Ch. 27) we have experienced so far. I believe that those results speak for themselves and demonstrate a remarkable success in this high-risk venture.

Although I have relocated to a different position and do not work with the project on a day-to-day basis, it is clearly a subject of important local interest. Anglers of all ages and interests debate its benefits and shortcomings. In my view, we have educated a whole generation of local anglers and other recreational groups about the important relationship between water quality management and fisheries management and how the different interest groups must work together.

Over the past several years, more and more support for cooperative projects has developed within our department as well as in other states and countries. Graduate students and postdoctoral researchers who participate in this project will likely find employment beyond Wisconsin's borders. I believe that their experience here will produce initiatives elsewhere that will greatly influence the direction of fisheries management in this country.

WDNR managers and researchers are exploring ways to apply some of the project's findings and to improve on the design of new projects. Currently, a program of similar scale is developing that will evaluate aquatic macrophytes and fishery relationships. Both the scientific and the administrative lessons we learn from these efforts are of statewide significance as managers struggle to deal with nuisance aquatic plants, water quality problems, and recreational fishing.

Today, there is a much stronger interagency research and management team working together on important resource management problems. We passed through a very difficult period of time when trust was weak between managers and university researchers. Today, I see both groups working together and in conjunction with groups of interested citizens to solve problems. Almost daily, the research-management team discusses ways of dealing with problems that they would not have dreamed about taking on several years ago.

During top management strategic planning meetings within the WDNR, the management team frequently cites the Lake Mendota Pro-

ject as an example of the sort of integrated management activity that we believe to be critical to our future. Acid depositions research activities, integrated resource management planning of the Milwaukee River system, the new Littoral Zone Fisheries Project, and other team efforts reflect the development of similar collaborative approaches.

In my view, the Lake Mendota Project has allowed us to see beyond the usual constraints imposed on managers. It has resulted in a different vision of how we can deal with future resource management and research issues. The impact of that change will be the most lasting and important benefit of the project.

### Some Practical Advice

Wisconsin worked hard and closely with a team of agency staff members from other states, the fishing industry, conservation groups, and anglers to expand funding for fisheries restoration and management. We chose to dedicate part of the new funding to innovative projects. The Lake Mendota Project was one of the first we started. We believe the results justify the cost and effort used. How should other states deal with this issue?

As I said earlier, this was not a spur-of-the-moment decision. The WDNR and the UW system had a long and effective working relationship. We could not have taken the shared risk that we did without mutual trust. Earlier projects laid the groundwork for the study. Others, too, must start by building a strong and mutually supportive working relationship. Agency people must take the time to meet and share their problems with faculty and researchers at the university. While the latter are often more skilled in new research techniques, they too rarely understand the complexities of resource management issues. Both parties must recognize that they bring particular strengths and weaknesses to the partnership. Both the academicians and the managers need one another to solve real-world problems.

Some practical suggestions for agency persons include hiring students as limited-term employees, finding ways to bring faculty to your agency on sabbatical or other exchanges, and helping faculty obtain extramural funding for research. Most of all, build a common understanding of what needs to be done. That common understanding is the key to developing integrated research management programs.

If managers and researchers approach administrators with a united front, one that is rigorous both in its science and in its awareness of public need, they will gain support. Again, a proven track record of working together to produce effective results is the key to administrative support. There is no shortcut. Only through systematic and increasingly complex

cooperation can we expect to gain the trust and innovative approaches required of research and management for the future.

### **Reference**

Carpenter SR, Kitchell JF, Hodgson JR (1985) Cascading trophic interactions and lake productivity. *BioScience* 35:634–639



A



B

**Plate 2.** A. Aerial photograph of Lake Mendota looking west toward the agricultural land of its drainage basin. The city of Madison is evident in the foreground (east) and to the south. B. Aerial photograph looking south across the Madison chain of lakes. Lake Mendota is in the foreground.

# 3

## Lake Mendota and the Yahara River Chain

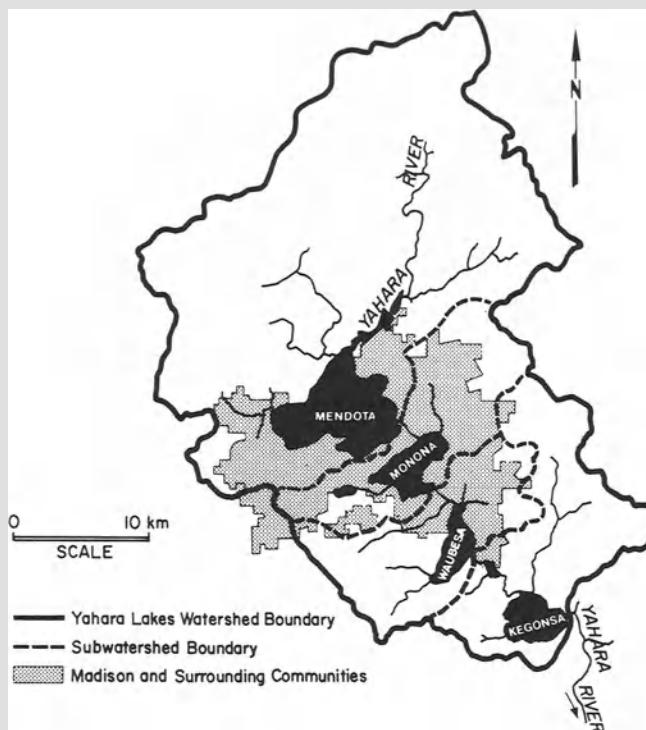
**Richard C. Lathrop**

### Drainage Basin Description

Lake Mendota is located near Madison (Dane County) in south central Wisconsin, USA ( $43^{\circ}6'N$ ,  $89^{\circ}24'W$ ). It is the uppermost lake in the Yahara River chain of lakes, which also include Lakes Monona, Waubesa, and Kegonsa (Figure 3.1; Plate 2). After leaving Lake Kegonsa, the Yahara River drains south to the Rock River, which is tributary to the Mississippi River.

The drainage basin or watershed of all four Yahara lakes encompasses  $996\text{ km}^2$  (Table 3.1) of gently rolling to hilly, glaciated terrain. The watershed is bounded on the west by moraines and on the east by a region of drumlins and marshes (Martin 1965). Much of the watershed is prime agricultural land because of fertile soils. Upland soils are mostly silt loams or loams characterized as well drained. Lowland soils are mostly poorly drained silts with mineral and organic material underlain by alluvial deposits (Cline 1965). Wetlands adjacent to the Yahara lakes have extensive peat deposits.

The Yahara River originates in a marshy area in southern Columbia County (bordering Dane County to the north). Upstream from Lake Mendota, the Yahara River is only a meandering creek of relatively low discharge during baseflow. However, before entering Lake Mendota, the Yahara River joins with Token Creek, a stream with a higher baseflow. Other streams entering Lake Mendota are Sixmile Creek and Spring Creek entering from the north and Pheasant Branch Creek entering from the west. Additional small discharges to Lake Mendota result from urban



**Figure 3-1.** Watersheds of the four Yahara lakes.

**Table 3-1.** Physical characteristics of the Yahara lakes and their watersheds.

Characteristic	Mendota	Monona	Waubesa	Kegonsa
<b>Lake</b>				
Surface area (ha)	3,985	1,326	843	1,299
Volume (million m <sup>3</sup> )	505	110	40	67
Maximum depth (m)	25.3	22.6	11.6	9.8
Mean depth (m)	12.7	8.3	4.7	5.1
Shoreline length (km)	35.2	21.2	15.1	15.4
Shoreline development factor <sup>a</sup>	1.57	1.64	1.47	1.21
Flushing rate (yr <sup>-1</sup> )	0.15	0.91	3.2	2.2
<b>Watershed</b>				
Direct drainage area (km <sup>2</sup> )	562	105	113	141
Total drainage area <sup>b</sup> (km <sup>2</sup> )	602	720	842	996

<sup>a</sup>Ratio shoreline length to circumference of circle that equals lake area.

<sup>b</sup>At lake outlet.

**Table 3-2.** Annual water budgets (in millions of m<sup>3</sup>) for Lake Mendota for 1976–77.<sup>a</sup>

Year	Precipitation	Surface inflow	Evaporation	Outlet flow	Storage change	Groundwater <sup>b</sup>
1976	21.9	88.6	37.3	80.3	-1.2	5.9
1977	31.7	49.9	33.2	54.6	+1.9	8.1

<sup>a</sup> Source: Lathrop 1979.

<sup>b</sup> Groundwater calculated by difference from mass balance equation using other components.

drainage. Water budgets for Lake Mendota for 1976–77 indicate the wide annual variation in surface runoff (Table 3.2).

Lake Mendota's watershed or drainage basin is largely agricultural with some urban area. The direct drainage area to Lake Monona, the next lake below Mendota, is mostly urban. The direct drainage areas are much smaller for all three of the lower Yahara lakes than for Lake Mendota (Table 3.1). While the major source of nutrients to these lower lakes is from each upstream lake, the major source of nutrients to Lake Mendota is from land use activities in its large watershed (Lathrop, Ch. 6).

The Yahara drainage system has been changed by the agricultural and urban development in the area since the late 1840s. Lake Mendota's water level was raised 1.2–1.5 m in 1847 by a dam (Kanneberg 1936) to its current average level of 259.0 m mean sea level. Wetlands have been drained or filled, stream channels have been straightened, and many of the small springs have dried up because of lowered water tables. In 1835, approximately 4,120 ha of wetlands were present in Lake Mendota's drainage basin (Lathrop et al., 1992). By 1938 and 1974, wetland areas were reduced to 3,190 ha (−23%) and 2,060 ha (−50%), respectively. Lakes Monona, Waubesa, and Kegonsa lost 92%, 73%, and 70% of their wetlands by 1974.

## Geology

The Yahara River drainage basin and the four Yahara lakes were created during the last period of glaciation, which ended a little more than 10,000 years ago (Martin 1965). Thick layers of glacial till were deposited in the Yahara River valley, with some areas filled with over 100 m of unconsolidated debris. This deposition created one large lake (Lake Yahara) that later drained when the Yahara River eroded its outlet. This led to the formation of the four Yahara lakes, which were separated by dams of glacial debris. After the period of glaciation ended, the Yahara River became a stream characterized by a meandering channel, a relatively small number of tributaries, and extensive, undrained interlake areas with large wetlands.

Beneath the unconsolidated glacial deposits are different layers of sedimentary rocks, composed mostly of alternating layers of sandstone and dolomite. The tops of the highest hills in the area are capped with the erosion-resistant Black River limestone, while the lower hills are capped with Lower Magnesian limestone. The short, steep slopes between these layers of limestone are underlain by St. Peter sandstone, while the valley bottoms are underlain by Cambrian sandstone (Cline 1965; Martin 1965). Beneath the many layers of Cambrian sandstone are much older crystalline rocks—mostly rhyolite, granite, and basalt. These rocks lie 150–300 m below the land surface. They allow little penetration of water and therefore form a floor beneath the overlying, water-bearing sedimentary rocks or aquifers (Cline 1965).

### Climate

The climate at Madison is typical of interior North America. The annual temperature range is large, and short temperature changes are frequent. The mean annual temperature is 8°C (1960–89) with an absolute range from –39°C to 40°C (1900–89) (National Oceanic and Atmospheric Administration, 1988; Pam Naber, Wisconsin State Climatologist, pers. comm.). January, the coldest month, averages –8°C (1960–89), while July, the warmest month, averages 22°C. Average annual precipitation is 78 cm (1960–89) with a range of 54–99 cm (1937–89). About 68% of this falls in April through September; much of the rainfall during this period occurs during heavy thunderstorms. Snowfall averages 107 cm per year (1960–89) with a range of 32–193 cm (1948–89).

### Lake Description

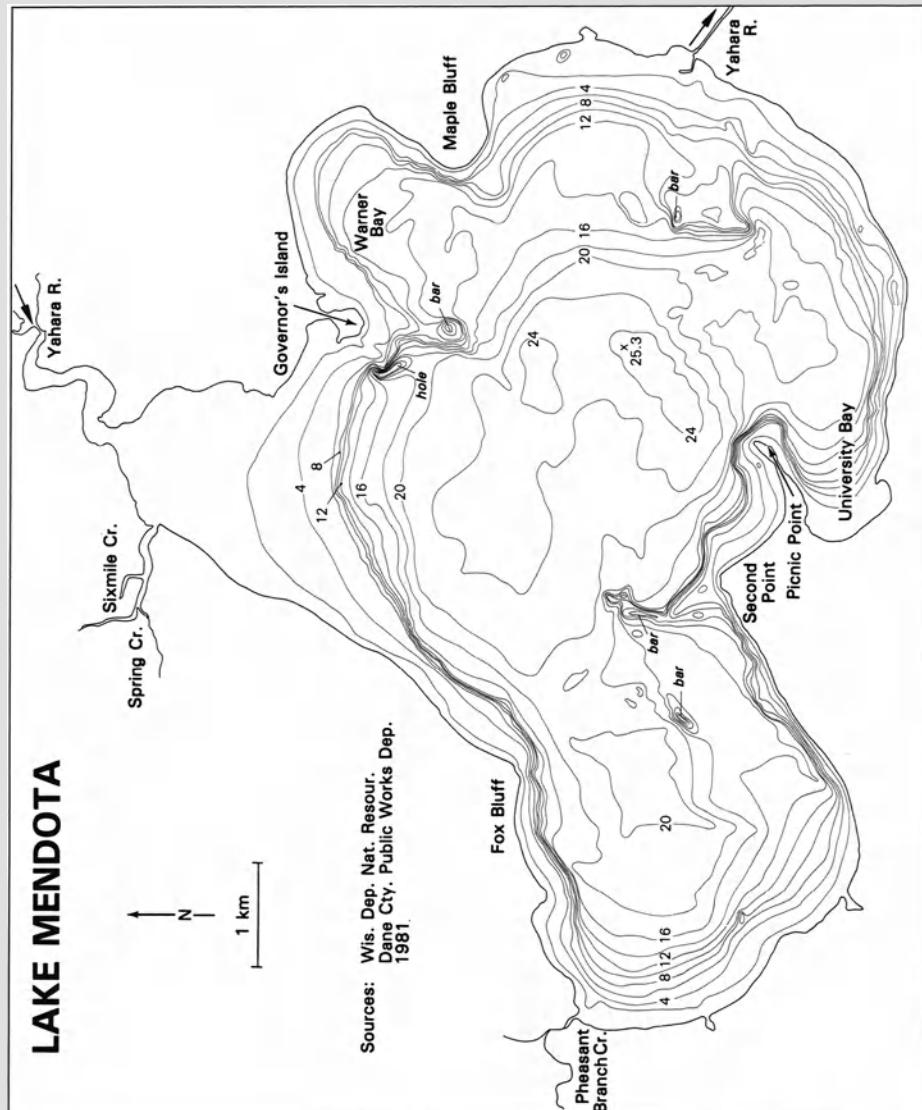
#### Morphometry

Lake Mendota is the largest (3,985 ha) and deepest (25.3 m) lake of the Yahara lakes. Physical characteristics for all four lakes are summarized in Table 3.1. A map of Lake Mendota depicting important shoreline and hydrologic features as well as depth contours is given in Figure 3.2. The area of the lake at 2-m depth contour intervals is given in Table 3.3.

Lake Mendota has an extensive pelagic zone. While the littoral zone (0–4 m) represents important habitat, particularly for many fish species through all or part of their life cycles (Magnuson and Lathrop, Ch. 11), nutrient recycling and primary production are dominated by pelagic processes. For example, the entrainment of nutrients across the thermocline

---

**Figure 3-2.** Hydrographic map of Lake Mendota showing depth contours in 2-m intervals.



**Table 3-3.** Morphometric data for Lake Mendota.

Depth contour (m)	Area (ha)
0	3,985
2	3,482
4	3,094
6	2,864
8	2,686
10	2,525
12	2,336
14	2,034
16	1,683
18	1,313
20	855
22	368
24	62

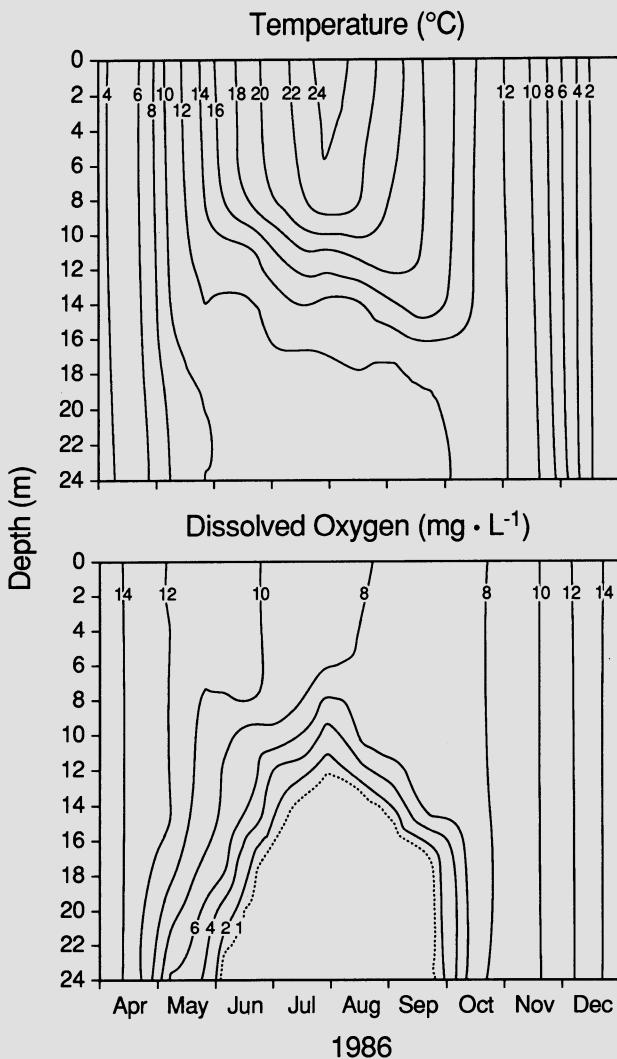
during windy summer periods causes phytoplankton blooms to develop (Stauffer and Lee 1973; Stauffer 1974). Large masses of nutrients are released from the bottom sediments and build up in the hypolimnion by late summer; these nutrients are transferred to the entire water column during fall turnover and remain high through the following spring (Sonzogni 1974; Lathrop 1990).

In another example of the importance of pelagic processes in Lake Mendota, phytoplankton blooms during the summer months restrict the depth distribution of littoral macrophytes (Nichols et al., Ch. 9). However, there is no evidence that extensive macrophytes and associated filamentous and epiphytic algae can reduce in-lake concentrations of nutrients and thereby restrict phytoplankton growth, as has been suggested for other lakes where the littoral zone composes a much larger proportion of the lake surface area.

### Temperature

Lake Mendota is dimictic. A typical thermal structure for the open-water period (1986) at the deep-hole area is depicted in Figure 3.3. The rate of spring warming varies from year to year. Surface water temperatures (0–2 m) extrapolated to 1 May have ranged between 7°C and 11°C during 1976–89. Rapid water temperature changes in a given spring may hamper successful reproduction of some fish species, while more moderate temperature increases may enhance reproduction in other years.

Although the lake may experience temporary stratification for brief periods during spring turnover until strong winds cause isothermal conditions, the lake permanently stratifies sometime in May, usually around



**Figure 3-3.** Isopleths for water temperatures and dissolved oxygen concentrations during April–December 1986 in Lake Mendota.

mid-May. Hypolimnetic temperatures in the deepest part of the lake (>22 m water depth) remain relatively constant throughout the summer months, but temperatures have ranged between 10°C and 15°C during 1976–89. Summer surface temperatures generally are 24–27°C, although 28°C was recorded during the summers of 1983 and 1987. Somewhat cooler temperatures occur in lower epilimnetic waters. Long-term average July temperatures for the epilimnion and hypolimnion (volume

weighted) were 23.1°C (range 20.6–26.3°C) and 12.6°C (range 8.6–16.4°C), respectively (Robertson 1989).

By late summer, Lake Mendota's epilimnetic temperatures start to decrease, which causes the thermocline to erode. Destratification is usually complete by mid-October. Fall turnover continues until water column temperatures cool to about 1°C, which allows ice to form during a calm, cold period. Although smaller lakes freeze at warmer water temperatures, wind mixing in Mendota prevents the surface cooling needed for ice formation.

Since records were first collected during the winter of 1855–56, the average ice formation date for Lake Mendota has been 20 December, but dates have varied by as much as 2–3 weeks earlier or later in a given year. The long-term average spring ice-out date is 5 April, but dates also have regularly varied by as much as 2 weeks. However, Robertson (1989) determined that the total period of ice duration has declined since 1856 as a response to warmer air temperatures. During the 3 years of intensive research covered in this volume, ice formation dates were 2 January 1988, 29 December 1988, and 12 December 1989. Ice-out was on 12 March 1987, 30 March 1988, and 5 April 1988.

### Dissolved Oxygen

Dissolved oxygen (DO) isopleths for a typical year (1986) are given in Figure 3.3. DO conditions in Lake Mendota have not changed since the early 1900s when detailed measurements were first recorded by E.A. Birge (Stewart 1976). Hypolimnetic DO depletion rates also have not changed since the early 1900s (Stewart 1976; Brock 1985). By early July, the entire hypolimnion becomes anoxic, a condition that remains until the water column is reoxygenated after destratification at the onset of fall mixing around mid-October. DO depletion of Mendota's bottom waters also occurs during the late winter, usually in March, but generally only in depths >20 m. Reoxygenation is rapid at the onset of spring turnover after ice-out.

### Major Water Chemistry Constituents

Recent concentration data for some of the major water chemistry constituents in Lake Mendota's surface waters are given in Table 3.4. Data on phosphorus, nitrogen, and silica, the primary nutrients that most likely have a role in controlling phytoplankton growth, are discussed later (Lathrop, Ch. 6; Lathrop and Carpenter, Ch. 7). The high pH, alkalinity, calcium (Ca), and magnesium (Mg) concentrations reflect the regional geochemistry. The large deposits of limestone and dolomite cause the lake waters to be alkaline. In 1987–89, midsummer Ca concentrations in the surface waters averaged  $24\text{ mg L}^{-1}$ , while concentrations averaged

**Table 3-4.** Mean concentration of major water chemistry constituents in the surface waters of Lake Mendota, 1980–89.<sup>a</sup>

Constituent	Concentration
pH	8.5
Alkalinity (meq L <sup>-1</sup> )	3.4
Calcium (mg L <sup>-1</sup> )	32
Magnesium (mg L <sup>-1</sup> )	32
Sulfate (mg SO <sub>4</sub> L <sup>-1</sup> )	22
Chloride (mg L <sup>-1</sup> )	27
Sodium (mg L <sup>-1</sup> )	11
Potassium (mg L <sup>-1</sup> )	3.2
Specific conductance ( $\mu\text{S cm}^{-1}$ )	410
Total dissolved solids (mg L <sup>-1</sup> )	260

<sup>a</sup> Data collected by WDNR Bureau of Research and analyzed at Wisconsin State Laboratory of Hygiene except for specific conductance and total dissolved solids, which were collected and analyzed by City of Madison Department of Public Health for 1984–89. Calcium, magnesium, potassium, and sodium data for 1987–89 only. Chloride reported for 1989 because concentrations have been steadily increasing in Lake Mendota.

32 mg L<sup>-1</sup> for the winter, spring, and fall seasons. This summer Ca decrease was probably due to the precipitation of calcium carbonate (CaCO<sub>3</sub>). Hurley (1988) recorded a large deposition of CaCO<sub>3</sub> in sedimentation traps during the summer of 1987 in Lake Mendota.

The high sulfate (SO<sub>4</sub>) concentrations in Lake Mendota are significant, because SO<sub>4</sub> in anoxic conditions is reduced to sulfide, which combines with reduced iron (Fe) to form insoluble iron sulfide (FeS). Fe is therefore unavailable under oxic conditions to form hydrous iron oxides, which adsorb/coprecipitate inorganic phosphorus (P) and thereby restrict its recycling. Consequently Lake Mendota has a high capacity for internal recycling of P, as compared to other lakes where SO<sub>4</sub> levels are lower and Fe is not tied up as FeS (Holdren 1977; Stauffer 1987).

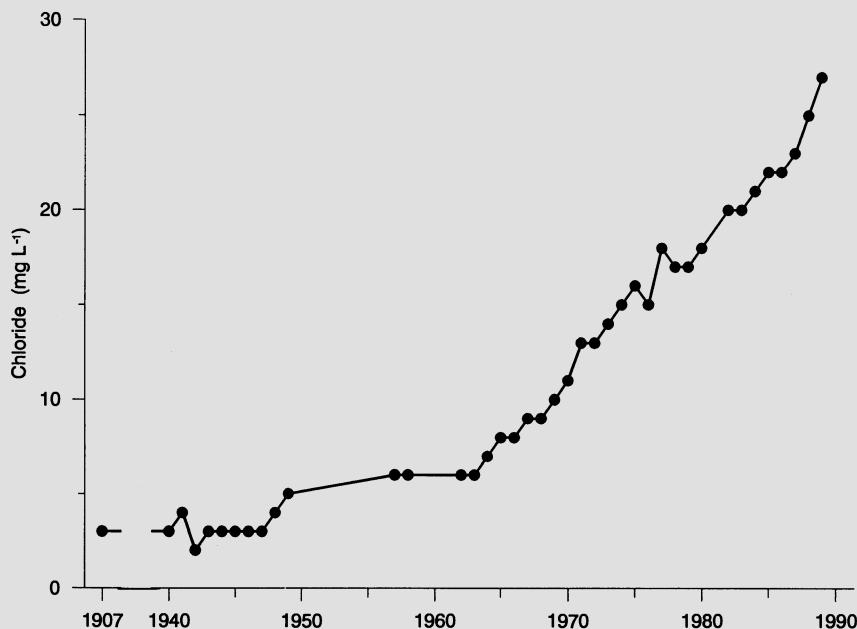
SO<sub>4</sub> concentrations in Lake Mendota's surface waters have been analyzed at different periods. During 1948–50, SO<sub>4</sub> concentrations were 8–12 mg L<sup>-1</sup>, based on extensive testing by different University of Wisconsin (UW) Civil Engineering students (Lee 1962). By the mid-1960s, SO<sub>4</sub> concentrations had increased to about 20–22 mg SO<sub>4</sub> L<sup>-1</sup> (UW Water Chemistry students, unpubl. data; Hawley 1967). These concentrations were similar to other data obtained by both the Wisconsin Department of Natural Resources (WDNR) Bureau of Research (unpubl. data) and Brock (1985) in the late 1970s and to more recent concentrations (Table 3.4). SO<sub>4</sub> was also measured on four occasions during

**Table 3-5.** Total sulfide concentrations (in  $\text{mg S L}^{-1}$ ) in the anoxic hypolimnion of Lake Mendota.<sup>a</sup>

Depth (m)	1967				1978 18 Sep	1979a 12 Sep	1979b	
	1908 22 Sep	6 Sep	19 Sep	30 Sep			2 Sep	18 Sep
20	0.7	2.2	2.1	2.6	—	—	2.2	3.0
21	—	—	2.5	2.7	—	—	3.2	3.3
22	0.8 <sup>b</sup>	2.3	—	3.5	—	—	3.0	4.3
23	—	—	—	—	—	—	3.4	4.1
24	—	—	—	—	3.6	3.3	—	—

<sup>a</sup>Sources of data: 1908 (Birge and Juday 1911), 1967 (Delfino 1968), 1978–79a (Stauffer 1987), 1979b (Ingvorsen and Brock 1982; Brock 1985).

<sup>b</sup> Sampled at 21.5 m.



**Figure 3-4.** Chloride concentrations in the surface waters of Lake Mendota for selected years during 1907–89.

1907–10 (Birge and Juday 1911). Concentrations were lower than current data, but I considered the early data too variable to be reliable.

Hydrogen sulfide is very noticeable in Lake Mendota's deep hypolimnetic waters during late summer. Total sulfide concentrations during the late 1970s were  $>3 \text{ mg S L}^{-1}$  in depths  $>20 \text{ m}$  by mid-September (Table 3.5). Concentrations reported for 1967 were only slightly lower, but concentrations reported for 1908 were considerably

lower ( $<1\text{ mg L}^{-1}$ ). An iodometric procedure was used for these early analyses (Birge and Juday 1911), but I did not evaluate the method for possible biases. Iodometric tests are currently recognized as a “standard method” for sulfide determinations. Whether the apparent increase in  $\text{SO}_4$  concentrations has resulted in a similar increase in hypolimnetic sulfide concentrations is not known. Deep-hole sediment cores taken in 1987 and 1990 did not show a pronounced change in total sulfur concentrations in sediments deposited since the 1940s.

As already mentioned, dissolved Fe (reduced) concentrations in the hypolimnetic waters of Lake Mendota are low. Concentrations recorded in late summer 1987 at 20 m were  $<0.1\text{ mg Fe L}^{-1}$  (WDNR Bureau of Research, unpubl. data). Stauffer (1987) recorded dissolved Fe of 0.06 and  $0.04\text{ mg L}^{-1}$  in September of 1977 and 1978, respectively. Holdren (1977) found that interstitial concentrations of Fe were so low in anoxic sediments in Lake Mendota that P release to the overlying water was not retarded even when surficial sediments were oxygenated.

Chloride (Cl) concentrations in Lake Mendota are perhaps of less limnological importance than some of the other major water chemistry constituents, but long-term trends are interesting. Concentrations remained low throughout the early 1900s (Figure 3.4) but have been steadily increasing since the early 1950s. Cl levels in 1989 were  $27\text{ mg L}^{-1}$  (Table 3.4). The reason for this change is the increased winter use of road salt. Beginning in the 1970s, the use of road salt was restricted by as much as 50% from that in peak usage years in the 1960s, but concentrations in area lakes and the local groundwater have continued to steadily increase (M.E. Testen, Madison Department of Public Health, unpubl. rep.).

Sodium (Na) concentrations have increased, but not as dramatically as Cl concentrations during the same period. Na in Lake Mendota was recorded at about  $3\text{ mg L}^{-1}$  in 1907,  $5\text{--}6\text{ mg L}^{-1}$  in the 1960s,  $8\text{--}9\text{ mg L}^{-1}$  in the 1970s, and  $10\text{--}11\text{ mg L}^{-1}$  in the mid-1980s (Lathrop 1988). Na was  $12\text{ mg L}^{-1}$  in 1989. Possible reasons why Na has not increased as much as Cl are: (1) calcium chloride ( $\text{CaCl}_2$ ) was also used as a road salt, and (2) cation exchange reactions on soil particles may remove some of the Na before the water enters the lake as groundwater or surface runoff (D.E. Armstrong, UW-Madison Water Chemistry Program, pers. comm.).

In this chapter I have provided a general description of Lake Mendota and the surrounding area. While the information is not central to the food web research presented in this volume, it is useful for understanding Lake Mendota’s basic limnology. This general lake description should also assist readers wishing to compare Lake Mendota to other temperate-latitude lakes.

**Acknowledgments.** I thank S.R. Carpenter and J.J. Magnuson for their critical reviews of this chapter and S.H. Nehls for editorial assistance. Data collection was principally funded by the WDNR.

## References

- Birge EA, Juday C (1911) The inland lakes of Wisconsin: The dissolved gases of the water and their biological significance. Bull. No. 22. Madison: Wis. Geol. Nat. Hist. Surv.
- Brock TD (1985) A eutrophic lake: Lake Mendota, Wisconsin (Ecol. Stud. Vol. 55). Springer-Verlag, New York
- Cline DR (1965) Geology and groundwater resources of Dane County, Wisconsin. Water Supply Pap. No. 1779-U. U.S. Geol. Surv., Washington
- Delfino JJ (1968) Aqueous environmental chemistry of manganese. Ph.D. Thesis, University of Wisconsin, Madison
- Hawley JE (1967) Calcium carbonate equilibrium in Lake Mendota. M.S. Thesis, University of Wisconsin, Madison
- Holdren GC (1977) Factors affecting phosphorus release from lake sediments. Ph.D. Thesis, University of Wisconsin, Madison
- Hurley JP (1988) Diagenesis of algal pigments in lake sediments. Ph.D. Thesis, University of Wisconsin, Madison
- Ingvorsen K, Brock TD (1982) Electron flow via sulfate reduction and methanogenesis in the anaerobic hypolimnion of Lake Mendota. Limnol. Oceanogr. 27:559–564
- Kanneberg A (1936) The dam at the outlet of Lake Mendota. In Lake Mendota: Origin and history, The Technical Club of Madison, Madison, Wisconsin, pp 17–19
- Lathrop RC (1979) Appendix H: Lake management. In Dane County water quality plan, Vol. 2, Dane County Regional Planning Commission, Madison, Wisconsin, pp H-1–H-77
- Lathrop RC (1988) Chloride and sodium trends in the Yahara lakes. Res. Manage. Find. No. 12. Wisconsin Department of Natural Resources, Madison
- Lathrop RC (1990) Response of Lake Mendota (Wisconsin, U.S.A.) to decreased phosphorus loadings and the effect on downstream lakes. Verh. Int. Verein. Limnol. 24:457–463
- Lathrop RC, Nehls SH, Brynildson CL, Plass KR (1992) The fishery of the Yahara lakes. Technical Bulletin (in press), Wisconsin Department of Natural Resources, Madison
- Lee GF (1962) Studies on the iron, manganese, sulfate and silica balances and distributions for Lake Mendota, Madison, Wisconsin. Trans. Wis. Acad. Sci. Arts Lett. 51:141–155
- Martin L (1965) The Physical Geography of Wisconsin. University of Wisconsin Press, Madison
- National Oceanic and Atmospheric Administration (1988) Local climatological data: Annual summary with comparative data Madison, Wisconsin. Environ. Data and Inf. Serv., Natl. Clim. Cent., Asheville, North Carolina.
- Robertson DM (1989) The use of lake water temperature and ice cover as climatic indicators. Ph.D. Thesis, University of Wisconsin, Madison
- Sonzogni WC (1974) Effect of nutrient input reduction on the eutrophication of the Madison lakes. Ph.D. Thesis, University of Wisconsin, Madison
- Stauffer RE (1974) Thermocline migration: Algal bloom relationships in stratified lakes. Ph.D. Thesis, University of Wisconsin, Madison

- Stauffer RE (1987) A comparative analysis of iron, manganese, silica, phosphorus, and sulphur in the hypolimnia of calcareous lakes. *Water Res.* 21:1009–1022
- Stauffer RE, Lee GF (1973) The role of thermocline migration in regulating algal blooms. In Middlebrooks EJ, Falkenborg DH, Maloney TE (eds) *Modeling the eutrophication process*, Ann Arbor Science, Ann Arbor, Michigan, pp 73–82
- Stewart KW (1976) Oxygen deficits, clarity, and eutrophication in some Madison lakes. *Int. Rev. Ges. Hydrobiol.* 61:563–579

# 4

## Paleolimnological Evidence of Food Web Dynamics in Lake Mendota

James F. Kitchell and Patricia R. Sanford

### Introduction

Paleolimnological techniques have been extensively used in reconstructing vegetation dynamics, biogeochemical processes, and lake productivity (Frey 1986). More recently, this approach has been employed in reconstructing limnetic food webs (Kerfoot 1974; Kerfoot and Sih 1987; Leavitt et al. 1989). Its merits include an integrated view of trophic interactions derived from the relative abundance, size, and species composition of the pelagic zooplankton. In addition, the deposition rate of zooplankton fossils provides quantitative estimates of secondary production as an indicator of system productivity.

As attested throughout this book, the relative abundance and size of herbivorous Cladocera serve as the nexus of food web interactions. In particular, the dynamics of large *Daphnia* spp. are critically related to relative intensities of both grazing on phytoplankton and predation by zooplanktivorous fishes. Dominance by large *Daphnia* indicates intense grazing pressure, relatively low levels of predation by small fishes, and, by extension, higher levels of piscivory. Abundances of *Bosmina* spp. are often reciprocally related to those of large *Daphnia* and serve as independent evidence of less intense and more selective herbivory, strong size-selective zooplanktivory by fishes, and low levels of piscivory. While these generalities derive primarily from theory and neolimnological studies, they are substantiated by paleolimnological evidence from a range of lake types, productivities, and food web structures (Kerfoot

1974; Kitchell and Kitchell 1980; Kitchell and Carpenter 1987; Leavitt et al. 1989).

Given the encouragement of previous successes in using the paleolimnological record as a surrogate for long-term observations, we sought to reconstruct the general history of food web interactions in Lake Mendota based on the evidence provided by fossil zooplankton typical of the pelagic system. As developed in the overviews of plankton and nutrient studies (Lathrop, Ch. 6) and that of the fish community (Magnuson and Lathrop, Ch. 11), the observational records are both incomplete and sometimes inconsistent. In particular, evidence of recent and continuing reductions in nutrient loading poses a logical question about the distant past of Lake Mendota. We seem to be moving to a system state quite different from that of contemporary observations and are probably affecting that more rapidly through fisheries management practices that will continue to alter the role of food web interactions (Addis, Ch. 2). Logically, the paleolimnological record can offer some basis for expectation as well as a more continuous documentation of changes corresponding with those known from the history of observations.

Our initial expectations were that the unexploited piscivore population of the distant past would suppress populations of planktivorous fishes, yielding a zooplankton community dominated by large Cladocera (Carpenter et al. 1985). We also anticipated that the cultural eutrophication known from the advent of agricultural practices would alter zooplankton community structure to favor eutrophication-tolerant species. In more general terms, we expected that the highest levels of system productivity would be recorded prior to the domestic wastewater diversions accomplished in the middle of this century (Lathrop, Ch. 6).

## Methods

The coring techniques chosen for this study were selected to maximize the resolution offered in recent sediments. Freeze-coring from the stable platform offered by ice cover allows minimal disturbance to the flocculent surficial materials yet can provide a core of sufficient depth to contain material that predates the appearance of anthropogenic effects on the lake's food web.

Sediments were cored with a 2.3-m-long aluminum freeze corer filled with a slurry of dry ice and ethanol (Swain 1973). Coring was done on 15 January 1985, over the Deep Hole of University Bay in 20 m of water. A continuous column of 115 cm of sediment was recovered, of which the top 69 cm was dark-colored and the remainder, buff marl (Twenhofel 1933). On removal from the core barrel, the frozen tube of sediment was cut horizontally into three pieces of convenient length. Each section was then cut longitudinally into four quarters.

The top 10 cm was divided into nine subsamples. The interval from 10 to 50 cm was subsampled at ca. 5-cm intervals. The remainder of the core was subsampled at ca. 10-cm intervals. Subsampling was carried out at room temperature, and some thawing of the core surface occurred during the process. In order to minimize contamination that may have occurred as the core was withdrawn from the sediment and through lake water, sectioned samples were carefully scraped on all sides with a metal spatula before subsamples were taken.

Each subsample was thawed, homogenized by stirring with a toothpick, and packed into a 0.5-ml spoon. A second 0.5-ml aliquot for each was dried and weighed to obtain dry weight of the volumetric sample, and then burned in a muffle furnace (550°C) to obtain loss of weight on ignition.

Chemical processing followed procedures selected from Frey's protocol (Frey 1986). Because Lake Mendota's sediments are heavily impregnated with  $\text{CaCO}_3$ , samples were treated with 10% HCl. A 10% KOH solution was used to remove humic acids and disperse clastics. Samples were rinsed several times with distilled water after each chemical process. Residue was transferred from water to glycerine by simply pipetting off most of the water, adding glycerine, and evaporating the remaining water.

Cladoceran zooplankton remains in our samples represent both molts of the exoskeleton and mortalities. Because those cannot be readily distinguished, we refer to them collectively as zooplankton fossils. Unfortunately, other major groups such as the Copepoda and Rotifera are poorly or indistinguishably included in the fossil record. Based on general principles, the effects of size-selective predation, competition, and nutrient enhancement allow members of the Cladocera to serve as an effective analogue for the total zooplankton community (Kitchell and Carpenter 1987).

In order to obtain quantitative results that could be used to calculate deposition rates, two different techniques were used: weight-to-weight (modified from Traverse and Ginsberg 1966) or an exotic pollen "spike" (Benninghoff 1962).

The weight-to-weight technique uses the formula:

$$X = AC/B$$

where  $X$  = number of fossils per 0.5-ml spoon,  $A$  = total grams maceration residue plus glycerine,  $B$  = grams residue plus glycerine on slides counted, and  $C$  = cladoceran sum.

The exotic pollen spike method involves adding a tablet of a known number of *Eucalyptus* pollen grains ( $16,180 \pm 1,460$ , Stockmarr Batch No. 903,722) to each sample before chemical processing, tallying the number of *Eucalyptus* grains encountered while counting cladoceran remains, and using the results in the formula:

$$X = DF/E$$

where  $X$  = number of fossils per 0.5-ml spoon,  $D$  = number of *Eucalyptus* grains in pollen tablet (16,180),  $E$  = number of *Eucalyptus* grains counted, and  $F$  = cladoceran sum. Both methods yield the concentration of cladoceran fossils in a known volume of sediment (0.5 ml). Deposition rate, loading rate, or influx is expressed as the number of cladoceran fossils deposited per square centimeter per year using the formula:

$$(\text{No. cladoceran fossils/cm}^3)/[\text{deposition time (years/cm)}]$$

Each processed subsample was stirred with a toothpick for 10 min to achieve a uniform suspension. Approximately 0.02 g of maceration residue was transferred a drop at a time on the end of a toothpick to a weighed slide. Slide and maceration residue were weighed and additional glycerine was added until there was enough residue to spread out uniformly under a 22-mm<sup>2</sup> cover slip. Counts were made using a Nikon Labophot compound binocular microscope with 20 $\times$  and 40 $\times$  objectives and 10 $\times$  oculars. Routine counting was done at 200 $\times$  magnification, and difficult determinations and measurement at 400 $\times$  magnification. Contiguous transects were scanned from one edge of the cover slip to the other until the whole slide had been examined.

Fragments of cladoceran exoskeletons were identified using Brooks (1957) and Frey (1964). Based on identifications by S.I. Dodson (pers. comm.), the large *Daphnia* in Lake Mendota is considered to be *D. pulicaria*, a representative of the *D. pulex* group. Three types of daphnid postabdominal claws were seen: those with three pectens of uniformly small teeth < ca. 8  $\mu\text{m}$  long were attributed to *D. galeata*; claws with a middle pecten of 3 to 8 stout teeth ca. 10 to 25  $\mu\text{m}$  long were attributed to the *D. pulex* group; and claws less than 60  $\mu\text{m}$  long, with no obvious pectens of fine teeth, and lacking a circlet of small teeth, were attributed to cf. *Ceriodaphnia*. In Lake Mendota, the *D. pulex* group includes both *D. pulicaria* and *D. retrocurva*. The latter is discernible as much smaller than *D. pulicaria* and typically comprises only 1–5% of the total *Daphnia* in both the annually averaged neolimnological plankton samples and the paleolimnological record. For that reason, we do not specifically differentiate and discuss its responses in the fossil record.

Daphnid postabdominal claws, bosminid carapaces, rostra, and separate antennules, *Leptodora kindtii* caudal furcae and mandibles, and *Chydorus* spp. carapaces were counted. In addition, *Filinia longiseta* (Rotifera) resting eggs could be recognized and were tabulated. Minimum numbers of individual fossils represented by tabulated exoskeleton parts for each taxon were calculated using formulas presented in Frey (1986). The cladoceran sum in this analysis is the minimum number of fossils of *D. galeata mendotae* Birge + *D. pulex* Leydig group + *Bosmina*

*longirostris* O.F. Muller + *Eubosmina coregoni* Baird. Ten slide preparations were made for each sample, and counts were continued until the cladoceran sum plus *Chydorus* fossils equaled 200 or all 10 slides were counted. The cladoceran sum was used to calculate simple percent composition among the four taxa of interest for each sampling interval.

Daphnid postabdominal claws and bosminid mucrones and antennules were measured as they were encountered. Because postabdominal claws exhibited varying degrees of curvature, presumably due to postburial distortion, measurements taken in a straight line from the distal tip of the claw to the point of union with the postabdomen (as in Dodson 1981, Figure 4E) seemed likely to yield misleading results as regards estimates of body size of a living organism. Therefore all claw measurements were made following the curvature of the claw by a series of chords. *D. galeata* claws were measured from the proximal edge of the proximal pecten to the distal tip. *D. pulicaria* claws were frequently broken at or near the junction of the proximal pecten and the middle pecten. Thus *D. pulicaria* claw measurements are of the distal pecten only, measured from the proximal end of the distal pecten to the distal tip of the claw. *Bosmina* mucrones were measured from the ventral notch to the tip; *Bosmina* and *Eubosmina* antennules from the base of the "tooth" to the tip (Kerfoot, 1975). Curvature was also encountered in *Bosmina* mucrones and antennules; consequently, these were measured by a series of chords as necessary.

### Dating

The 1985 core sediments are dated using features internal to the core: the water-sediment interface, the stratigraphic change from buff marl to dark-colored marl (heavily mottled with ferrous sulfides) at -70 cm, and the *Ambrosia* pollen rise between -70 and -50 cm. Both of the latter mark the time when Euroamerican agricultural activities increased and the rich prairie soils of the Yahara basin were disturbed by the iron plow. Each of these features was used to correlate the 1985 core with other Lake Mendota cores which have been dated using radiocarbon or cesium-137. Those are WC-86 and WC-89 (Bortelson and Lee 1972), core C (Winkler 1985), and a core taken in 1987 (Hurley 1988; Hurley et al., Ch. 5). In dating the upper 70-cm component of our core, we adopted the sedimentation rate calculations developed by Hurley (1988). This method accounts for changes in particle size and compaction with sediment depth and was the basis for our calculations of zooplankton fossil deposition rates. It is fully described in Hurley (1988) and employed by Hurley et al. (Ch. 5) in their estimates of plant pigment deposition and degradation.

The depth to buff-colored marl is similar in all cores when adjustments are made for deposition since the earlier coring efforts. In the 1985 core, ragweed pollen, calculated as percent of upland pollen, rises from 8.5%

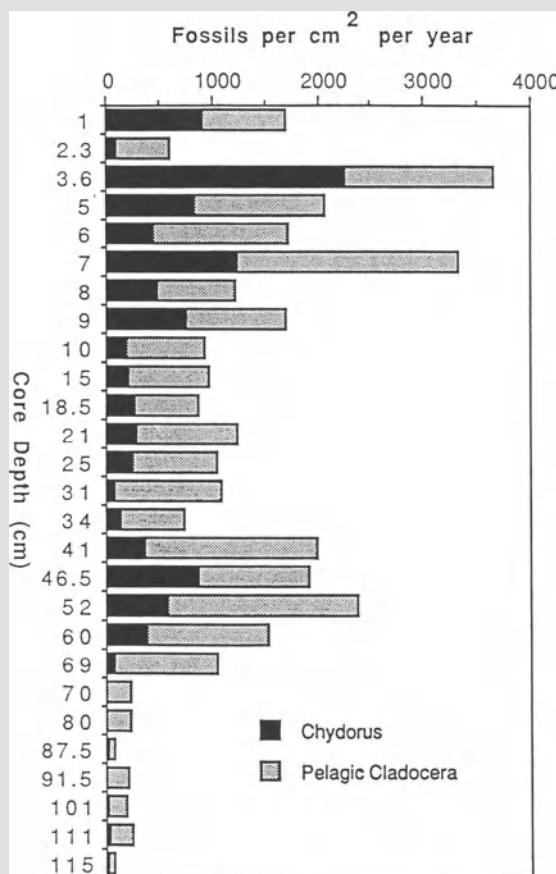
at 68–69 cm to 48% at 45.5–46.5 cm, which corresponds quite well with the ragweed rise determined for WC-86 (Winkler 1985). The 1985 and 1987 cores are very comparable in particle density and porosity, as well as depth to marl; therefore deposition rates derived for the mottled marl portion of the 1987 core can be applied with confidence to the 1985 core.

The buff marl underlying the postsettlement mottled marl is not well dated. Sediments from the 90- to 95-cm level of core WC-89, equivalent to ca. 100–105 cm in the 1985 core, yielded a radiocarbon date <200 years BP, ca. 1770 AD (Bortelson and Lee 1972). Sediments at the interface from inshore core C yielded a radiocarbon date of  $1,310 \pm 70$  carbon-14 years BP (Wis No. 1449), ca. 640 AD (Winkler 1985). Extrapolating from a second radiocarbon date from core C at 1.2 m below the interface of  $3,280 \pm 70$  years BP (Wis No. 1454), marl was deposited at a rate of 1 cm in 16 years or 0.6 mm/year. This rate is an order of magnitude lower than the overall average for postsettlement sedimentation (Hurley 1988). Clearly the radiocarbon date from WC-89 is too young, given the slow rate of marl deposition indicated by dates from core C. Applying the core C marl deposition rate to the 1985 core indicates that the deepest marl sample analyzed for cladocera (114–115 cm) might represent the period ca. 1100 AD.

Results derived from our analyses are ascribed to a year at the midpoint of each group of years represented in the core cut of that sample. Although cores from Lake Mendota are not annually varved, they do exhibit distinct banding patterns, indicating that bioturbation is modest. Sediment resuspension and focusing during spring and fall mixing events prevent identification of a discrete time for each core cut. In general, we interpret our individual results to represent something analogous to a running average of several years. Given that the average sedimentation rate since the early 1800s has been about 0.6 cm per year (Hurley 1988), a core cut of 1 cm thickness will contain material deposited over 2 or 3 years as well as the unknown effects of resuspension and mixing. When strong effects are known from the neolimnological record, they will be recorded but weakened by the dilution of the previous and subsequent years. Accordingly, we interpret the paleolimnological record with an aggregate view that represents the equivalent of several years of data. Where possible, we assessed that approach by comparing our results with those made in previous neolimnological studies representative of plankton communities now archived in the fossil record.

## Results

The results of our analyses are presented at three levels. First, we provide a general description of the entire core and the evidence of changes in system productivity over the nearly 1,000-year record represented in this

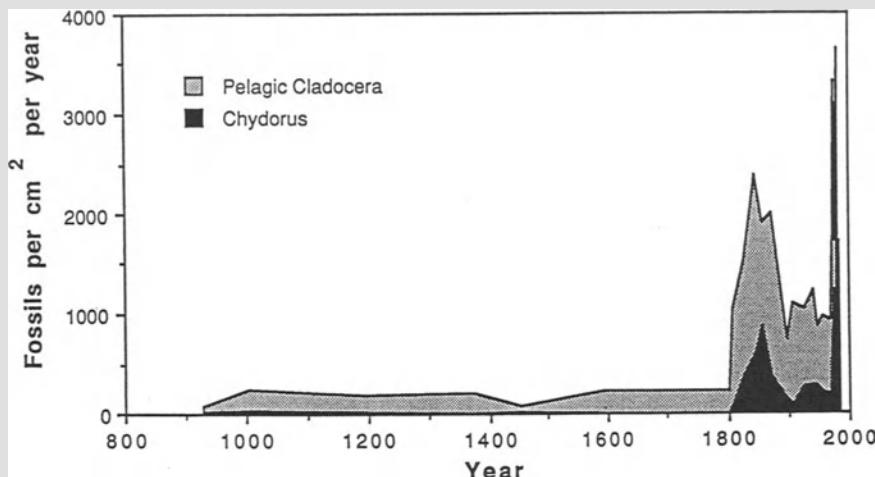


**Figure 4-1.** Estimated deposition rates for pelagic and littoral (*Chydorus*) Cladocera from each core sample. Core depth corresponds with the lower margin of each core cut.

core. Next, we describe the dynamics of the zooplankton community as they represent changing food web conditions. Further, we present evidence comparing the fossil record with historical observations of both the plankton and the fish communities.

### Fossil Deposition Rates

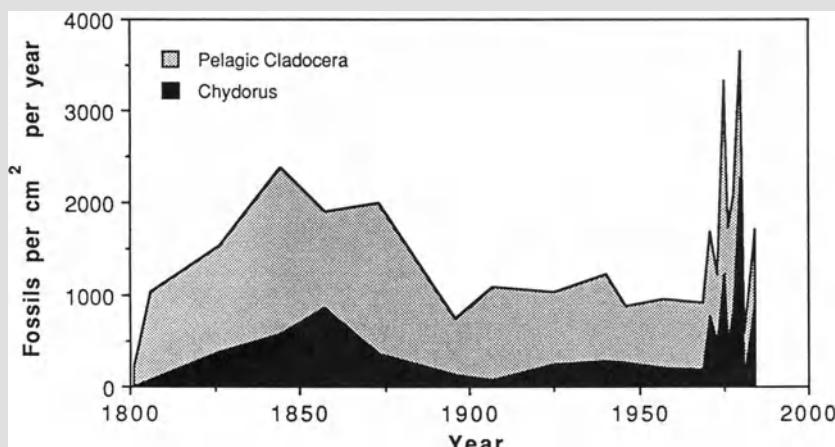
The dominant feature of this core corresponds with the well-known change in lake productivity that accompanied the advent of agriculture in Lake Mendota's drainage basin (Murray 1956). In combination, increases in sedimentation rate, nutrient loading, and more extensive anoxia of the hypolimnion produce the striking change in sediment color that marks the



**Figure 4-2.** Fossil deposition rates for pelagic and littoral Cladocera presented as a function of time based on the core dating protocol described in text.

cultural horizon. As described by Hurley (1988), sedimentation rates after about 1800 were approximately an order of magnitude greater than those in the preceding years. Remarkably, changes in sedimentation rate were not accompanied by increases in the organic fraction. As recorded by other studies (Bortelson and Lee 1972; Hurley 1988; Hurley et al., Ch. 5), the organic fraction of our core subsamples typically ranged from 15% to 20% and remained relatively constant throughout its length. A single value of 30% organic near the top of the core corresponds with a year (1976) of high runoff and productivity, as discussed in the following.

Calculated fossil deposition rates for each core cut are presented in Figure 4.1. Littoral forms (*Chydorus* spp.) are distinguished from pelagic Cladocera, and the estimated date of each sample was used to create the equivalent of a long-term data set for the entire core (Figure 4.2) and a greater resolution for the past two centuries (Figure 4.3). The deposition rate of all Cladocera increased dramatically at the cultural horizon, which occurs between our samples at -79 to -80 cm and -68 to -69 cm (Figures 4.1 and 4.2). This corresponds with the increase in ragweed pollen known to occur when agricultural practices intensified (Winkler 1985). Deposition rates continue to increase into the middle of the past century, documenting a continuous increase in nutrient loading as agriculture expanded. Although variable, deposition rates were reduced during the late 1800s and the first half of this century (core depths of -41 to -10 cm) (Figures 4.1 and 4.3). We interpret this period as indicative of a relative stabilization in agricultural development. In general, fossil loading rates decreased to about half of those recorded during the peak of agricultural expansion.



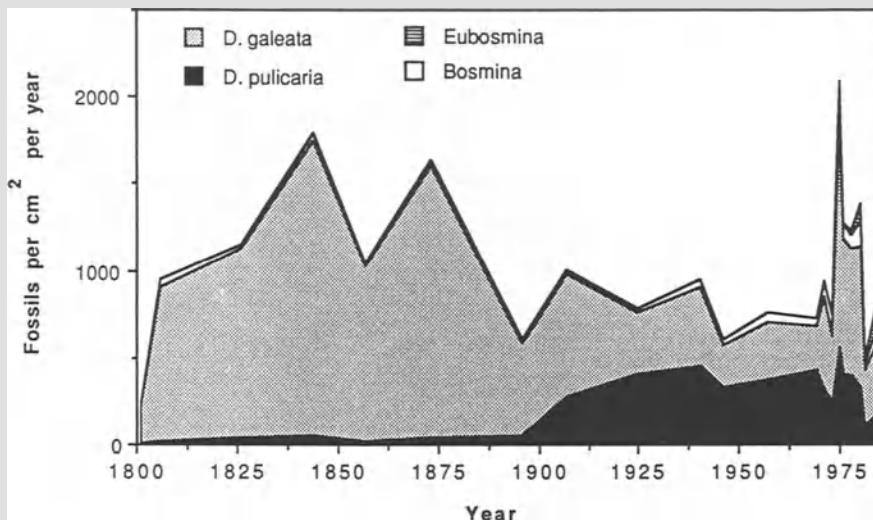
**Figure 4-3.** Fossil deposition rates for pelagic and littoral Cladocera for the period 1800–1985.

During more recent years, urban areas within the Yahara River basin have grown rapidly. The annual nutrient load has been further enhanced by construction activities and urban runoff. Zooplankton fossil deposition rates have been highly variable, including both the highest and the lowest rates observed since agriculturalization. The high rate at  $-6$  to  $-7$  cm corresponds with Hurley's (1988) estimate of a deposition rate of nearly 1 cm of new sediment in 1976. That year was reported by Lathrop (Ch. 6) as having unusually high runoff. All zooplankton species exhibited high productivity in that interval (Figures 4.1 and 4.3).

As documented by Nichols et al. (Ch. 9), the period from 1960 to the present includes the invasion, expansion, and reduction of *Myriophyllum spicatum* as the littoral zone of Lake Mendota underwent dramatic changes in macrophyte abundance. Corresponding with these changes is a variable but general increase in the loading of *Chydorus* spp. fossils. *Chydorus* spp. inhabit the littoral but are known to "raft" to the pelagic during blooms of blue-green algae (Frey 1960).

The highest deposition rate recorded in this core occurred at  $-2.3$  to  $-3.6$  cm and represents sediments deposited during 1979–81. *Chydorus* loading was particularly enhanced, suggesting a confounding effect of changes in the littoral habitat (Figures 4.1 and 4.3). Interpretation of this event is incomplete. It does, however, correspond with a period when macrophyte harvesting in the Madison lakes was at its nadir and, by extension, littoral vegetation offered substantial habitat to *Chydorus*. Pelagic Cladocera were also more abundant at that time, although not as remarkably so as *Chydorus*.

Low deposition rates observed in the recent past (core depths of  $-1$  to  $-2.3$  cm) cover the period of 1981–83, which includes a summer of



**Figure 4-4.** Fossil deposition rates of the most abundant pelagic Cladocera for the period 1800–1985.

unusually clear water (1983) documented by Lathrop (Ch. 6) and Vanni et al. (1990). Deposition rates recorded for that interval are the lowest observed since the advent of agriculture in the basin (Figures 4.1 and 4.3). The recent reductions in deposition rates are associated with the general reduction in nutrient status over the past 10 years as described by Lathrop (Ch. 6) and with food web dynamics more fully discussed in the following.

### Pelagic Zooplankton Community Dynamics

Fundamental changes in relative abundance of the commonly occurring pelagic cladoceran taxa indicate major changes in Lake Mendota's food web. The dynamics of the most abundant forms are presented in Figure 4.4. The dramatic increase in productivity initiated at the cultural horizon saw little change in relative abundance; *D. galeata* dominated the pelagic fauna. Subsequent changes in percent composition of *Daphnia* spp. divide the core into two major zones (Figure 4.4). For the period prior to about 1900 AD (core depths of –115 to –33 cm), *D. pulicaria* was consistently less than 5% of total Cladocera. Beginning about 1900 (core depth of –31 cm), the larger *D. pulicaria* continually increased and remained the most abundant of the pelagic zooplankton until the mid-1970s when it gradually declined to about 20% of the total (Figure 4.4).

The general increase in *D. pulicaria* followed by a gradual decline corresponds with the large-scale changes observed in fish populations. One of the primary planktivores in Lake Mendota is the cisco (*Coregonus*

*artedii*). Cisco die-offs were reported in the late 1800s, intensified about the beginning of this century with a major die-off reported in 1884, and continued intermittently for many years. During this period, populations of other major planktivores, the yellow perch (*Perca flavescens*) and white bass (*Morone chrysops*), were also known to diminish due to die-offs and variable recruitment success. In addition, exploitation by the sport fishery for yellow perch expanded dramatically during the first half of this century (Johnson and Staggs, Ch. 17). *D. pulicaria* became an important member of the pelagic community only after these documented reductions of its major predators (Luecke et al., Ch. 20; Magnuson and Lathrop, Ch. 11).

The decline of *D. pulicaria* over the most recent 15 years (Figure 4.4) of the core corresponds with the general recovery of the cisco population initiated by strong recruitment events in 1976 and 1977 (Magnuson and Lathrop, Ch. 11). These interpretations are consistent with the well-documented (Vanni et al. 1990) changes in zooplankton that occurred during the 1987–89 period when a massive cisco mortality resulted in a sudden change from *D. galeata* dominance to dominance by *D. pulicaria*.

Unlike the most recent changes evidenced in 1988, when *D. pulicaria* was more than 95% of the total *Daphnia*, *D. pulicaria* and *D. galeata* remained of similar abundance throughout the period 1925–70 (Figure 4.4). We interpret this difference to represent some combination of two effects. Core cuts include more than one year's sediment and, therefore, yield an average of two or more years. Second, several lines of evidence developed in other contributions to this volume indicate that Lake Mendota is experiencing a series of changes expressed as increased inter-annual variability in its plankton community. The paleolimnological record offers only a general indication of that, in that the surficial core cuts (1981–84) show zooplankton loading rates among the lowest since the increases recorded at the cultural horizon. In addition, the most recent sediments are buff-colored marl, similar to those deposited before the early 1800s.

Other paleolimnological reconstructions of food web interactions have successfully used changes in zooplankton size as an indicator of the intensity of size-selective predation by fishes (Kerfoot 1974; Kitchell and Kitchell 1980; Kitchell and Carpenter 1987). For samples ranging over nearly the entire length of the core, our estimates of body size for *D. galeata* consistently averaged 1.35–1.45 mm, while those for *D. pulicaria* were 1.4–1.55 mm. The two most recent samples yielded a different result; both decreased in size (to 1.25 and 1.3 mm, respectively) at core depths of –1.0 to –2.3 cm, and both increased to greater than 1.55 mm in the surface cut. Otherwise, *Daphnia* sizes appear little altered by the changes in productivity and fish community structure. This unexpected result may be associated with the relatively large adult sizes of *D. galeata* regularly observed in Lake Mendota. Size-selective predation effects may

be sufficient to account for the wax and wane of *D. pulicaria*, but not so strong as to diminish the compensatory capacity of the *D. galeata* population. Changes in the relative abundance and sizes of different *Daphnia* species are the responses indicative of predation intensity by visual predators whose size selectivity may be confounded in a dynamic light regime such as that of Lake Mendota (Kitchell and Kitchell 1980; Leavitt et al. 1989). *Daphnia* is generally a superior competitor among the Cladocera. When total predation on *Daphnia* is reduced as during the cisco die-offs, the largest *Daphnia* comes to dominance.

Other zooplankton species are a small component of the pelagic zooplankton community (Figure 4.4). *Bosmina longirostris* comprised a small and variable (5–37%) percentage of the total. It is more than 10% only in the very old sediments and in the recent sediments, in conjunction with a gradual reduction in *D. pulicaria*. *Ceriodaphnia* spp. and *Leptodora kindtii* are represented throughout the core but are consistently less than 2% of fossil cladocerans. *Eubosmina coregoni*, a European exotic that invaded the Great Lakes in the early 1960s, appeared only in the more recent samples and increased to 19% of the total at the core surface. Dodson (pers. comm.) found *E. coregoni* in nearby Lake Monona and Lake Waubesa during the early 1980s. *E. coregoni* continues to appear in recent zooplankton samples from Lake Mendota but is generally less abundant than during the mid-1980s.

### Neolimnological vs. Paleolimnological Results

One advantage of working on Lake Mendota is the long record of previous research efforts. Accordingly, we attempted to take advantage of this unique opportunity by assessing the comparability of neolimnological results which are now represented in a paleolimnological archive.

Independent observations of relative abundance confirm our interpretations based on fossils. Birge (1898) made a series of regular zooplankton collections during the period of 1894–96. He reported two years of *D. galeata* dominance and one year of higher abundance of *D. pulicaria*. Averaging his data yields a general result of 80% *D. galeata* and 20% *D. pulicaria*. Our core sample for that period (–34 to –33 cm), which is dated at about 1896, reflects a comparable composition of 88% *D. galeata* and 12% *D. pulicaria*.

In a later study, Frey (1960) sampled both the zooplankton and the surficial sediments to test for congruence. He reported that his samples of sediments contained 92% *Daphnia* spp. and 8% *Bosmina*. He also stated that *Daphnia* “with large middle pecten” were most common. His sampling occurred during 1958, which corresponds to our core cut at –15 to –14 cm that was dated as 1956–59. We observed 93% *Daphnia* spp., 7% *Bosmina*, and dominance by *D. pulicaria*, whose large middle pecten is a diagnostic key character. Again, our core samples appear to directly

reflect results from independent neolimnological observations of the zooplankton community.

The general patterns of zooplankton composition represented by the 1969–84 sediment record correspond with those reported by Lathrop and Carpenter (Ch. 8). *D. galeata* and *D. pulicaria* were the dominant cladocerans with substantial interannual differences in relative importance. After 1975, *D. pulicaria* exhibited an overall decline in relative abundance as the pelagic planktivore community reflected the general increase in cisco abundance recorded prior to the major mortality of 1987.

## Discussion

Our 1,000-year record of zooplankton fossils can be summarized in three general periods. The presettlement history of the lake included low levels of productivity and low variability. That record was dominated by *D. galeata* with only modest representation by smaller (*Bosmina*) and larger (*D. pulicaria*) zooplankton. In general, this community was indicative of an intermediate level of planktivory by fishes such as the cisco and yellow perch. At no time was the system dominated by small cladocerans (e.g., *Bosmina*) or heavily dominated by the largest (e.g., *D. pulicaria*). By inference, levels of herbivory and piscivory were also of intermediate intensity.

The period of the nineteenth century included the appearance of agriculture and a surge of productivity corresponding with increased erosional load of allochthonous nutrients. Both the sedimentation rate and the zooplankton production rate increased dramatically. However, zooplankton community composition remained similar throughout this period. Although productivity at all trophic levels may have been enhanced, we see no evidence of qualitative changes in food web structure.

The early decades of this century reflected a general decrease in system productivity, which we interpret as indicative of a stabilization of agricultural activities. While remaining substantially higher than in presettlement history, overall productivity declined to about one-half of that recorded as agricultural development was expanding and soil disturbance rates were at their peak. In keeping with this observation, the human population density of the Lake Mendota watershed was about 10,000 in 1870 and increased to only about 15,000 by 1960.

The zooplankton community began to change about the turn of the century as periodic die-offs of major planktivores diminished the intensity of size-selective predation. The largest zooplankton, *D. pulicaria*, gradually increased over this period to become the dominant herbivore and remained as such until the 1970s, when a series of strong year classes reestablished the cisco population. *D. pulicaria* diminished subsequently and *D. galeata* resumed dominance.

Two surges of increased zooplankton production dominate the record of the past two centuries (Figure 4.3). This period corresponds with the sediment core analyzed by Hurley et al. (Ch. 5). In fact the general patterns of their indicator of grazing intensity—a ratio of pheophorbide to total pheopigments—correspond well with our record of zooplankton loading. The first increase in both corresponds with the cultural horizon and is followed by a period of sustained but lower grazing intensity. A second increase in both grazing and zooplankton production occurs in the past two decades. Patterns of variability are also similar; the recent periods evidenced both high rates and high variation. During the period of 1960–80, the human population density of the watershed increased from 15,000 to more than 40,000.

The 15-year period of 1969–84 includes both the highest and the lowest fossil deposition rates since the early 1800s. The variability evident in our data derives from two sources. First and most obvious is our sampling resolution. We sampled our core at more frequent intervals near the top, which will generally yield both higher resolution and greater variability. Hurley et al. (Ch. 5) got a similar result. In addition, as reported by many contributors to this volume (e.g., Carpenter et al., Ch. 22), Lake Mendota's food web appears to be going through a period of heightened instability due to both the inherent variability of predation effects and the continuous reduction in nutrient loading that became more apparent in the past decade. As our core includes only the beginning of that record, the long-term results of direct observation are a more appropriate source of evidence (Lathrop and Carpenter, Ch. 7 and 8; Magnuson and Lathrop, Ch. 11), while the mechanistic basis for dynamics is represented in the results of experimental studies (Luecke et al., Ch. 14; Post et al., Ch. 15; Vanni et al., Ch. 21).

Our original goal in undertaking this study was to offer some of the insights of history as a basis for developing more realistic expectations for the experimental studies and whole-lake manipulations. Three aspects of our results surprised us:

1. *D. galeata* was the dominant zooplankter well before cultural eutrophication and fishery exploitation effects appeared. The overall change in productivity due to the plow did not result in an apparent change in zooplankton community structure. We conclude that piscivory has been of only intermediate importance in governing the presettlement structure of the pelagic system. Returning Lake Mendota to its ancestral state would probably not yield maximum possible grazing pressure on the algal community.
2. Strong dominance by *D. pulicaria*, as exhibited in 1988 (Vanni et al., Ch. 21), is unknown from the fossil record. This may derive from the averaging of seasons and years represented by core samples and/or from the fact that the events of 1987–88 are unique. In either case,

neolimnological studies indicate that lower nutrient loading rates and very low levels of planktivory occurred in a combination without clear precedence in the historical record.

3. In terms of overall productivity, agricultural effects dominated the paleolimnological record and, surprisingly, diminished after the initial effects of soil disturbance. However, zooplankton accumulation rates indicated that maximum production occurred in the mid-1970s. Within the past three decades, system productivity has increased and decreased in concert with the effects of urbanization and the subsequent diversion of sewage (Lathrop, Ch. 6). Food web effects, due largely to population dynamics of the cisco, further amplified water quality improvements observed when nutrient loading rates were low.

Throughout this volume are many kinds of evidence suggesting that Lake Mendota's water quality is both highly variable and gradually improving over the past two decades. If the trends are to be sustained, nutrient loading must not be allowed to increase. The results summarized herein demonstrate that management of the food web can enhance water quality in periods when nutrient loading is low. Those periods cannot increase in frequency and duration if urbanization occurs without the constraints that will minimize nutrient runoff. In fact, recent limnological events in this lake (e.g., 1988) are without historic precedent. Food web enhancements of water quality are at or near their maximum potential. Although of academic interest, these lessons are of little or no practical consequence unless local institutions accept the responsibility for continued vigilance against increases in allochthonous nutrient loading.

At this writing, communities to the north and west of Lake Mendota continue to grow at remarkable rates. Fully one-third of the nutrient load to the lake now derives from urbanized areas. Uncontrolled urban growth is additive to the extant non-point loading from agricultural areas and, in fact, yields more nutrient per unit area than farming. It is imperative that controls on these sources be maintained if not enhanced.

The essential combination of basic limnological understanding, fisheries management practices, and public support is now established in ways that will provide the maximum benefits of food web management in Lake Mendota. Continued improvement in the water quality of this eutrophic, urban lake requires the complement of effective controls on nutrient loading.

*Acknowledgments.* We thank Majorie Winkler for use of the facilities of the Palynology Laboratory, Center for Climatic Research, University of Wisconsin-Madison. We also thank Jim Hurley, Peter Leavitt, Lars Rudstam, and Majorie Winkler for manuscript reviews. This report was funded in part by the Federal Aid in Sport Fish Restoration Act under Project F-95-P and the Wisconsin Department of Natural Resources (WDNR).

## References

- Benninghoff WS (1962) Calculations of pollen and spores density in sediments by addition of exotic pollen in known quantities. *Pollen Spores* 4:332–333
- Birge EA (1898) Plankton studies on Lake Mendota. II. The crustacea of the plankton from July, 1894, to December, 1896. *Trans. Wis. Acad. Sci. Arts Lett.* 11:274–448
- Bortelson GC, Lee GF (1972) Recent sedimentary history of Lake Mendota, Wisconsin. *Env. Sci. Technol.* 6:799–808
- Brooks JL (1957) The systematics of North American *Daphnia*. *Mem. Conn. Acad. Arts Sci.* 13:1–180
- Carpenter SR, Kitchell JF, Hodgson JR (1985) Cascading trophic interactions and lake productivity. *BioScience* 35:634–639
- Dodson SI (1981) Morphological variation of *Daphnia pulex* Leydig (Crustacea: Cladocera) and related species from North America. *Hydrobiologia* 83:101–114
- Frey DG (1960) The ecological significance of cladoceran remains in lake sediments. *Ecology* 41:684–699
- Frey DG (1964) Remains of animals in Quaternary lake and bog sediments and their interpretation. *Arch. Hydrobiol. Beih. Ergeb. Limnol.* 2:1–114
- Frey DG (1986) Cladocera analysis. In Berglund BE (ed) *Handbook of holocene palaeoecology and palaeohydrology*, John Wiley and Sons, New York, pp 667–692
- Hurley JP (1988) Diagenesis of algal pigments. Ph.D. Thesis, University of Wisconsin, Madison
- Kerfoot WC (1974) Net accumulation rates and the history of cladoceran communities. *Ecology* 55:51–61
- Kerfoot WC (1975) Seasonal changes of *Bosmina* (Crustacea: Cladocera) in Frains Lake, Michigan: Laboratory observations of phenotypic changes induced by organic factors. *Freshwat. Biol.* 5:227–243
- Kerfoot WC, Sih A (eds) (1987) *Predation: Direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, New Hampshire
- Kitchell JA, Kitchell JF (1980) Size selective predation, light transmission, and oxygen stratification: Evidence from the recent sediments of manipulated lakes. *Limnol. Oceanogr.* 25:389–402
- Kitchell JF, Carpenter SR (1987) Piscivores, planktivores, fossils, and phorbins. In Kerfoot WC, Sih A (ed) *Predation: Direct and indirect impacts on aquatic communities*, University Press of New England, Hanover, New Hampshire, pp 132–146
- Leavitt PR, Carpenter SR, Kitchell JF (1989) Whole lake experiments: The annual record of fossil pigments and zooplankton. *Limnol. Oceanogr.* 34:700–717
- Murray RC (1956) Recent sediments of three Wisconsin lakes. *Bull. Geol. Soc. Am.* 67:883–910
- Swain AM (1973) A history of fire and vegetation in northeastern Minnesota as recorded in lake sediments. *Quat. Res.* 3:383–396
- Traverse A, Ginsberg RN (1966) Palynology of the surface sediments of Great Bahama Bank, as related to water movement and sedimentation. *Mar. Geol.* 4:417–499

- Twenhofel WH (1933) The physical and chemical characteristics of the sediments of Lake Mendota, a freshwater lake of Wisconsin. *J. Sed. Petrol.* 3:68–76
- Vanni MJ, Luecke C, Kitchell J, Allen Y, Temte J, Magnuson JJ (1990) Effects on lower trophic levels of massive fish mortality. *Nature* 344:333–335
- Winkler MG (1985) Late glacial and Holocene environmental history of south-central Wisconsin: A study of upland and wetland ecosystems. Ph.D. Thesis, University of Wisconsin, Madison

# 5

## **Historical Interpretation of Pigment Stratigraphy in Lake Mendota Sediments**

**James P. Hurley, David E. Armstrong, and  
Andrea L. DuVall**

### **Introduction**

Algal pigments are important biomarkers of lake productivity and trophic interactions. Our understanding of organic matter production, sedimentation, and decomposition, phytoplankton–zooplankton interactions, and historical changes in lakes has benefited from pigment-derived information. However, several pitfalls may be encountered in interpreting pigment data. Algal pigments must be distinguished from those produced by higher plants and photosynthetic bacteria. Influences of production on pigment types and concentrations in the water column must be resolved from effects of photodegradation and chemical or biological alteration. Biases in historical sedimentary records toward pigments preferentially preserved during diagenesis must be quantified. With these complications in view, algal pigments provide important insights into lake biogeochemistry and paleolimnology.

Recent advances in pigment methodologies have enabled rapid separation and identification of individual phorbins, carotenoids, and their degradation products (Mantoura and Llewellyn 1983; Bidigare et al. 1985). Thus, common absorbance and fluorescence techniques for chlorophyll analysis (Holm-Hansen et al. 1965; Lorenzen 1967) can be replaced by compound-specific measurements which can yield information on algal biomass, senescence, and processing. Several important phorbin transformations have been characterized. Chlorophyll *a*, used to estimate phytoplankton biomass, can be transformed to pheophytin or pheophorbide. Conversion to pheophytin (Mg removal) is generally

associated with cell senescence and aging (Daley 1973; Daley and Brown 1973). Pheophorbide *a* (dephytollated, demetalled chlorophyll) forms during passage through the gut and may be used as an indicator of heterotrophic processing (Welschmeyer et al. 1984; Carpenter et al. 1986).

Carotenoids in the water column and sediments are particularly useful in providing information on specific algal groups: Chlorophyta (lutein, violaxanthin, neoxanthin, and  $\beta$ -carotene), Chrysophyta (fucoxanthin, diadinoxanthin, and diatoxanthin), Cryptophyta (alloxanthin), Cyanophyta (zeaxanthin, myxoxanthophyll, echinenone, and oscillaxanthin), and Pyrrophyta (peridinin and diadinoxanthin) (Goodwin 1965). Although individual carotenoid contents may vary among cells or species, the abundances of major carotenoids in the water column clearly reflect major distributions of phytoplankton types.

Phytoplankton-derived phorbins and carotenoids which remain in sediments are those resistant to degradation within the water column or sediments. Dominance in a sediment core may not mean that a particular phytoplankton type was dominant in the water column. It may mean that the pigment has resisted degradation. Similarly, a dominant water column pigment may be absent from a sediment core due to complete degradation. These influences can be assessed by measurement of water column concentrations, fluxes to sediments, and accumulation in sediments.

Information on degradation is emerging. Processes of degradation in the water column include photolysis, cell lysis, and processing by heterotrophs (Welschmeyer et al. 1984; Carpenter et al. 1986; Leavitt and Carpenter 1990a,b). Losses depend on the length of time particles are subjected to these processes. Pigments in slowly sinking particles may be preferentially degraded. At the sediment–water interface, degradation occurs both biologically and chemically, increasing under oxic conditions (Furlong and Carpenter 1988; Hurley and Armstrong 1990). However, rates are reduced after pigments are buried below the surface mixed layer. Rates are also pigment-specific, depending on pigment structure (Repeta and Gagosian 1987; Hurley and Armstrong 1990). Stable end products of some carotenoids have been identified (Repeta 1989). Eventually, coupling of information on rates and products of degradation in diagenetic models will provide quantitative assessment of sedimentary pigment profiles.

Here we summarize recent information on algal pigments in Lake Mendota. We compare water column pigment distribution to pigments contained within the permanent sediment record. The incorporation of pigments into sediments is evaluated by identifying major components and processes which affect preservation. The effects of diagenesis—the combined physical, chemical, and mineralogical changes taking place during and after their deposition (Lerman 1979)—are examined. After the effects of diagenesis are considered, the sedimentary pigment signature may be assessed.

## Methods

In this study, it was necessary to obtain information on standing pigment content of the water column, gross sedimentation fluxes, and net accumulation fluxes of pigments and major elemental phases prior to interpretation of pigment distributions in sediments. Details of individual techniques employed are described by Hurley (1988a) and Hurley and Armstrong (1990).

Water column pigment distribution was determined weekly by standard filtration, followed by extraction with 90% acetone and preparation for high-performance liquid chromatography (HPLC) analysis. Settling particulate matter was collected by installing sedimentation traps (Shafer 1988) in the hypolimnion. Trap material was collected every 3 weeks during the ice-free period. Subsamples of collected material were taken for analysis of mass, major elemental composition, and pigment content.

The sediment core was obtained in June 1987 from the Deep Hole Basin of Lake Mendota, using a frozen crust sampling device (Swain 1978). The core was sectioned at 1-cm intervals for the first 10 cm, 2-cm intervals from 10 to 20 cm, and 5-cm intervals for the remainder of the core. Subsamples for pigment analysis were taken, and the remainder of the core was freeze-dried for further analyses.

Sedimentation rates were calculated based on the nondestructive cesium-137 method (Robbins and Edgington 1975). The strong 1963 peak in cesium-137 input was easily distinguished in the 14- to 16-cm interval (Hurley and Armstrong 1990). Identification of this horizon, together with mass depth information, yielded a sedimentation rate of  $88.9 \text{ mg cm}^{-2} \text{ y}^{-1}$  (not corrected for sediment focusing). Table 5.1 summarizes the percent dry weight, mass depth, extrapolated deposition date, and linear sedimentation rate for each interval. Due to compaction, linear sedimentation rates for intervals at the top of the core are substantially greater than midcore rates. Greater percent solids results in lower linear sedimentation rates through the middle section of the core.

It must be noted that the measured sedimentation rate from cesium-137 dating is most accurate down to the 1963 horizon. A constant annual mass sedimentation rate above this layer is assumed. Below this point in the core, it is assumed that the mass deposition rate is the same as the rate measured for sediments deposited after 1963. Our assumption is strengthened by the comparison of our linear sedimentation rate of  $0.63 \text{ cm y}^{-1}$  to a rate of  $0.6 \text{ cm y}^{-1}$  obtained by Bortleson (1970) using ragweed pollen. Bortleson's core was taken approximately 20 years prior to our core, and his sedimentation rate represents the entire post-settlement section. Information on sedimentation rates obtained from our core is applied to other sediment-related aspects of Lake Mendota by Kitchell and Sanford (Ch. 4) and Lathrop (Ch. 6).

Pigments were measured using HPLC (Mantoura and Llewellyn 1983) with modifications in mobile phases and gradients (Hurley 1988a,b). Stan-

**Table 5-1.** Sediment core information for Deep Hole core, obtained in June 1987. Mass sedimentation data are based on cesium-137 dating. Peak in cesium-137 occurred in the 14- to 16-cm interval (Hurley and Armstrong 1990). Linear sedimentation rates for intervals reflect differences in compaction and porosity in the core.

Depth interval (cm)	% dry wt.	Mass depth (g/cm <sup>2</sup> )	Date <sup>a</sup>	Linear sed. rate <sup>b</sup>
0–1	3.52	0.028	1987	1.67
1–2	5.26	0.083	1986	1.29
2–3	7.16	0.112	1985	0.91
3–4	6.88	0.304	1984	0.81
4–5	7.36	0.416	1982	0.80
5–6	7.32	0.531	1981	0.77
6–7	8.39	0.655	1980	0.72
7–8	9.12	0.792	1978	0.65
8–9	9.63	0.939	1976	0.60
9–10	10.6	1.10	1974	0.56
10–12	10.8	1.35	1972	0.53
12–14	12.6	1.72	1968	0.48
14–16	13.8	2.13	1963	0.43
16–18	15.7	2.60	1958	0.38
18–20	16.8	3.11	1952	0.35
20–25	16.6	4.03	1942	0.34
25–30	17.0	5.34	1927	0.34
30–35	20.0	6.80	1911	0.31
35–40	20.7	8.40	1892	0.28
40–45	16.2	9.85	1876	0.31
45–50	15.7	11.1	1862	0.36
50–55	14.2	12.3	1849	0.38
55–60	12.4	13.2	1837	0.43
60–65	13.0	14.3	1826	0.45
65–70	12.8	15.3	1815	0.44
70–75	11.7	16.3	1804	0.46
75–80	11.2	17.2	1794	0.50

<sup>a</sup>Extrapolated date of midpoint of interval, based on mass sedimentation rate of 0.0889 g cm<sup>-1</sup> y<sup>-1</sup>.

<sup>b</sup>Linear sedimentation rate in cm y<sup>-1</sup> for depth interval in core.

dards were obtained from suppliers (Sigma Co., Hoffman LaRoche) or extracted from algal cultures of known pigment composition. Results presented for *a* phorbins represent the four major groupings (chlorophyllide, pheophorbide, chlorophyll, and pheophytin), although each group may contain a number of derivatives. For example, chlorophyll *a* represents the sum of chlorophyll *a*, allomerized (oxidized) chlorophyll *a*, and epimerized chlorophyll *a'*, while pheophytin *a* represents the sum of three pheophytin peaks (Hurley 1988a). Carotenoid analysis is restricted to

fucoxanthin, diadinoxanthin, diatoxanthin, alloxanthin, peridinin,  $\beta$ -carotene, echinenone, and lutein + zeaxanthin (chromatographically inseparable). It is unfortunate that the latter two carotenoids could not be distinguished from each other, since zeaxanthin is a major carotenoid of blue-green algae, while lutein is common in green algae (Goodwin, 1965).

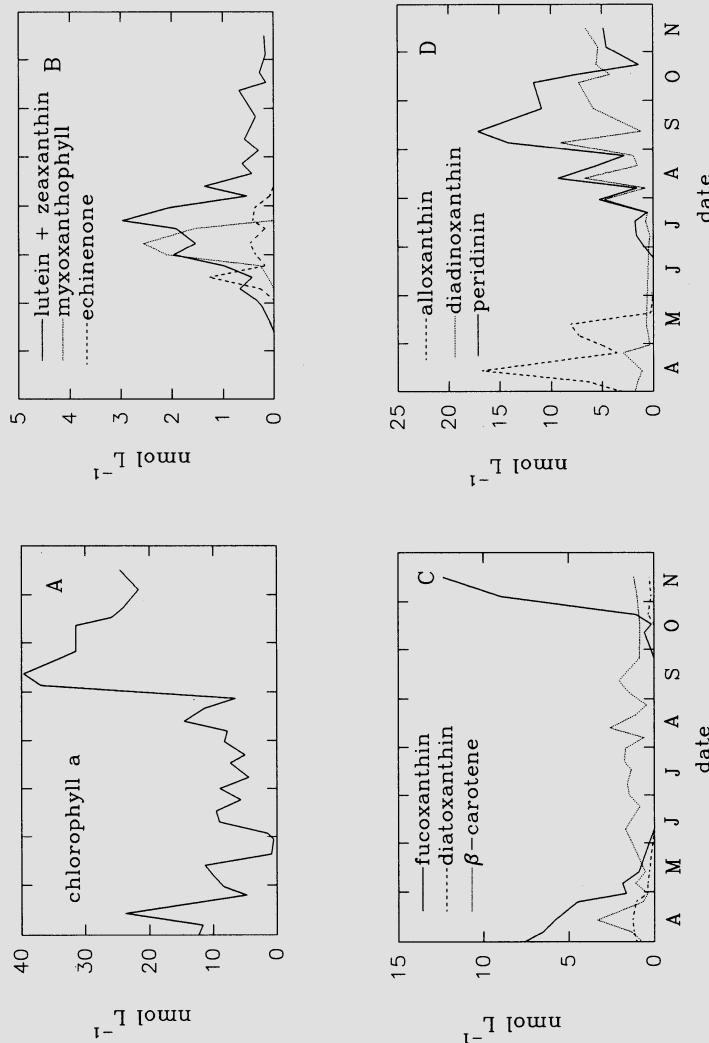
Total C was determined by dry combustion to CO<sub>2</sub>. Inorganic C was determined after a precombustion step at 450°C, and organic C was calculated by difference. Biogenic silica was determined by a wet alkaline digestion procedure followed by colorimetric analysis (DeMaster 1979; Krausse et al. 1983) with modifications by DuVall (1990). Total Ca and Al were determined by inductively coupled plasma (ICP) analysis of digested sediment extracts. Sediment compositional phases were calculated from elemental information, based on molar compositions of chemical phases (Shafer 1988). The four phases modeled were organic matter (from organic C), calcite (from Ca and inorganic C), biogenic silica (direct), and shale (from Al). The remaining fraction contains other phases not modeled, including nonbiogenic silica (sand).

### Transformations in the Water Column

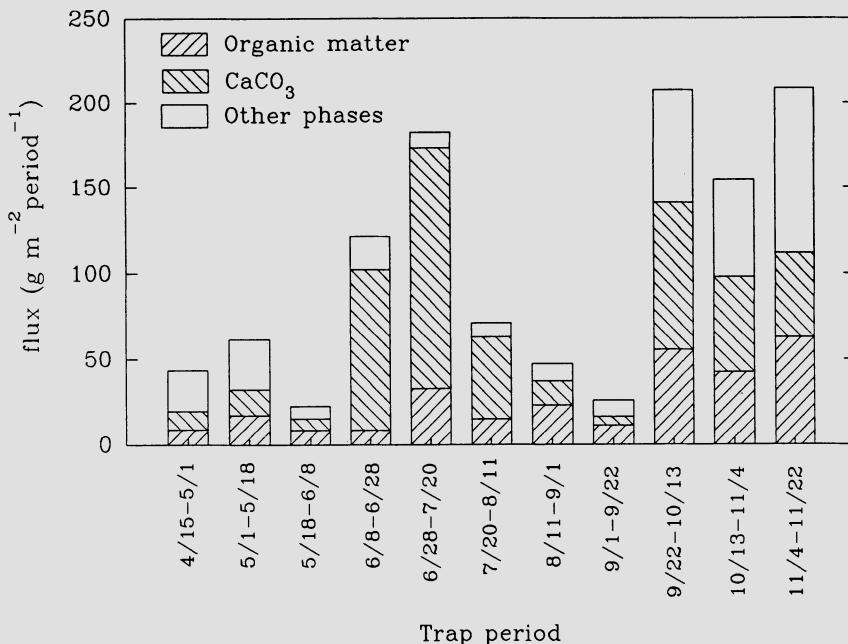
During 1987, samples for phorbins and carotenoids were measured weekly in the epilimnion (0–10 m) of Lake Mendota (Hurley 1988a; Hurley and Armstrong 1990). Phytoplankton distribution was also determined (Vanni and Temte 1990; Vanni et al., Ch. 13). Comparisons were made with pigments deposited in sediment traps to obtain information on pigment losses within the water column.

Chlorophyll distribution (Figure 5.1a) was bimodal, with highest concentrations ( $>20 \text{ nmol L}^{-1}$ ) occurring after complete mixing in early spring and fall. Lowest chlorophyll concentrations, after thermal stratification in mid- to late May, were concurrent with a period of maximum zooplankton abundance and grazing activity (Vanni et al., Ch. 13). This so-called clear-water phase is typical of Lake Mendota (Lathrop and Carpenter, Ch. 7).

Carotenoid distribution reflected shifts in phytoplankton dominance through the ice-free period (Figure 5.1b–d). In early spring, following ice-out, both chrysophytes (fucoxanthin) and cryptophytes (alloxanthin) were dominant. Similar to chlorophyll *a*, the concentrations of fucoxanthin and alloxanthin dropped dramatically during May. Although alloxanthin was absent after late spring, fucoxanthin exceeded spring values following fall overturn. Blue-green algal blooms are common during midsummer in Lake Mendota (Lathrop and Carpenter, Ch. 7). Although intense midsummer algal blooms developed near the surface, depth-integrated (0–10 m) chlorophyll *a* ( $0–10 \text{ nmol L}^{-1}$ ) and carotenoid concentrations ( $0–4 \text{ nmol L}^{-1}$ ) were low compared to other bloom periods. Cyanophytes



**Figure 5-1.** Chlorophyll *a* and carotenoid content of 0- to 10-m integrated samples in Lake Mendota, 1987. Adapted from Hurley and Armstrong (1990) with permission of Limnology and Oceanography.



**Figure 5-2.** Flux and composition of particulate matter to sediment traps in Lake Mendota, 1987. Adapted from Hurley and Armstrong (1990) with permission of Limnology and Oceanography.

containing zeaxanthin (although not quantitatively separated from lutein) appeared to dominate in midsummer, along with a secondary peak of echinenone producers.

Chlorophyll levels in excess of  $15 \text{ nmol L}^{-1}$  were produced by dinoflagellates (see peridinin, Figure 5.1). Peridinin appeared in early July, peaked in mid-September, and remained through November. In late October and November, peridinin was replaced by fucoxanthin as the dominant carotenoid, a result of a strong fall diatom bloom. This pattern of phytoplankton succession in 1987 is generally typical of Lake Mendota, although interyear variability is high (Lathrop and Carpenter, Ch. 7).

Water column processes play a key role in determining which pigments will be preserved in bottom sediments. Direct settling of phytoplankton may be slow, allowing degradation to occur within the water column, especially through photolysis. Processing by zooplankton may package pigments into quickly settling fecal material and aid preservation (Soohoo and Kiefer 1982a,b). Conversely, gut passage may degrade or transform specific pigments. Also, pigment deposition during periods of high sedimentation or anoxia may aid preservation (Sanger 1988).

Particulate matter fluxes to sediments during the ice-free period (Figure 5.2) reflected both organic and inorganic sedimentation events. Calcite

**Table 5-2.** Sediment-trap fluxes, permanent accumulation (burial) fluxes (corrected for sediment focusing), and calculated loss (%) of phorbins and selected carotenoids in Lake Mendota surface sediments (0–3 cm). Flux units are  $\mu\text{mol m}^{-2} \text{yr}^{-1}$ . Table reprinted with permission from Limnology and Oceanography.

	Trap flux	Accum. flux	% loss
<b>Phorbin class</b>			
Total <i>a</i> phorbins	952	337	65
Chlorophyll <i>a</i>	376	170	58
Pheophytin <i>a</i>	34.8	115	-230
Chlorophyll <i>a</i> + pheophytin <i>a</i>	411	185	31
Pheophorbide <i>a</i>	280	42.8	85
Chlorophyllide <i>a</i>	262	8.82	96
Chlorophyllide <i>a</i> + pheophorbide <i>a</i>	541	51.6	90
<b>Carotenoids</b>			
Total carotenoids	738	217	71
Fucoxanthin	414	43.7	89
Diadinoxanthin	96.6	ND	100
Diatoxanthin	42.4	31.5	26
Alloxanthin	22.2	40.4	-82
Peridinin	20.9	ND	100
$\beta$ -Carotene	63.1	58.5	7
Myxoxanthophyll	7.61	ND	100
Echinonone	12.3	ND	100
Lutein + zeaxanthin	59.2	42.5	28

precipitation ( $\text{CaCO}_3$ ) was a major sedimentation process throughout midsummer in 1987, as shown by sediment trap measurements (Hurley and Armstrong 1990). Fallon and Brock (1980) suggest that mass flux in midsummer is due to sedimentation of blue-green algae. Our results from 1987 show organic matter sedimentation increased in late July (suggesting blue-green algal sedimentation), but the midsummer mass flux is mainly calcite. Postovertturn calcite in sediment traps (9/22–11/22) was attributed to calcite in resuspended sediments, since surface sediments contain approximately 30% calcite and conditions (temperature, pH) for precipitation within the water column are less favorable than in midsummer. Sedimentation after overturn (9/22) results from both sediment resuspension and settling of the fall diatom bloom. We did not measure biogenic silica in the trap material, but the fucoxanthin content of trap material during this period (Hurley and Armstrong 1990) suggests biogenic silica is a major component of “other phases” present. Similarly, biogenic silica was probably abundant in the spring bloom and corresponding sedimentation from 4/15 to 6/8.

Pigment fluxes to the bottom sediments, measured by sediment traps and corrected for resuspension, were dominated by chlorophyll *a*,

pheophorbide *a*, and chlorophyllide *a* (Table 5.2). Sedimentation of untransformed chlorophyll *a* was high, suggesting that direct settling of phytoplankton was the dominant transport route to sediment for plankton-derived material. Pheophorbide sedimentation indicates that water-column processing by heterotrophs (Welschmeyer et al. 1984) and transport through fecal material are also important. Intense zooplankton grazing (and pheophorbide deposition) mainly occurred during the clear water phase in spring (Hurley and Armstrong 1990). The chlorophyllide flux occurred mostly in late fall in association with diatoms. High chlorophyllase activity in diatoms enhances chlorophyllide formation (Jeffrey and Hallegraeff 1987).

Carotenoid sedimentation was dominated by fucoxanthin, diadinoxanthin, and  $\beta$ -carotene, due largely to high fluxes of diatoms during the fall bloom (Table 5.1) (Hurley and Armstrong 1990). Bluegreen algal pigment fluxes (myxoxanthophyll, echinenone, and lutein + zeaxanthin) were lower. Sedimentation of peridinin, the most important water column carotenoid during 1987, was low relative to its abundance in the water column. Apparently, peridinin is susceptible to degradation (i.e., photo-degradation) during whole-cell sedimentation (see also Leavitt and Carpenter 1990b). Since dinoflagellates were not grazed extensively (Vanni and Temte 1990), their transfer to bottom sediments probably occurred through direct settling.

## Transformations in Sediment

Comparisons of sediment trap fluxes to the focus-corrected sediment accumulation fluxes (Table 5.2) indicate that overall degradation of phorbins and carotenoids at the sediment surface was of similar magnitude (65% and 71% of the trap-deposited flux). However, individual phorbins and carotenoids differ widely in the degree of susceptibility to degradation.

Dephytollated derivatives of chlorophyll *a* (pheophorbide + chlorophyllide) are degraded more extensively than phytol-containing derivatives (chlorophyll + pheophytin). A large fraction of the chlorophyll loss is accounted for by pheophytin gain, suggesting that transformation to pheophytin is a dominant sedimentary transformation process (Daley et al. 1973; Keely and Brereton 1986). Preferential degradation of dephytollated derivatives decreases pheophorbide accumulation in sediments relative to chlorophyll and pheophytin. Therefore, sedimentary pheophorbide (a grazing indicator) levels are low relative to the proportion deposited at the sediment surface.

Among the carotenoids, diadinoxanthin, peridinin, myxoxanthophyll, and echinenone were not detected in surface (0–3 cm) sediments. Fucoxanthin, which represented the largest trap-collected carotenoid

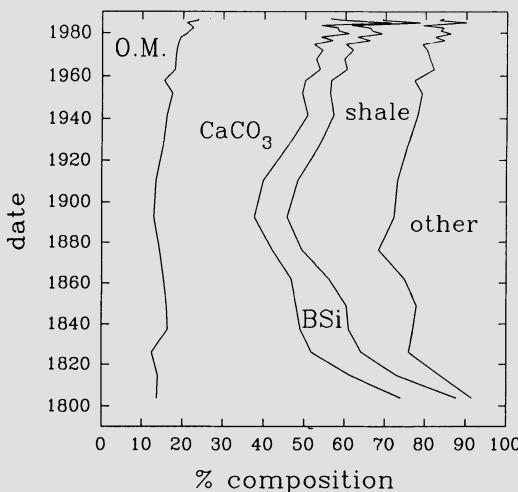
flux, is similarly reduced in surface sediments. Therefore, the two major carotenoids present in the water column substantially degraded during incorporation into surface sediments. Since fucoxanthin also undergoes postdepositional diagenesis (see below), fucoxanthin and peridinin in sediments are not useful for paleolimnology under these conditions. Similar trends in fucoxanthin diagenesis were observed in oligotrophic lake sediments (Hurley 1988a; Hurley and Armstrong 1991) and in coastal Peruvian sediments (Repeta 1989). Susceptibility to degradation of fucoxanthin and peridinin, relative to other carotenoids, is likely a result of their chemical structure, i.e., epoxide groups on end-member rings (Repeta and Gagosian 1984, 1987).

In contrast, the carotenoids diatoxanthin, alloxanthin, lutein + zeaxanthin (all diols, -OH substitution on end rings), and  $\beta$ -carotene (hydrocarbon) are preserved in surface sediments. Accumulation of alloxanthin exceeded the trap-deposited flux by about a factor of two, possibly due to inefficient trapping of cryptophytes, production in the hypolimnion (not accounted in trap fluxes), or greater abundance of cryptophytes in previous years. The latter explanation appears unlikely based on available data on historical plankton trends (Brock 1985). Diatoxanthin, a minor carotenoid, may be a better indicator of diatom presence than fucoxanthin. Lutein and zeaxanthin are major carotenoids of greens and blue-greens, respectively. Additionally,  $\beta$ -carotene is ubiquitous in algae and may be useful as an estimator of biomass, similar to chlorophyll.

### Stratigraphic Information

Sediment trap measurements showed that both organic matter and calcite deposition were major components of the sedimenting particle flux in Lake Mendota (Figure 5.2). Biogenic silica is also a major component, due to production and settling of diatoms. Similarly, major phases of bottom sediments (Figure 5.3) are organic matter, calcite, and biogenic silica. The greatest shift in sediment composition occurred after about 1830, where sediment was dominated by calcite. The decrease in percent calcite in recent sediments likely results from dilution by other phases that increased after farming practices developed in the watershed and eutrophication increased (Murray 1956; Bortleson 1970). Figure 5.3 reveals an increase in the proportion of sediment attributed to shale and “other” phases, which may include silt and sand.

Murray (1956) suggests that the shift in basin use during cultural eutrophication resulted in a sediment transition from “marl to sludge.” Our results from trap and sediment analyses show that marl deposition remains an important depositional process in Lake Mendota. Marl (calcite) continues to comprise a dominant fraction of the bottom sedi-



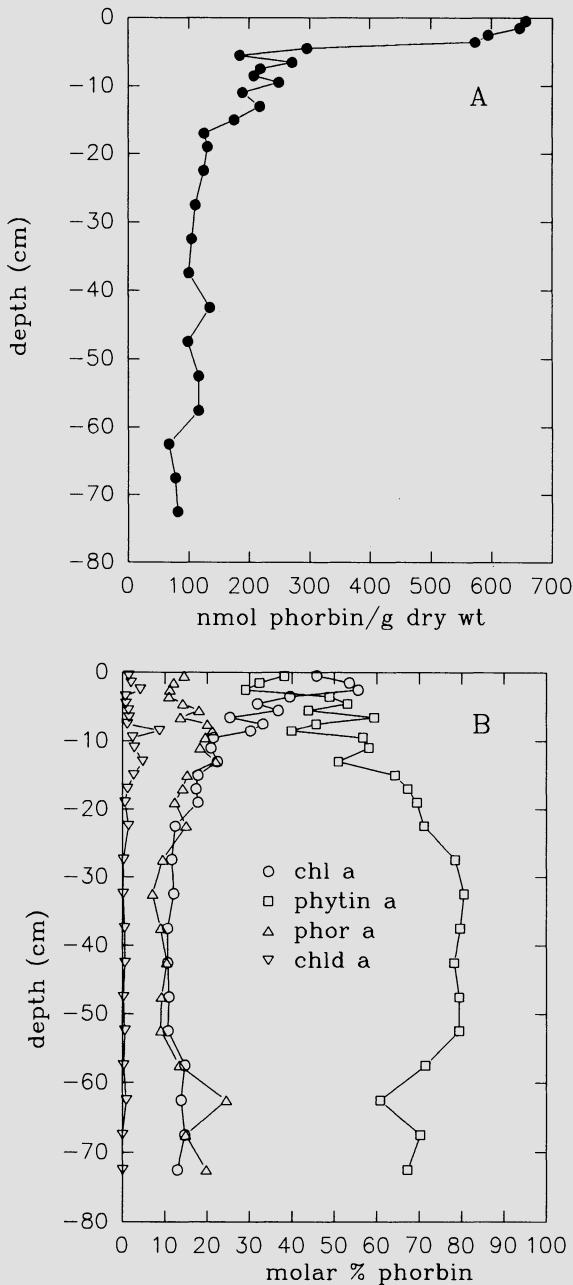
**Figure 5-3.** Major phase composition of sediments in Lake Mendota. OM, Organic matter; BSi, biogenic silica.

ment. Organic matter increases only slightly in the “cultural horizon.” Perhaps the change in color noted by Murray (1956) reflects inorganic constituents (iron sulfides) rather than organic matter. Biogenic silica, derived mainly from diatoms, accounts for a significant sediment fraction. Additionally, shale represents an important component, increasing in abundance about 1830. The remaining fraction, calculated by difference, probably contains quartz and other mineral phases.

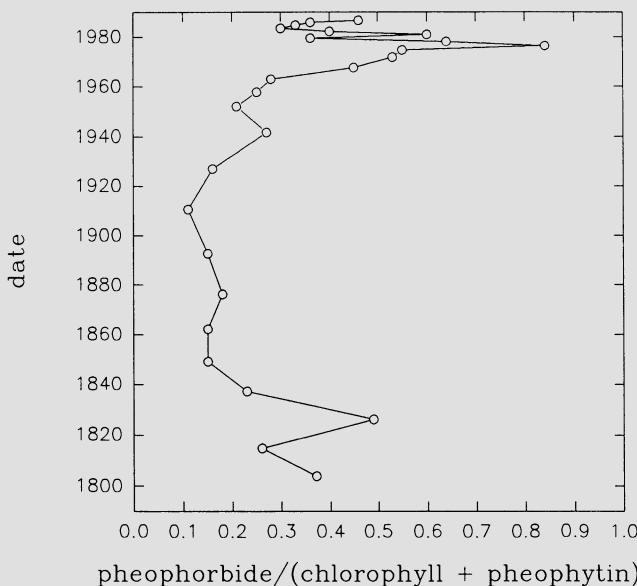
Surface sediments (top 5 cm) are a zone of intense diagenesis and transformation of algal pigments. Total phorbins (Figure 5.4a) decline from about 650 to 350 nmol g<sup>-1</sup>. Below about 10 cm, changes with depth are relatively small, indicating preservation of phorbin and carotenoid residues buried below the surface layer. Phorbin levels in the 10- to 20-cm section remain near 200–300 nmol g<sup>-1</sup>, then decline to about 100 nmol g<sup>-1</sup>.

In addition to total degradation, parent phorbins are partially transformed to other phorbins. In particular, conversion of chlorophyll to pheophytin occurs within the top 15 cm of sediment (Figure 5.4b). Chlorophyll was the dominant phorbin deposited, yet decreased to levels similar to pheophorbide downcore. Chlorophyllide and pheophorbide, are degraded more extensively at the sediment surface (Table 5.2), and appear to have similar degradation rates to chlorophyll + pheophytin, since the relative abundance does not change substantially downcore.

Historical trends in the importance of grazing in transport of organic matter were explored using sedimentation rates derived from cesium-137 and information on both surface sediment diagenesis (Table 5.2) and postdepositional diagenesis (Hurley 1988a). Since a major fraction of chlorophyll was transformed to pheophytin after deposition, we use



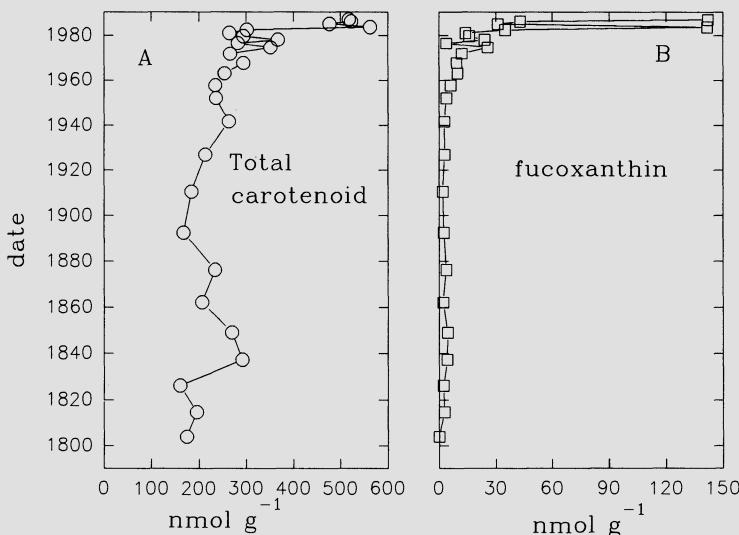
**Figure 5-4.** Phorbin concentration and molar composition in Lake Mendota sediments.



**Figure 5-5.** Changes in grazing intensity as inferred from phorbins in Lake Mendota sediments. High ratio values (pheophorbide/chlorophyll + pheophytin) indicate periods of high grazing.

the sum of chlorophyll + pheophytin to represent material that settled directly to the sediment surface. Pheophorbide, the grazing indicator, can be compared to chlorophyll + pheophytin after the effects of differential diagenesis are incorporated.

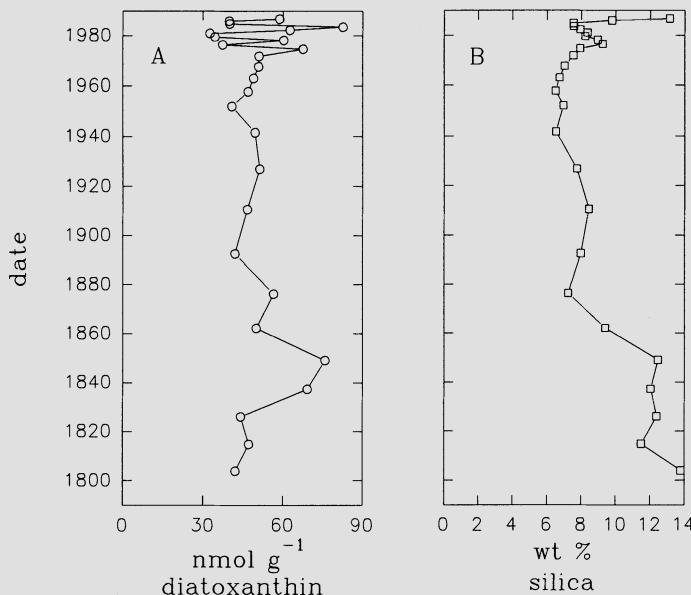
Corrections must be made for two degradative processes, sediment surface diagenesis and postdepositional diagenesis. Postdepositional diagenesis was examined using a model similar to Henrichs and Farrington's (1987) to calculate degradation rate constants ( $k$ ). Based on profiles from three Deep Hole cores from Lake Mendota, we calculated  $k$  values of  $0.093$  and  $0.193 \text{ yr}^{-1}$  for pheophorbide and chlorophyll + pheophytin, respectively (Hurley 1988a). The decay constants were then used to correct pigment concentration profiles for degradation occurring within the surface layer (upper 3 cm) during burial. A second correction factor, accounting for diagenesis at the sediment surface (after deposition from the water column), was calculated from a comparison of sediment trap fluxes and sediment accumulation rates. Since pheophorbide degrades  $2.7\times$  faster than chlorophyll + pheophytin at the sediment surface, this correction factor was applied to the ratio of pheophorbide/(chlorophyll + pheophytin) over the entire length of the core. The reconstructed ratio was then used as a relative indication of grazing intensity. A plot of the ratio (Figure 5.5) suggests downcore shifts in grazing intensity, with peaks during the 1830s and from 1960 to 1980.



**Figure 5-6.** Total carotenoid and fucoxanthin profiles of Lake Mendota sediments.

Diagenesis largely removes some of the more important carotenoids from the sedimentary record (Figure 5.6a). Roughly half of the carotenoid loss is accounted for by the rapid diagenesis of fucoxanthin. Surficial sediment diagenesis for fucoxanthin appears to occur in deeper sediments, as the concentration of fucoxanthin continues to decrease downcore. Levels of fucoxanthin (Figure 5.6b) are reduced from  $>140$  to  $<10\text{ nmol g}^{-1}$  over a depth equivalent to 30 years of deposition. It is unfortunate that diagenesis of fucoxanthin, a dominant sedimented carotenoid and diatom marker, is so extensive, making it less useful for paleolimnological interpretation of the core.

Diatoxanthin, a minor carotenoid of diatoms, appears to be useful as a sedimentary marker for diatoms. Since diatoxanthin is not extensively degraded at the sediment surface (Table 5.2), its abundance in sediment cores likely reflects past trends in abundance of diatoms (and other chrysophytes). The biogenic silica profile (Figure 5.7b) also reflects diatom abundance and is probably less susceptible to rapid diagenesis than fucoxanthin. The parallel trends upcore from 1850 of biogenic silica and diatoxanthin indicate diatoxanthin was derived from chrysophytes, rather than from other algal types (e.g., *Euglena*) that may contain small amounts of diatoxanthin. Below the 1850 level the relationship is not as clear, as the two profiles diverge. This may reflect a shift in preservation conditions due to eutrophication. The phase distribution (Figure 5.3) suggests that calcite and diatoms were the major precultural sediment constituents. Precultural sedimentation rates were probably lower, expos-



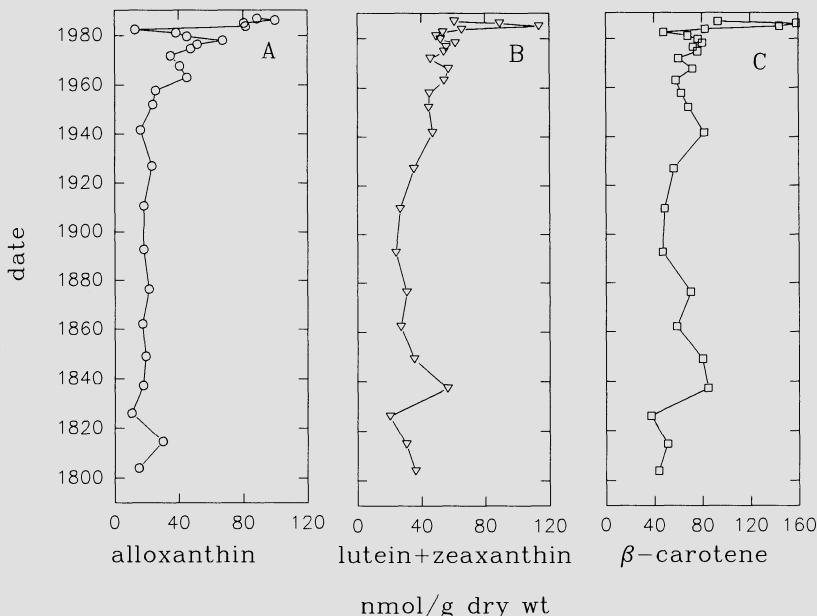
**Figure 5.7.** Profiles of diatoxanthin and biogenic silica in Lake Mendota sediments.

ing labile constituents such as carotenoids to surface sediment diagenesis for a longer time period.

Profiles of more “stable” carotenoids—alloxanthin, lutein + zeaxanthin, and  $\beta$ -carotene—also reveal trends over the last 200 years (Figure 5.8). Lutein + zeaxanthin and  $\beta$ -carotene increase sharply following cultural eutrophication, again suggesting a shift in preservation character. Since lutein + zeaxanthin were chromatographically inseparable, the relative importance of greens and blue-greens can not be resolved in the core. Alloxanthin increased between 1960 and 1980, suggesting the growing importance of cryptophytes in the recent (30 years) history of the lake. A low value occurring about 1982 suggests the earlier peak is not diagenetic. Apparent increases after 1982 in alloxanthin,  $\beta$ -carotene, and lutein + zeaxanthin are likely diagenetic in origin.

## Discussion

Relations between pigment production, sedimentation, and sedimentary accumulation in Lake Mendota are influenced by pigment diagenesis and by deposition and diagenesis of major sediment components. Calcite precipitation in summer and diatom production in fall produce major sedimentation events. Smaller fluxes are associated with the spring



**Figure 5-8.** Profiles of alloxanthin, lutein + zeaxanthin, and  $\beta$ -carotene in Lake Mendota sediments.

phytoplankton bloom, zooplankton grazing, and blue-green algal sedimentation. In sediments, calcite remains a dominant phase. Although reduced substantially by diagenesis, organic matter and biogenic silica remain as important secondary phases. Relatively high deposition/accumulation of “shale” + unidentified (possibly quartz) components between about 1830 and 1900 reduced concentrations of other components by dilution. After 1900, the proportion of  $\text{CaCO}_3$  as shale and “other” phases decreased. Both calcite and biogenic silica were major phases prior to eutrophication in the lake.

The extent of diagenesis varies widely among individual phorbins and carotenoids. Surface sediment diagenesis differs between phytol-containing and dephytolated phorbin derivatives (Table 5.2). Carotenoid diagenesis is extreme, especially for peridinin, the most important water column carotenoid, which was not present in sediments due to degradation. Thus, other pigment residues or ancillary information (e.g., algal cysts) would be needed to assess dinoflagellate abundance over time. Similarly, fucoxanthin, the major carotenoid deposited from the water column to the sediment surface, has been removed from historical sediments by diagenesis. However, a minor carotenoid (diatoxanthin) is partially preserved and reflects diatom abundance. Alloxanthin, lutein + zeaxanthin, and  $\beta$ -carotene profiles reveal downcore trends. Both lutein + zeaxanthin and  $\beta$ -carotene content increased around 1830–40, but

these increases likely reflect differences in preservation associated with changes in sedimentation rate and conditions at the sediment–water interface. Profiles from more recent sediments (last 100 years), however, can be used to assess changes in the system.

Parallel trends between diatoxanthin and biogenic silica after 1850 indicate that relative trends in biogenic silica deposition are preserved in buried sediments in spite of substantial surficial diagenesis of biogenic silica. The importance of comparing biogenic silica and diatoxanthin is shown by divergence of the two profiles prior to 1850. Diatoxanthin alone suggests a rapid increase in diatom abundance during the initial stages of eutrophication. Biogenic silica, however, indicates diatoms were dominant prior to this period.

After the 1850s, biogenic silica declined, reaching a minimum about 1940. Similarly, diatoxanthin declined from about  $80 \text{ nmol g}^{-1}$  at the 1850 peak to about  $40 \text{ nmol g}^{-1}$  by 1950. A trend of increasing biogenic silica and diatoxanthin after 1960, peaking about 1970, may reflect a period of increased nutrient loading and productivity followed by a decrease in the 1980s, as also suggested by Lathrop (Ch. 6). Surface peaks at the top of the core for both constituents probably represent diagenetic fronts and should not be interpreted as a recent increase in productivity.

Other carotenoids (Figure 5.8) are consistent with an increased supply in the 1960s and early 1970s. Both alloxanthin and  $\beta$ -carotene show subsurface peaks during this period, declining in the early 1980s. The subsurface peak of lutein + zeaxanthin in the mid-1980s suggests increased deposition of green and/or blue-green algae.

The reconstructed phorbin ratio, corrected for the effects of diagenesis (Figure 5.5), indicates downcore shifts in grazing intensity. Precultural levels ranged from 0.2 to 0.5, followed by a decrease to 0.1–0.2 for the period from 1850 to about 1935. Apparently, after the onset of cultural eutrophication (1850s), grazing pressures were lowered, and direct settling became the dominant sedimentation process for phytoplankton until about 1940. A significant shift toward higher grazing intensities occurred from 1940 through about 1975, reaching a maximum about 1975. In the 1980s, however, the phorbin ratio decreased to values similar to those in the 1940s to 1950s, suggesting a decrease in grazing intensity. Correction of the ratio for downcore diagenesis strengthens the validity of the subsurface peak during 1960–75. Lake nutrient supply may have been high during this period due to development in the watershed (Kitchell and Sanford, Ch. 4), and a greater fraction of phytoplankton produced may have been processed by zooplankton.

It is difficult to evaluate a specific annual event, such as the grazing-produced clear-water phase in the spring, through its effect on sedimentation of phytoplankton and associated pigments. Although maximum zooplankton biomass occurred in late May of 1987, the greatest pigment flux occurred after fall overturn (Hurley and Armstrong 1990).

Apparently, entrainment of nutrient-rich hypolimnetic water at fall overturn had a major influence on plankton production and pigment sedimentation. Therefore, pigments produced during the spring clear-water period may be masked by pigments produced during the fall bloom.

Sedimentary pigments reflect some of the changes that have occurred in productivity, plankton types, and grazing in Lake Mendota over the past 100 years. Although much of the sedimentary record has been altered or eliminated by pigment diagenesis, evidence of changes in diatom sedimentation and grazing has been preserved. Diagenetic modeling aided interpretations of changes in sedimentary profiles. Grazing intensities, as reflected in pheophorbide, were greater than indicated by uncorrected pheophorbide profiles. Although some carotenoids were preserved in the sediment core, identification and measurement of stable end products of carotenoids produced by blue-greens and dinoflagellates would greatly enhance the sedimentary historical record.

### References

- Bidigare RR, Kennicutt MC, Brooks JM (1985) Rapid determination of chlorophylls and their degradation products by high performance liquid chromatography. *Limnol. Oceanogr.* 30:432–435
- Bortleson GC (1970) The chemical investigation of recent lake sediments from Wisconsin lakes and their interpretation. Ph.D. Thesis, University of Wisconsin, Madison
- Brock TD (1985) A eutrophic lake: Lake Mendota, Wisconsin. Springer-Verlag, New York
- Carpenter SR, Elser MM, Elser JJ (1986) Chlorophyll production, degradation and sedimentation: Implications for paleolimnology. *Limnol. Oceanogr.* 31:112–124
- Daley RJ (1983) Experimental characterization of lacustrine chlorophyll diagenesis. 2. Bacterial, viral and herbivore grazing effects. *Arch. Hydrobiol.* 72:409–439
- Daley RJ, Brown SR (1983) Experimental characterization of lacustrine chlorophyll diagenesis. 1. Physiological and environmental effects. *Arch. Hydrobiol.* 72:277–304
- DeMaster DJ (1979) The marine budgets of silica and  $^{32}\text{Si}$ . Ph.D. Thesis, Yale University, New Haven, Connecticut
- DuVall AL (1990) Historical trends in diatom production in Lake Mendota: Evidence from the sedimentary record. Water Chemistry Program Report, University of Wisconsin, Madison
- Fallon R, Brock TD (1980) Planktonic blue-green algae: Production, sedimentation and decomposition in Lake Mendota, Wisconsin. *Limnol. Oceanogr.* 25:72–88
- Furlong ET, Carpenter R (1988) Pigment remineralization in oxic coastal marine sediments. *Geochim. Cosmochim. Acta* 52:87–99
- Goodwin, TW (1965) Distribution of carotenoids. In Goodwin TW (ed) Chemistry and biochemistry of plant pigments, Academic Press, New York, pp 127–142

- Henrichs SM, Farrington JW (1987) Early diagenesis of amino acids and organic matter in two coastal marine sediments. *Geochim. Cosmochim. Acta* 51:1–15
- Holm-Hansen OO, Lorenzen CJ, Holmes RW, Strickland JDH (1965) Fluorometric determination of chlorophyll. *J. Cons. Perm. Int. Explor. Mer.* 30:3–15
- Hurley JP (1988a) Diagenesis of algal pigments in lake sediments. Ph.D. Thesis, University of Wisconsin, Madison
- Hurley JP (1988b) Analysis of aquatic pigments by High Performance Liquid Chromatography. *J. Anal. Purif.* 3:12–16
- Hurley JP, Armstrong DE (1990) Fluxes and transformations of aquatic pigments in Lake Mendota, Wisconsin. *Limnol. Oceanogr.* 32:384–398
- Hurley JP, Armstrong DE (1991) Pigment preservation in lake sediments: a comparison of sedimentary environments in Trout Lake, Wisconsin. *Can. J. Fish. Aquat. Sci.* 48:472–486
- Jeffrey SW, Hallegraeff GM (1987) Chlorophyllase distribution in ten classes of phytoplankton: A problem for chlorophyll analysis. *Mar. Ecol. Prog. Ser.* 35:293–304
- Keely BJ, Brereton RG (1986) Early chlorin diagenesis in a Recent aquatic sediment. In Leythaeuser W, Pullkotter J (eds) *Advances in organic geochemistry 1985*, pp 975–980, Pergamon, London
- Krausse GL, Schelske CL, Davis CO (1983) Comparison of three wet alkaline methods of digestion of biogenic silica in water. *Freshwat. Biol.* 13:73–81
- Leavitt PR, Carpenter SR (1990a) Aphotic pigment degradation in the hypolimnion: Implications for sedimentation studies and paleolimnology. *Limnol. Oceanogr.* 35:520–534
- Leavitt PR, Carpenter SR (1990b) Regulation of pigment sedimentation by photo-oxidation and herbivore grazing. *Can. J. Fish. Aquat. Sci.* 47:1166–1176
- Leavitt PR, Carpenter SR, Kitchell JF (1989) Whole-lake experiments: The annual record of fossil pigments and zooplankton. *Limnol. Oceanogr.* 34:700–717
- Lerman A (1979) *Geochemical processes: Water and sediment environment*. Wiley, New York
- Lorenzen CJ (1967) Determination of chlorophyll and phaeopigments: Spectrophotometric equations. *Limnol. Oceanogr.* 12:343–346
- Mantoura RFC, Llewellyn CA (1983) The rapid determination of algal chlorophyll and carotenoid pigments and their breakdown products in natural waters by reverse-phase high performance liquid chromatography. *Anal. Chim. Acta* 151:297–314
- Murray RC (1956) Recent sediments of three Wisconsin lakes. *Bull. Geol. Soc. Am.* 67:883–910
- Repeta DJ (1989) Carotenoid diagenesis in recent marine sediments: II. Degradation of fucoxanthin to loliolide. *Geochim. Cosmochim. Acta* 53:699–707
- Repeta DJ, Gagosian RB (1984) Transformations and recycling of carotenoids and chlorins in the Peru upwelling region (15°S, 75°W). *Geochim. Cosmochim. Acta* 48:1265–1277
- Repeta DJ, Gagosian RB (1987) Carotenoid diagenesis in recent marine sediments- I. The Peru continental shelf (15°S, 75°W). *Geochim. Cosmochim. Acta* 51:1001–1009

- Robbins JA, Edgington DN (1975) Determination of recent sedimentation rates in Lake Michigan using Pb-210 and Cs-137. *Geochim. Cosmochim. Acta* 39:285–304
- Shafer MM (1988) Biogeochemistry and cycling of water column particulates in Southern Lake Michigan. Ph.D. Thesis, University of Wisconsin, Madison
- SooHoo JB, Kiefer DA (1982a) Vertical distribution of phaeopigments—I. A simple grazing and photooxidative scheme for small particles. *Deep-Sea Res.* 29:1539–1552
- SooHoo JB, Kiefer DA (1982b) Vertical distribution of phaeopigments—II. Rates of production and kinetics of photooxidation. *Deep-Sea Res.* 29:1553–1564
- Swain AM (1978) Environmental changes during the past 2000 years in north-central Wisconsin: Analysis of pollen, charcoal and seeds from varved lake sediments. *Quat. Res.* 10:55–68
- Vanni MJ, Temte J (1990) Seasonal patterns of grazing and nutrient limitation of phytoplankton in a eutrophic lake. *Limnol. Oceanogr.* 35:697–709
- Welschmeyer NA, Copper AE, Vernet M, Lorenzen CJ (1984) Diel fluctuation in zooplankton grazing rate as determined from the downward vertical flux of phaeopigments. *Mar. Biol.* 83:263–270

# 6

## Nutrient Loadings, Lake Nutrients, and Water Clarity

**Richard C. Lathrop**

### Introduction

Nutrient loadings and lake water quality are inextricably linked. Excessive loadings of nitrogen and, particularly, phosphorus cause lakes to become eutrophic and often to exhibit noxious algal blooms (Vollenweider 1968; Schindler 1977). While the role of nutrients in lake eutrophication is widely accepted, the ability of zooplankton such as *Daphnia* to graze algae and thus ameliorate water quality problems is less certain for eutrophic lakes (McQueen 1990). Because blue-green algae can be inedible, eutrophic lakes that have excessive summer blue-green algal blooms may not respond to fish population manipulations that have produced "top-down" responses in less eutrophic lakes (Carpenter, Ch. 23; Gulati et al. 1990; Elser and Goldman 1991).

In Lake Mendota, blue-green algal blooms have occurred since at least the 1880s (Lathrop and Carpenter, Ch. 7). Concern about the lake's water quality problems was raised soon after the mid-1940s, and problems have been severe since the early 1960s. While much attention has been given to reducing nutrient loadings to remedy these problems, the feasibility of increasing grazing to improve water quality was not addressed prior to the food web research summarized in this book.

In this chapter, I present long-term nutrient and water clarity data for Lake Mendota, most of which have not been summarized previously. My objective is to examine water clarity response throughout this century to changes in both external loadings and in-lake concentrations of nutrients, as well as to differences in herbivory (grazing by *Daphnia*) and

planktivory. This treatment is more qualitative than statistical, because the data for all variates were not available. In other chapters in this volume, Lathrop and Carpenter (Ch. 7 and 8) report more rigorous tests of these interrelationships based on extensive nutrient and plankton data available for 1976–89. Finally, Vanni et al. and Luecke et al. (Ch. 13 and 14) present detailed experimental evidence about the relative importance of nutrients, herbivory, and planktivory based on work conducted in 1987–89. My hope is that the long-term data presented here can provide evidence to support the statistical and mechanistic conclusions discussed by these and other authors in this volume.

## Methods

### Estimates of External Nutrient Loadings

Because accurate external loadings of phosphorus (P) and nitrogen (N) are difficult to compute without extensive monitoring data, annual loadings to Lake Mendota were not estimated for 1987–89, the years of the food web research presented in this volume. Stream flow data were not collected on most of the major tributaries to the lake (except for Pheasant Branch Creek), and nutrient concentration data were even less available. Therefore, loading data for N and P developed previously are summarized in this chapter. Estimates for loadings of total P (TP), total reactive P (TRP), organic N, and inorganic N ( $\text{NH}_4\text{-N}$  +  $\text{NO}_2\text{-N}$  +  $\text{NO}_3\text{-N}$ ) were calculated for 1976–77 (based on detailed monitoring data), and a long-term average was computed (Lathrop 1979). P loadings were also computed from monitoring data for the Yahara River upstream from Lake Mendota for 1976–80 (Lathrop 1986). N loadings were computed for the same river and period but were not previously published.

These P loading estimates along with past sewage effluent discharges to Lake Mendota were related to annual loadings of biologically available P (BAP) by Lathrop (1990). Annual volumes of spring runoff (excluding baseflow) for Black Earth Creek, a stream draining a watershed adjacent to Lake Mendota, were used to indicate which years had low, normal, or high spring loadings of BAP. This stream was selected for this analysis because its runoff was highly correlated with runoff from the Yahara River, the main tributary to Lake Mendota. Because spring runoff contained the highest dissolved nutrient concentrations during a year (Lathrop 1986), runoff during this period was considered very important in predicting a response in lake P concentrations.

For this chapter, runoff volumes for Black Earth Creek were computed for both the spring runoff period, defined as January to March, and for the remaining months of a “biological runoff year,” defined as starting on 1 October (of the previous year) and running through 30 September.

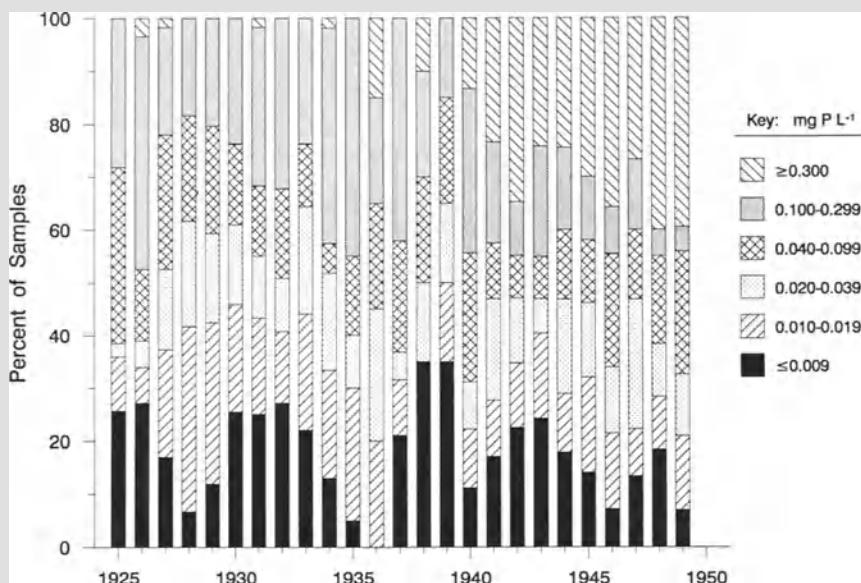
Runoff during October–September corresponds to annual external loadings that contribute to algal blooms during the summer, when epilimnetic inorganic N and inorganic P concentrations are typically very low in Lake Mendota. However, because average inorganic P concentrations in runoff for different seasons varied by as much as 400%, actual loadings for each biological runoff year were not calculated because this detailed analysis was beyond the scope of this chapter.

### In-Lake Phosphorus and Nitrogen Determinations

Long-term P concentration data for Lake Mendota were obtained from numerous sources: Madison Public Health Department (MPHD) under the direction of B.P. Domogalla (unpubl. data) for 1925–49; C.N. Sawyer, State Laboratory of Hygiene (SLH) (unpubl. data) for 1944; Wisconsin Committee on Water Pollution (1949) for 1945–47; Clesceri (1961 and unpubl. data) for 1959–61; University of Wisconsin (UW) Water Chemistry students, including unpubl. data for 1965–67, Torrey (1972) for 1970–71, Sonzogni (1974) for 1971–73, Stauffer (1974) for 1971–72, and Vigon (1976) for 1974–75; MPHD (unpubl. data) for 1974–75; and the Wisconsin Department of Natural Resources (WDNR) Bureau of Research for 1975–89. Additional P data were available from UW Civil Engineering student reports and theses for 1948–50 and from Brock (1985) for 1976 and 1978–81. N data were available from all of the above sources plus Domogalla et al. (1925, 1926) for 1923–25 and Goering (1963) for 1959–61.

Long-term analyses of water chemistry data usually assume that data from early sources are comparable to those produced with modern laboratory procedures and that data determined by students had sufficient quality assurances applied. Because I was placing a heavy reliance on the MPHD database for long-term P trends, I compared results of water samples analyzed by the MPHD's early methods with results obtained from the SLH using current U.S. Environmental Protection Agency procedures.

Methods of analysis for dissolved reactive P (DRP) (Atkins 1923; Juday et al. 1928) used by UW researchers by the mid-1920s were also employed by Domogalla and the MDPH. Minor modifications to the procedures were found in MDPH laboratory notes. These analyses were conducted using an ammonium molybdate, stannous chloride procedure that was eventually recognized as a “standard method” by the American Public Health Association and American Water Works Association (1946). The early method of Juday et al. (1928), Domogalla's modification, and the later standard method all produced results within a range of  $\pm 0.01$  mg P/L to results obtained from current procedures for DRP concentrations of 0.004–0.16 mg P/L.



**Figure 6-1.** Proportion of DRP concentration ranges found in water samples analyzed by the Madison Public Health Department for Madison area lakes during 1925–49.

TP data were first analyzed by the MDPH in 1937. The comparison of TP methods was less satisfactory than the comparison of DRP methods because a reliable standard curve could not be reproduced for the older method. The procedure required the heating and evaporation of a water sample after stepwise addition of sulfuric, nitric, and hydrochloric acids, diluting to volume, and then following the same procedure used for DRP (Robinson and Kemmerer 1930). Problems with acidity in the final solution may have affected the intensity of the blue color development. Another factor was the small volume of original sample used compared to the DRP test. Analytical errors would be compounded by dilution. Obviously, early water chemists would have had more experience with the TP procedure, but I felt that the data were not sufficiently reliable to detect relatively small changes in surface water concentrations in Lake Mendota.

In addition to the comparison of analysis methods, another evaluation that I performed on the DRP data base was a check of whether MDPH reported low concentrations as well as high ones during 1925–49. Laboratory effort may have focused on measuring the much higher DRP found in the lower Yahara lakes receiving Madison's sewage effluent. However, approximately 10–30% of the lab's analyses for most years were of DRP concentrations  $\leq 0.009 \text{ mg P/L}$  (Figure 6.1), often within a range of

0.002–0.005 mg/L. Based on these results and the analytical method comparison described above, I concluded that the lower limit of detection for DRP was at least 0.01 mg/L and that DRP differences of  $\geq 0.02$  mg/L in Lake Mendota's surface waters were most likely reliable in the MDPH dataset.

As mentioned earlier, P measurements for Lake Mendota were also performed by the SLH and by UW students in the 1940s. Corroboration between the SLH and the MDPH was good for DRP in lake surface waters. Additional analyses reported by the SLH on water samples collected from local springs during a 2-year period indicated relatively low concentrations of both DRP and TP (Wisconsin Committee on Water Pollution 1949). However, student data obtained from the same spring water in ensuing years were higher and more variable for DRP and particularly TP. Consequently, this data source was not considered reliable for comparing trends in Lake Mendota.

All more recent data sources were used to develop long-term DRP trends in Lake Mendota, except data collected in 1959 by UW Water Chemistry students. These data, collected at the lake outlet and along the south shoreline during the fall, were rejected because of high variability. Data for 1960–61 were less variable between sampling dates within each season and considered more reliable. TP was not analyzed during 1959–61. Only TP data reported since the mid-1960s were used to document long-term trends in Lake Mendota's surface waters.

I did not compare the early analytical methods for ammonia ( $\text{NH}_4\text{-N}$ ), nitrate ( $\text{NO}_3\text{-N}$ ), nitrite ( $\text{NO}_2\text{-N}$ ), and organic nitrogen (ON) because early “standard methods” were available (American Public Health Association 1923). However, hypolimnetic  $\text{NH}_4\text{-N}$  data in late summer were screened for inconsistencies. Recent data on acid-preserved samples have shown that, by late summer when dissolved oxygen has been absent for some time, the only form of inorganic N in the deeper waters of the hypolimnion is  $\text{NH}_4\text{-N}$ . Reported detections of appreciable  $\text{NO}_3\text{-N}$  or  $\text{NO}_2\text{-N}$  in earlier data may reflect sample aeration and storage, allowing removal of  $\text{NH}_4\text{-N}$  via nitrification. Such data were not used. Other data sources not used reported an erratic buildup of hypolimnetic  $\text{NH}_4\text{-N}$  or a large increase in organic N while  $\text{NH}_4\text{-N}$  remained relatively low. I attributed these characteristics to lab error.

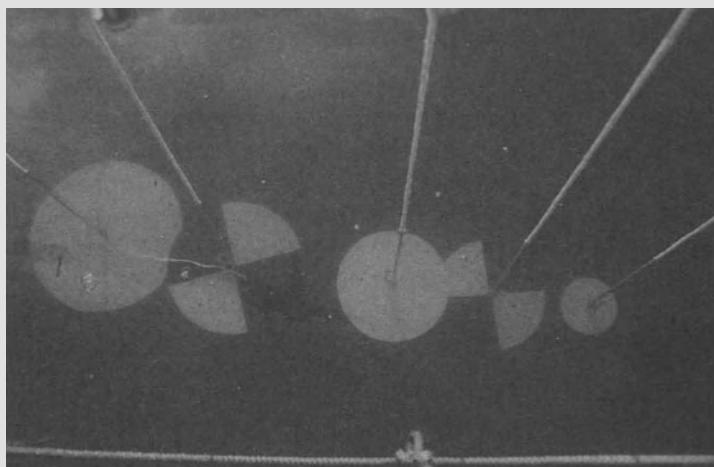
For this chapter, I have presented what I feel are the most useful indices of long-term nutrient concentrations in Lake Mendota. To depict surface water trends in P concentrations, summer DRP data were not used because concentrations were almost always near or below analytical detection. After fall turnover occurs, hypolimnetic DRP concentrations that build up during the summer are mixed throughout the water column, causing an increase in surface concentrations that remain high through the following spring. Therefore, fall, winter, and early spring concentrations were considered better indicators of long-term DRP supplies in

Lake Mendota. Surface water concentrations of TP in summer were also used to detect changes in the lake's trophic condition after the mid-1960s. Hypolimnetic DRP at the 20-m water depth on 1 September (extrapolated from dates in close proximity) was used as another indicator of P trends. Fall and winter inorganic N concentrations in Lake Mendota's surface waters and hypolimnetic NH<sub>4</sub>-N at 20m on 1 September were used to examine long-term trends in N availability in Lake Mendota.

### Water Clarity Measurements

The Secchi disk has been used to measure water clarity or algal bloom intensity of Lake Mendota's surface waters throughout much of the 1900s. To document trends in water clarity, Secchi readings from many data sources were compiled. The largest dataset was from E.A. Birge's and C. Juday's unpublished records collected between the fall of 1900 and the winter of 1931. Records were less extensive prior to 1913 and after 1920. In other years, multiple readings per sampling date were available, so daily averages could be computed. [D.M. Robertson (1989) transcribed a large portion of Birge and Juday's raw data and computed these daily averages.] After the mid-1920s, most of the records were probably collected by B.P. Domogalla, a former UW-Madison graduate student who began working for the MPHD. After that time, identical Secchi disk readings were found in unpublished city records.

A variety of sources compose the remainder of the readings reported from 1931 to date. Only a few readings taken by the MPHD from 1931 through 1946 were found; readings recorded only on field note sheets apparently were discarded. Prior to the early 1950s, a few readings were taken by Frey (1940) in 1939, Zimmerman (1953) in 1942, and Hasler and Wohlschlag (1951) in 1949. Ranges of Secchi disk readings for the mid-1940s were also noted by Hasler and Bardach (1949), but the raw data were not found. R.A. Ragotzkie (unpubl. data) took Secchi readings on Lake Mendota in the spring and summer of 1951. Secchi disk data for Lake Mendota were not found for the rest of the 1950s, although readings known to have been taken in 1955–56 may be located eventually. Sources of Secchi readings for the 1960s were: K.W. Stewart (unpubl. data) for 1961–62, 1966, and one reading in 1968; the UW Water Chemistry Program (unpubl. data) for 1965–67, including some additional data by Delfino (1968) for 1966–67; and Lueschow et al. (1970) for 1966. Sources of Secchi readings taken during 1970–75 were: Stewart (unpubl. data) for 1971, Sonzogni (unpubl. data) for 1971–74, Stauffer (1974) for 1971–72, Vigon (1976) for 1974–75, and the WDNR Bureau of Research (unpubl. data) for 1975. T.D. Brock and his students (unpubl. data) collected extensive Secchi disk readings during 1976–80. Beginning in 1976, the WDNR Bureau of Research began taking Secchi disk readings regularly throughout each year as part of our long-term research study of the four



**Figure 6-2.** Five different styles of Secchi disks used in recording water clarity readings on Lake Mendota throughout the 1900s. (Left to right: 30-cm W, 25-cm B/W, 20-cm W, 20-cm B/W, and 10-cm W.)

Yahara lakes. Since 1987, the UW Center for Limnology has also been taking regular Secchi disk readings.

Five different types of Secchi disks have been used on Lake Mendota (Figure 6.2). All Secchi readings by Birge and Juday (including the UW research in northern Wisconsin) and by the city of Madison prior to the early 1930s were taken with a 10-cm white disk (Domogalla 1926, 1935; Juday 1929; Juday and Birge 1933). By the mid-1930s, the UW had switched to a larger white disk for lake sampling in northern Wisconsin (R.W. Pennak, pers. comm.; R.E. Juday, pers. comm.). While a graduate student of Juday's, Frey (1940) used a 20-cm white disk during 1939 on the Yahara lakes. I could not determine in what year the MPH changed disks, but a larger disk was in use by the mid-1940s (T.W. Burnham, pers. comm.). A.D. Hasler remembered that a black and white (B/W) disk was used at the UW limnology laboratory in the 1940s, but R.A. Ragotzkie (pers. comm.) recounted that he used a white disk from the UW limnology laboratory in 1951. Secchi disks used since the early 1960s were: 20-cm white disk (Stewart); 25-cm B/W disk (UW Water Chemistry students including Delfino, Sonzogni, Stauffer, and Vigon); 30-cm white disk (Brock and his students); and 20-cm B/W disk (Lueschow et al., the WDNR Bureau of Research, and the UW Center for Limnology since 1987). The type of Secchi disk used by other sources not listed above could not be determined.

These five Secchi disks had large differences in their white surface areas. Because readings from these disks were not exactly comparable, a

**Table 6-1.** Mean correction factors for different Secchi disks used on Lake Mendota. (Disk readings standardized to a 20-cm black-and-white disk, based on 89 comparisons recorded on the four Yahara lakes in 1988.)

	Secchi disk				
	10-cm W	20-cm B/W	25-cm B/W	20-cm W	30-cm W
White area (cm <sup>2</sup> )	79	157	245	314	707
Correction factor <sup>a</sup>					
Mean	0.956	—	1.043	1.058	1.129
SEM	0.0048	—	0.0053	0.0059	0.0077

<sup>a</sup>20-cm B/W disk = other disk divided by correction factor.

study was initiated involving readings of the five disks taken by two persons on all four Yahara River lakes during the open water biweekly sampling in 1988. Algal densities varied greatly throughout the year on all four lakes, such that a wide range of Secchi disk readings was recorded. Readings were taken during different wind and cloud cover conditions normally encountered in lake sampling.

Correction factors between each of the four other disk readings and the 20-cm B/W disk reading were computed. To determine if a given disk's correction factor varied for different water clarity conditions, average factors for three different Secchi ranges were compared (<1.5 m, 1.5–2.9 m, and ≥3.0 m). For each of the four disks, average correction factors between the three Secchi ranges were not significantly different. All correction factors for each disk were then pooled, and an average disk correction factor was computed (Table 6.1). All historic Secchi disk readings were then standardized to the 20-cm B/W disk in order to make the long-term database more comparable. I did not apply any correction factor to disk readings taken by the UW, the MPHD, or other sources between 1935 and the late 1940s unless the type of disk was recorded.

To depict long-term trends in water clarity in Lake Mendota, I stratified the Secchi disk data into six different seasonal periods that corresponded to patterns of thermal stratification and to densities of phytoplankton and *Daphnia*. These seasonal periods were: (1) "winter" from 1 January to 1 March—days 1–60, (2) "spring turnover" from 22 March to 10 May—days 81–130, (3) "early stratification" from 11 May to 29 June—days 131–180, (4) "summer stagnation" from 30 June to 2 September—days 181–245, (5) "destratification" from 3 September to 12 October—days 246–285, and (6) "fall turnover" from 13 October to 16 December—days 286–350.

The only periods of a year not used in this analysis were early to mid-March and late December. Few Secchi readings were found for late December; these readings would have been taken in some years through the ice and in other years during turnover. I did not use data for early to

**Table 6-2.** Median DRP concentrations during baseflow in Sixmile Creek, the Yahara River, and Token Creek upstream from Lake Mendota.<sup>a</sup>

Year	Sixmile Cr.	Yahara R.	Token Cr.
1943–44	0.06	0.05	0.02
1945–46	0.09	0.06	0.02
1946–47	0.17	0.12	0.02
1948–49	0.28	0.17	0.03
1976–79	0.09	0.04	0.04

<sup>a</sup>Data sources: 1943–44 (Sawyer et al. 1945), 1945–47 (Wisconsin Committee on Water Pollution 1949), 1948–49 (Belter and Calabresa 1950), and 1976–79 (TRP collected by WDNR; means summarized in Dane County Regional Planning Commission 1980).

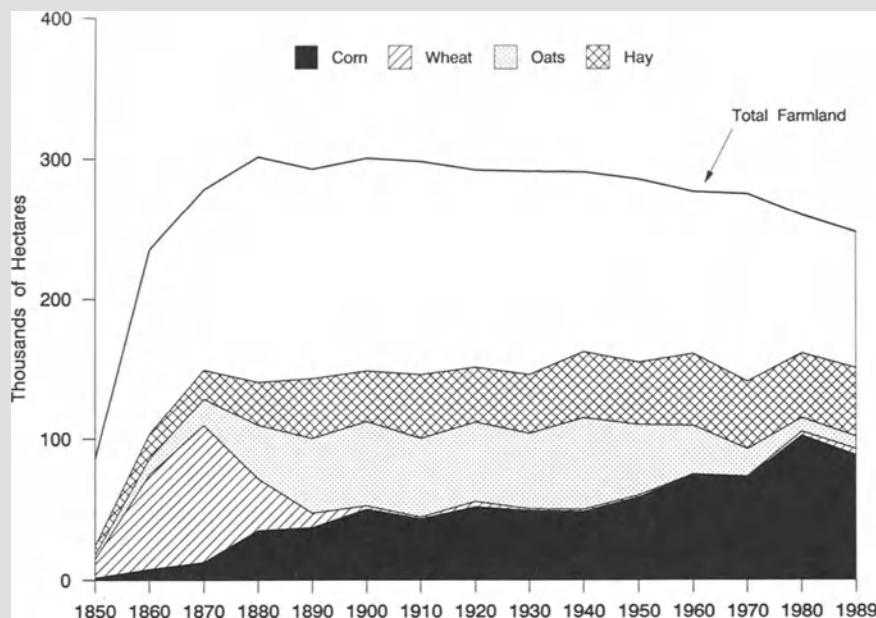
mid-March because the number of readings was small and algal blooms developing under a thinning ice cover could have biased midwinter averages. I included late March in the spring turnover period, even though the average ice-out date for Lake Mendota is 5 April, because sampling was only done during this period when an early ice-out occurred. Sampling normally was not done in late March because of unsafe ice.

For each of the six seasonal periods, annual means of the Secchi disk readings were computed. The long-term mean of the annual means in each period was also computed. To detect years of normal or abnormal water clarity in each season, the annual mean and the range representing maximum and minimum readings were plotted along with the long-term mean and its 95% confidence interval. These ranges were composed of many readings for a few years but of only a few readings for most years. For years represented by only one reading, no range was plotted.

## Results

### External Nutrient Loadings

External loadings of P to Lake Mendota prior to the mid-1950s were impossible to quantify. Sewage effluents from upstream communities began entering the lake in the 1920s via discharges to Sixmile Creek and the Yahara River. However, DRP concentration data at baseflow for these streams and Token Creek (a stream without sewage effluents) during the 1940s indicated that P loadings from the sewage effluents increased substantially after the end of World War II (Table 6.2). The increase was the result not only of population growth in these communities but also of additional sewage from another upstream community

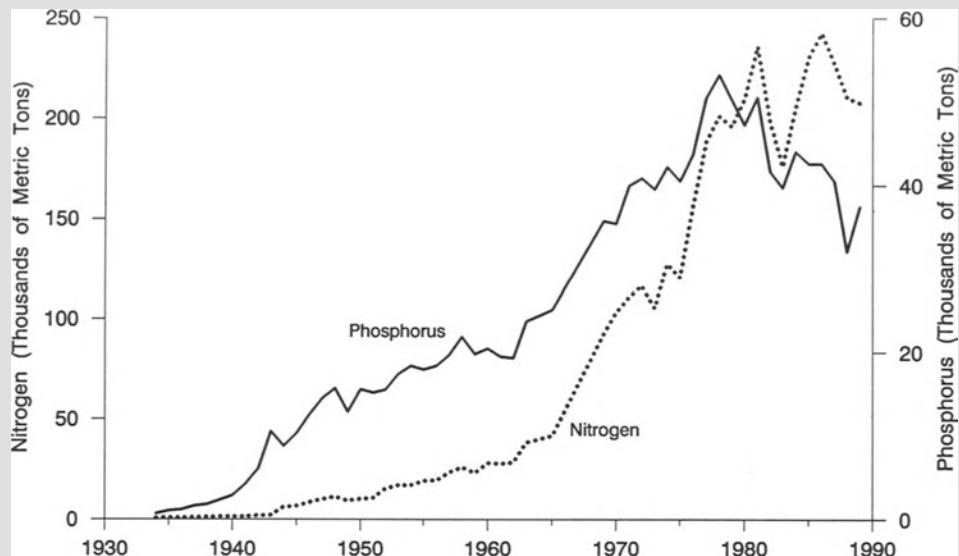


**Figure 6-3.** Land area used for major crop production and total farmland in Dane County by decade from 1850 to 1980 plus 1989. Other small grains included in oats; pastureland, woodlots, farm buildings, and misc. crops included in total farmland. (Source: Wis. Agric. Rep. Serv., Madison, Wis.)

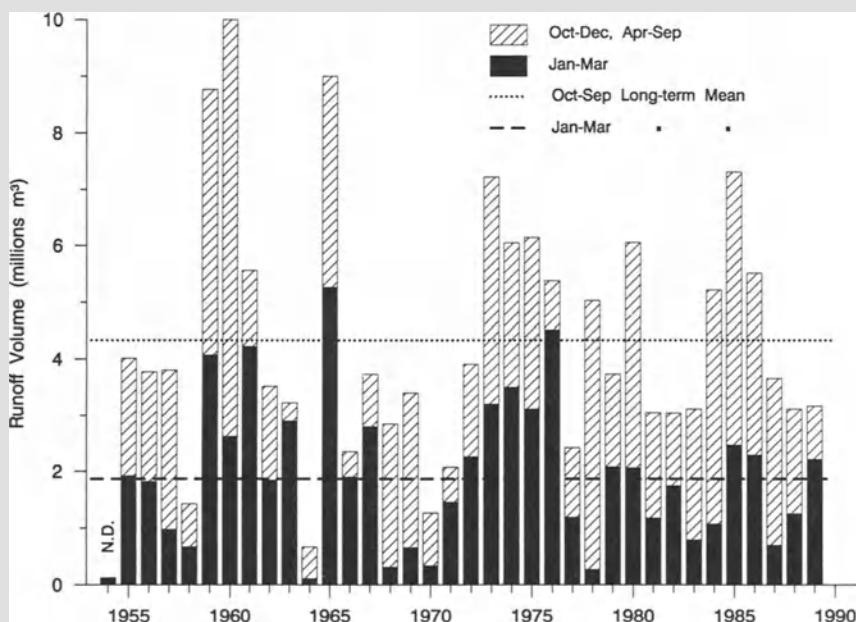
(Windsor) that entered the lake via the Yahara River in 1962. These effluents were discharged to Lake Mendota until the sewage was diverted in late 1971 (Sonzogni 1974). DRP concentrations in Sixmile Creek and the Yahara River in 1976–79 were lower, although cannery processing wastes continued to be discharged to Sixmile Creek.

While Dane County's entire drainage basin (including Lake Mendota's) reached its maximum agricultural development by 1870, an increase in corn production occurred soon after World War II (Figure 6.3). Corn exposes soil to erosion for longer periods of time than other grains. After the war, the use of artificial P and N fertilizers in Wisconsin also increased dramatically (Figure 6.4). As a result of these agricultural changes, non-point loadings most likely increased.

Annual nutrient loadings to Lake Mendota after the mid-1950s apparently have been highly variable. Year-to-year variations in loading are indicated by variations in seasonal runoff volumes, based on Black Earth Creek as an example (Figure 6.5), and by other nutrient loading data for Lake Mendota (Tables 6.3 and 6.4). Very high spring (January–March) and/or annual runoff (biological year, October–September) in 1959–61, 1963, and 1965, coupled with sewage discharges into Lake



**Figure 6-4.** Nitrogen and phosphorus fertilizers used in Wisconsin during 1934–89. (Source: Wis. Agric. Rep. Serv., Madison, Wis.)



**Figure 6-5.** Runoff volume (excluding baseflow) for Black Earth Creek for various months in October–September runoff year for 1954–89.

**Table 6-3.** Phosphorus and nitrogen loadings (kg) to Lake Mendota and from its outlet for 1976–77 and estimated annual averages (excluding sewage inputs) for the 1950s–1970s (from Lathrop 1979).

Nutrient	Source of loadings to lake					
	Rural runoff	Urban runoff	Stream baseflow	Other <sup>a</sup>	Total	Outlet
<b>Total P</b>						
1976	31,100	4,200	4,500	3,200	43,000	9,900
1977	10,500	5,100	3,700	3,600	22,900	7,000
Avg.	25,000	5,000	4,100	3,600	37,700	9,500
<b>TRP<sup>b</sup></b>						
1976	15,000	2,100	2,600	1,700	21,400	6,400
1977	6,300	2,500	2,300	2,000	13,100	5,100
Avg.	12,000	2,500	2,500	2,000	19,000	6,200
<b>Organic N</b>						
1976	74,000	15,000	30,000	80,000	199,000	63,000
1977	25,000	20,000	20,000	80,000	145,000	38,000
<b>Inorganic N</b>						
1976	86,000	5,000	150,000	130,000	371,000	50,000
1977	23,000	6,000	120,000	130,000	279,000	40,000

<sup>a</sup>P loading from precipitation, dry fallout, and groundwater; N loading estimated by Sonzogni and Lee (1974) for the same sources plus nitrogen fixation.

<sup>b</sup>TRP = unfiltered, molybdate reactive.

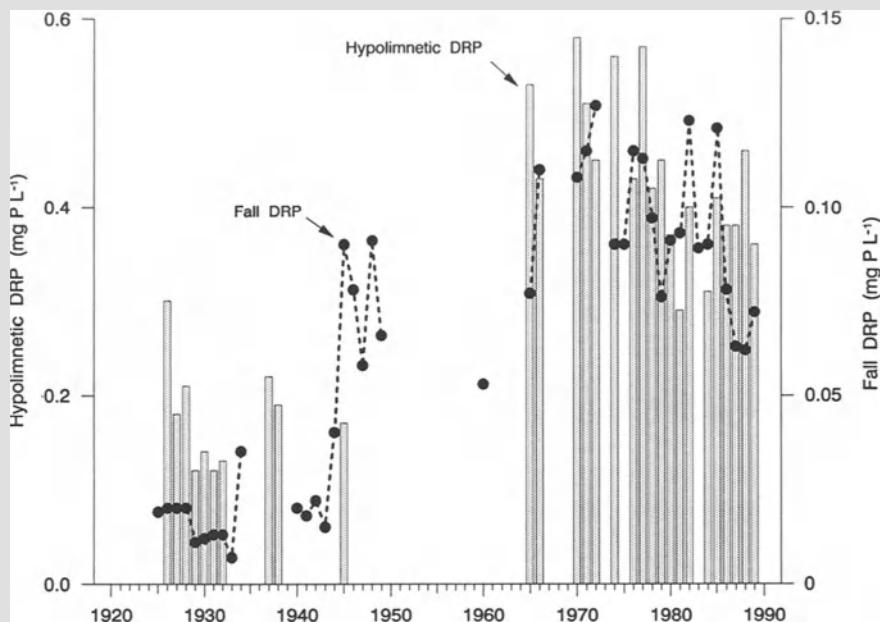
**Table 6-4.** Phosphorus and nitrogen loadings (kg) for the Yahara River watershed for 1976–80.<sup>a</sup>

Nutrient	1976	1977	1978	1979	1980
Total P	11,300	2,800	7,800	4,100	13,800
TRP <sup>b</sup>	5,600	1,700	2,200	1,900	4,400
Organic N	32,300	8,500	20,300	13,600	35,800
Inorganic N	63,500	30,200	39,900	51,400	58,800

<sup>a</sup>Watershed area at U.S. Geological Survey gauging station = 191 km<sup>2</sup>. P data from Lathrop (1986); N data computed in similar fashion but not previously published.

<sup>b</sup>TRP = unfiltered, molybdate reactive.

Mendota's upstream tributaries, likely produced the highest P loadings to Lake Mendota since the mid-1950s. Spring runoff was much lower in 1968–71, immediately prior to the sewage diversion in late 1971. However, spring runoff was again higher than normal for 1973–76. These high spring runoff volumes probably delivered more BAP to Lake Mendota than was removed by the sewage diversion, which represented about a 30% reduction in the average BAP loading to the lake (Lathrop 1990).



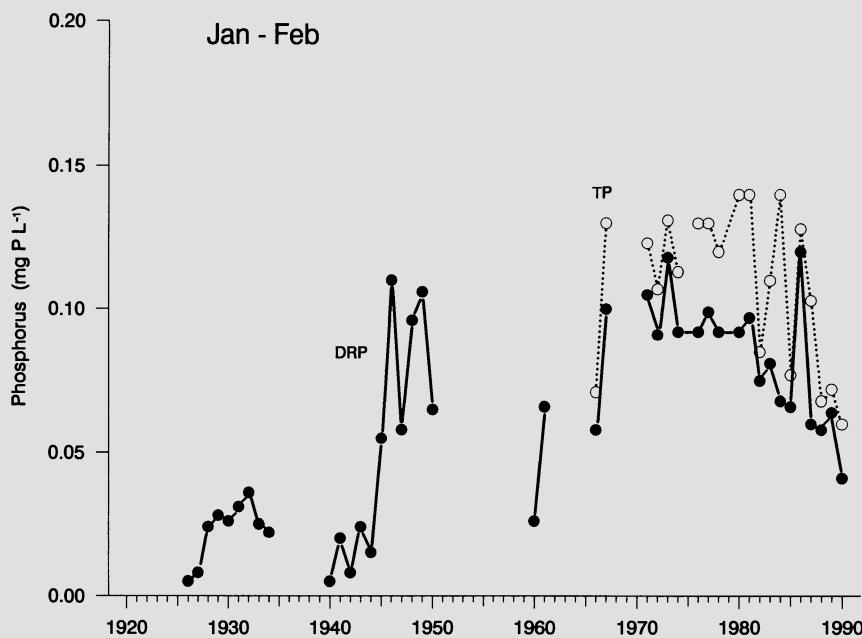
**Figure 6-6.** DRP surface concentrations during fall turnover (15 Oct–14 Dec) and DRP hypolimnetic concentrations at 20 m on 1 September for selected years during 1925–89 in Lake Mendota.

For many years since 1977, spring and annual runoff have been either normal or below normal, indicating average P loadings also have been low. Runoff was particularly low in 1987–88, the first 2 years of the food web research. Spring runoff was slightly above normal in 1989, although runoff for the rest of the biological runoff year was low.

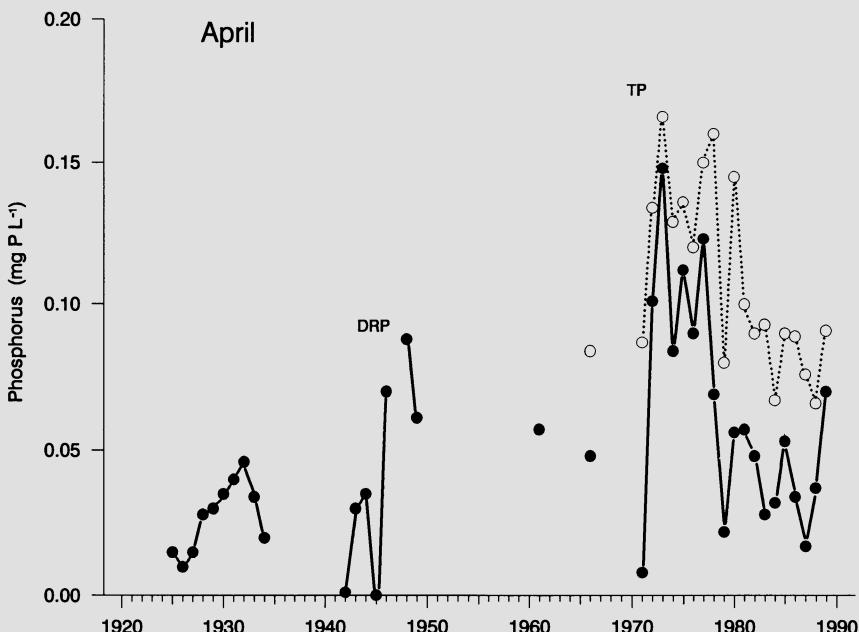
Annual loadings to Lake Mendota were probably less variable for N than for P. While organic N loadings were highly correlated with runoff, year-to-year variations in inorganic N loadings were not as great because they were dominated by high nitrate concentrations in streams with large baseflow discharges (Table 6.3). However, these high baseflow concentrations of nitrate may be partially depleted in the low-flow river reaches, possibly leading to overestimation of annual inorganic N loadings to Lake Mendota.

### Lake Phosphorus

Surface water concentrations of DRP in the fall, winter, and early spring months have changed considerably since measurements were first made in 1925 (Figures 6.6–8). Concentrations were relatively low until the mid-1940s, when a major increase occurred. Fall and early spring DRP were



**Figure 6-7.** Surface water concentrations of TP and DRP in January–February for selected years during 1926–89 in Lake Mendota.



**Figure 6-8.** Surface water concentrations of TP and DRP in April for selected years during 1925–89 in Lake Mendota.

even higher in the early to mid-1970s than concentrations recorded in the late 1940s; winter DRP was about the same in both periods. Late summer hypolimnetic DRP concentrations also exhibited a similar increase from the 1920s and 1930s to more recent years (Figure 6.6).

By the late 1970s, surface DRP concentrations began a downward trend in each season for most years. Throughout most of the 1980s, April DRP averaged only about 40% of levels recorded in 1972–77. Comparing the first 3 years of the food web research, April DRP was noticeably higher in 1989 than in 1987–88. TP also exhibited an overall downward trend between the 1970s and the 1980s. During this same period, hypolimnetic DRP concentrations dropped, corresponding with declines in surface DRP levels after fall turnover had begun. Considerable variation occurred from year to year during this downward trend in DRP and TP. Because the P concentration data do not measure inputs, incorporation by algae, and direct sedimentation or losses through grazing, further discussion of these yearly P differences would be speculative and beyond the scope of this chapter.

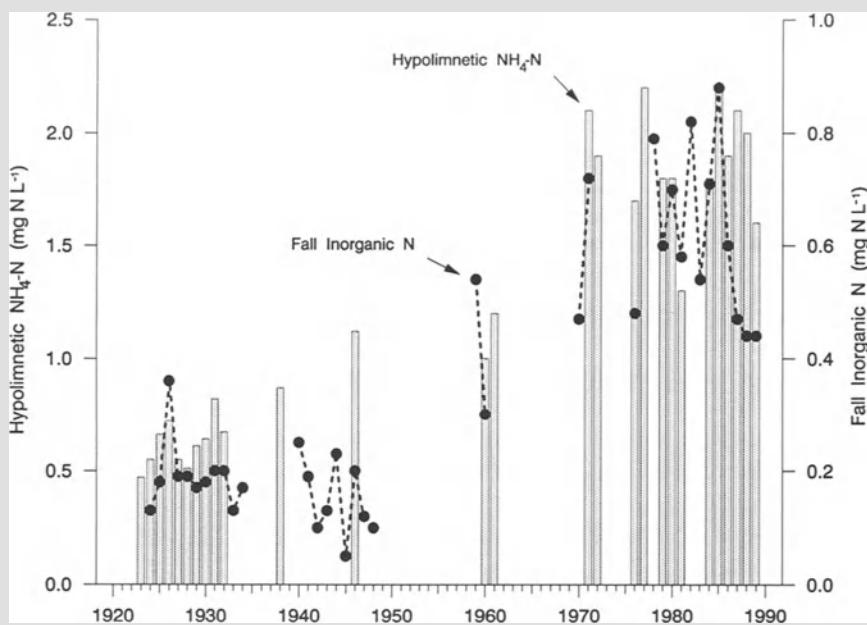
### Lake Nitrogen

Both fall inorganic N ( $\text{NH}_4\text{-N}$ ,  $\text{NO}_2\text{-N}$ , and  $\text{NO}_3\text{-N}$ ) in the surface waters and late summer  $\text{NH}_4\text{-N}$  concentrations in the hypolimnion increased by about a factor of three between the 1920s–30s and the 1970s–80s (Figure 6.9). Although not discussed in this chapter, similar increases in both the winter and the early spring months also occurred between these same periods. Fall inorganic N in the surface waters was lower in the food web research years (1987–89) than in most years since 1971. However, hypolimnetic  $\text{NH}_4\text{-N}$  did not decline in 1987–89.

### Water Transparency

Long-term mean Secchi disk readings for Lake Mendota during each of the six seasons that I defined above are given in Table 6.5. These mean readings followed the annual cycle observed in the food web research years (Vanni et al., Ch. 13). The greatest water clarity typically occurred during the winter, followed by a major decrease in clarity due to early spring algal blooms. A spring clear-water period then followed when *Daphnia* populations typically were high (Lathrop and Carpenter, Ch. 8; Luecke et al., Ch. 14). The lowest water clarity occurred during the summer months, followed by a gradual improvement through the fall.

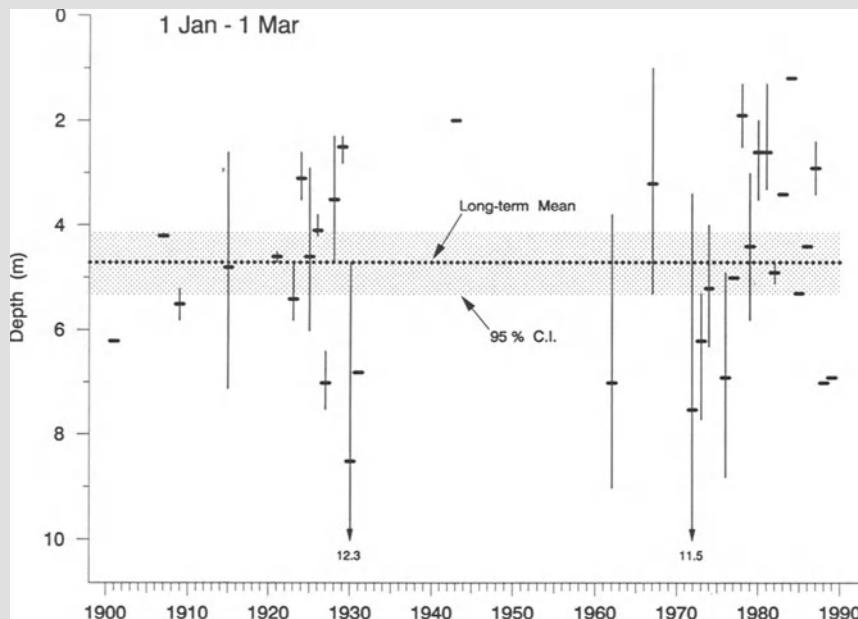
Long-term trends in Secchi disk readings for the winter period indicated that water clarity has been highly variable (Figure 6.10). In recent years, winters with exceptionally high clarity occurred in 1972–74, 1976, and 1988–89. Winters with relatively low clarity occurred in 1978, 1980–81, 1984–85, and 1987. Water clarity was similar to the long-term mean



**Figure 6-9.** Surface concentration of inorganic N during fall turnover (15 Oct–14 Dec) and hypolimnetic NH<sub>4</sub>-N concentrations at 20 m on 1 September for selected years during 1923–89 in Lake Mendota.

**Table 6-5.** Long-term means of Secchi disk readings (20-cm B/W) during different seasonal periods in Lake Mendota.

Periods	Mean (m)	N	SEM
Winter 1 Jan–1 Mar	4.74	34	0.31
Spring turnover 22 Mar–10 May	2.67	49	0.15
Early stratification 11 May–29 Jun	3.72	55	0.16
Summer stagnation 30 Jun–2 Sep	2.31	56	0.11
Destratification 3 Sep–12 Oct	2.45	51	0.10
Fall overturn 13 Oct–16 Dec	3.14	48	0.11

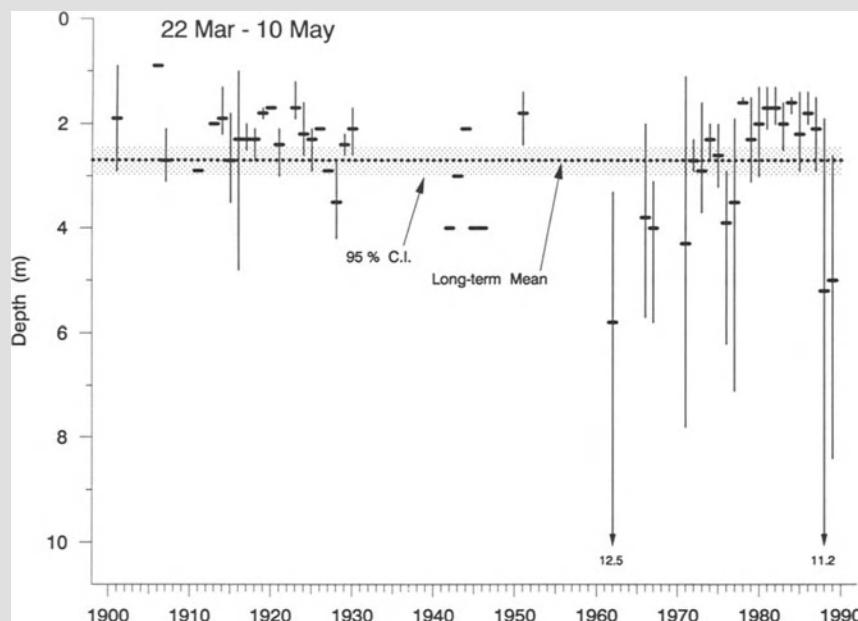


**Figure 6-10.** Secchi disk readings (converted to 20-cm B/W disk) collected during the winter period (1 Jan–1 Mar) for selected years during 1901–89 in Lake Mendota. Fat short bar is season mean for each year; thin vertical line is range if more than one reading was taken. Long-term mean is mean of each year's seasonal mean.

during much of the first part of this century until relatively low clarity occurred in 1923 and 1927–28, and high clarity occurred in 1926 and 1929–30. Poor clarity was also observed in 1943 and 1966, and high clarity in 1962.

Secchi disk readings were not as variable for the spring turnover period (Figure 6.11). Secchi readings were generally less than or similar to the long-term mean from the early 1900s through 1930, with the exception of 1928. During this 30-year period, Secchi readings averaged around 2.0–2.2 m. In recent years (1978–87) when Secchi data were also extensive, readings were less than the long-term mean of 2.7 m. Lake Mendota was especially clear during the spring turnover periods of 1962, 1966–67, and 1971, and also in 1976–77 and 1988–89. Secchi readings in 1971–75 were similar to the long-term average.

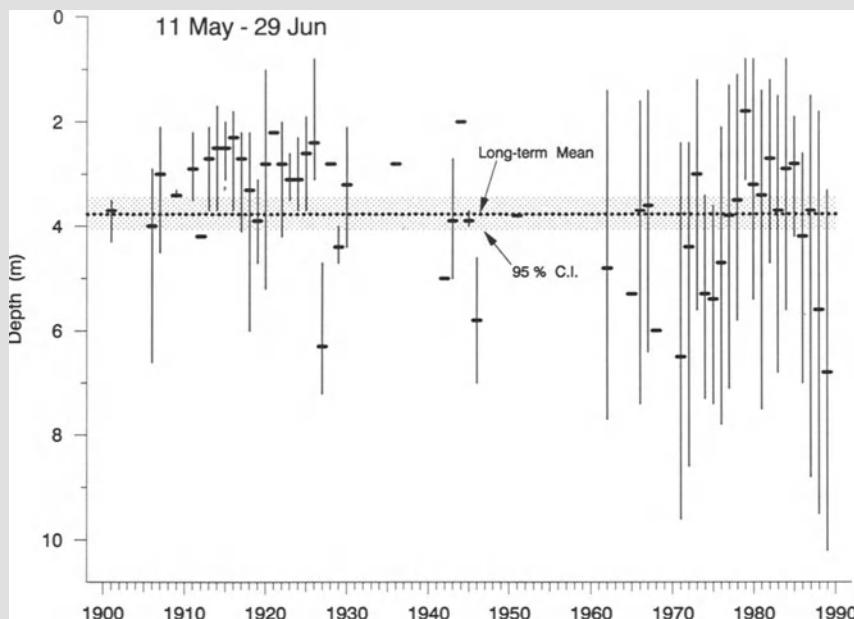
Long-term Secchi readings taken during the early stratification period indicated that highly variable water clarity occurred in many years (Figure 6.12). The maximum disk readings of the ice-free period were normally recorded at this time. Other differences in the long-term dataset are noteworthy. Most of the late springs prior to 1930 had average disk



**Figure 6-11.** Secchi disk readings (converted to 20-cm B/W disk) collected during the spring turnover period (22 Mar–10 May) for selected years during 1901–89 in Lake Mendota. Fat short bar is season mean for each year; thin vertical line is range if more than one reading was taken. Long-term mean is mean of each year's seasonal mean.

readings less than the long-term mean of 3.7 m. Better than average water clarity was recorded only in 1927. Maximum readings were <4.5 m in most years. Very high water clarity was recorded in the 1960s in the few years that had data and during 1971–72, 1974–76, and 1987–89. During 1977–87, most annual mean readings were either similar to or less than the long-term mean. In 1979, water clarity was relatively low. The maximum reading was less than the long-term mean, indicating that no true spring clear-water period occurred that year. Water clarity was also relatively poor in 1985. However, maximum Secchi disk readings exceeded 6.0 m during 1960 through 1977 (except for 1973) and in 1981, 1983, and 1986–89. In these years, water clarity was notably greater than in the early 1900s.

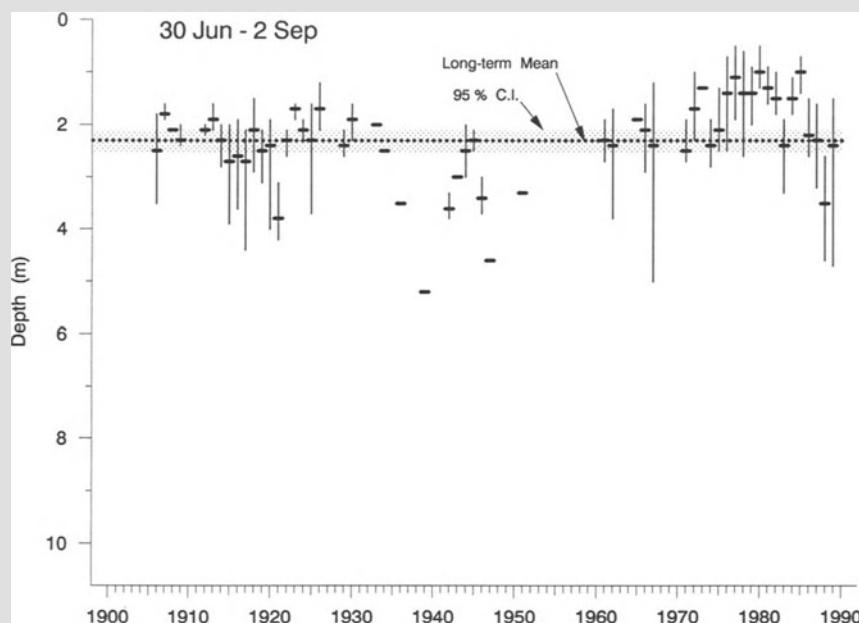
Average Secchi disk readings during the summer stagnation period for many years were similar to the long-term mean of 2.3 m (Figure 6.13). Prior to the early 1930s, readings varied little from summer to summer. Averages for a few years were significantly less than the long-term mean, but never less than 1.7 m; average readings in 1915–17 were slightly greater than the long-term mean. Only in 1921 was water clarity sig-



**Figure 6-12.** Secchi disk readings (converted to 20-cm B/W disk) collected during the early stratification period (11 May–29 Jun) for selected years during 1901–89 in Lake Mendota. Fat short bar is season mean for each year; thin vertical line is range if more than one reading was taken. Long-term mean is mean of each year's seasonal mean.

nificantly greater than the long-term mean. Although not many Secchi disk readings were taken from the mid-1930s to the early 1950s, water clarity was often high. Unusually high readings of around 5 m were recorded in 1939 and 1947. Hasler and Bardach (1949) reported a maximum reading of 7.3 m during the summer of 1947, a summer they considered to have unusually good water clarity. Secchi readings of 3–4 m were recorded in 1935, 1942–43, 1946, and 1951. Readings similar to the long-term average were recorded in 1944–45. Hasler and Bardach (1949) indicated that readings for the summers of 1943–46 averaged 1.5–3.0 m, but the actual unpublished measurements could not be located.

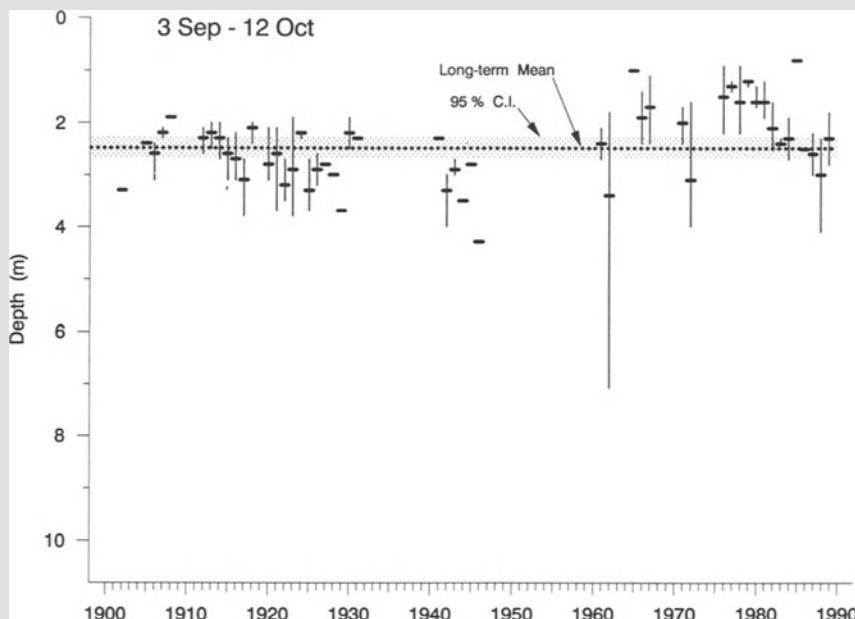
Average Secchi disk readings taken in the summer stagnation period of 1961–62, 1966–67, 1971, 1974–75, 1983, 1986–87, and 1989 were similar to the long-term mean reading. However, average readings in 1973–74, 1976–82, and 1984–85 were significantly less than the long-term mean. These readings averaged only slightly greater than 1.0 m and were consistently the lowest recorded during the summer months in this century on Lake Mendota. In recent years, only the summer of 1988 (the year following the massive cisco die-off) had an average disk reading significantly greater than the long-term mean.



**Figure 6-13.** Secchi disk readings (converted to 20-cm B/W disk) collected during the summer stagnation period (30 Jun–2 Sep) for selected years during 1906–89 in Lake Mendota. Fat short bar is season mean for each year; thin vertical line is range if more than one reading was taken. Long-term mean is mean of each year's seasonal mean.

Secchi disk readings during the destratification period exhibited trends similar to the summer stagnation period (Figure 6.14). Readings were similar to the long-term mean (2.45 m) in the early 1900s but were significantly greater than the long-term mean throughout the 1920s. Most readings were also greater during the 1940s. Readings were quite variable during the 1960s and early 1970s, with both high and low values recorded. Readings in 1976–81 and 1985 were significantly less than the long-term mean and often were only slightly greater than 1.0 m. Readings were nearer the mean during 1983–84, 1986–87, and 1989. The average reading in 1988 was greater than the long-term mean.

The Secchi depth during fall turnover was greater (long-term mean = 3.1 m) and seasonally more variable than during the destratification period (Figure 6.15). However, year-to-year trends in the two periods were similar. Average readings during the early 1900s appeared to increase slightly during these years. Water clarity in 1961–62, 1965–66, and 1975, and later in 1982, 1984, and 1986–89 was quite good. Secchi readings were significantly less than the long-term mean in 1967, 1971, 1976–81, 1983, and 1985. While very low water clarity was recorded in 1985, it was represented by only one reading on 15 October.

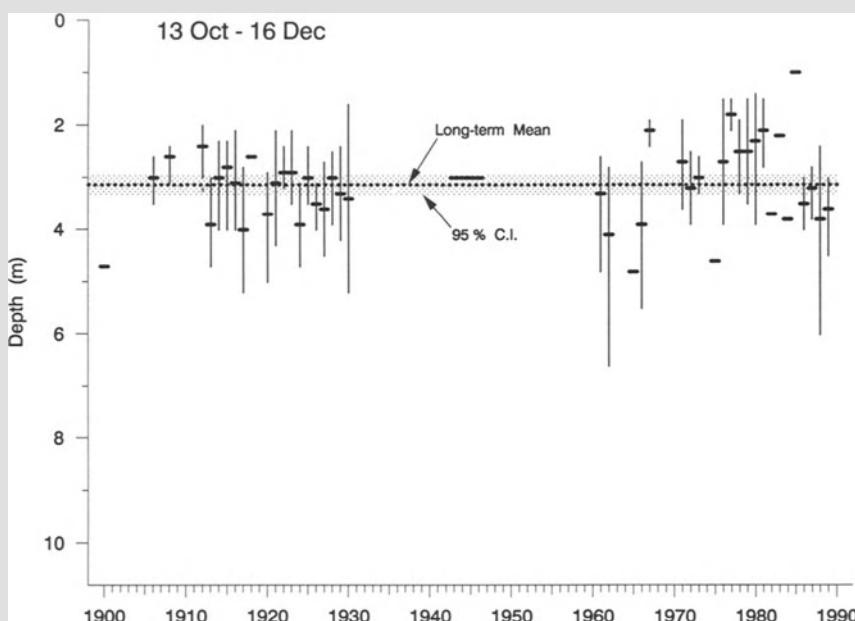


**Figure 6-14.** Secchi disk readings (converted to 20-cm B/W disk) collected during the destratification period (3 Sep–12 Oct) for selected years during 1902–89 in Lake Mendota. Fat short bar is season mean for each year; thin vertical line is range if more than one reading was taken. Long-term mean is mean of each year's seasonal mean.

## Discussion

Since the early 1900s, nutrient loadings, lake P and N concentrations, and water clarity have changed considerably in Lake Mendota. This finding contradicts earlier views that the lake has not experienced major changes in water quality during this century (Brock 1985). The long-term datasets collected and evaluated in this chapter document a dynamic and variable lake system. This variability illuminates the relative importance of both nutrient loadings (bottom-up) and herbivory (top-down) effects on algal densities and water clarity in Lake Mendota.

Nutrient loadings most likely increased during the 1920s when sewage discharges from upstream communities first entered Lake Mendota. However, a major increase in P loadings from the sewage effluents apparently did not occur until the mid-1940s, based on increases in both in-lake and stream DRP concentrations. Loadings probably continued to increase as agricultural fertilizers were used extensively after World War II. In ensuing years, loadings increased because of additional urban stormwater runoff as Madison grew. Additional sewage effluents were



**Figure 6-15.** Secchi disk readings (converted to 20-cm B/W disk) collected during the fall turnover period (13 Oct-16 Dec) for selected years during 1900–89 in Lake Mendota. Fat short bar is season mean for each year; thin vertical line is range if more than one reading was taken. Long-term mean is mean of each year's seasonal mean.

discharged to the lake in 1962. Because of high runoff, particularly during the early spring. P loadings to Lake Mendota remained high through 1977, even after the sewage effluents were diverted in late 1971. For many years from the late 1970s through the late 1980s, loadings were lower because of below-normal runoff and the lack of sewage inputs. In-lake P concentrations during this period experienced a downward trend.

Long-term Secchi disk data, including seasonal patterns, indicate that water clarity trends in Lake Mendota cannot be interpreted solely on the basis of nutrient loadings and lake P concentrations. While loadings and in-lake concentrations of P were relatively low during the early 1900s through the late 1920s, this was also a period of relatively high planktivory in Lake Mendota. The cisco population was large and the yellow perch population was dense in the early 1900s (Lathrop et al. 1992; Magnuson and Lathrop, Ch. 11). *Daphnia galeata mendotae* was the dominant spring *Daphnia* species, with large densities usually occurring after mid-May during the early stratification period (Lathrop and Carpenter, Ch. 8). As a result, Secchi disk readings during the spring turnover period in April and early May were low compared to the long-term mean.

Comparably low water clarity occurred during spring turnover from 1978 to 1987 when *D. galeata mendotae* also dominated. P loadings and lake P concentrations were also higher than in the 1900s–20s. Planktivory was high during 1978–87 because the cisco population was dense (Rudstam et al., Ch. 12). During the spring months, lake N and P concentrations normally were high and the phytoplankton were mostly edible forms readily consumed by *Daphnia* (Lathrop and Carpenter, Ch. 8; Vanni et al., Ch. 13). However, the cisco population was low in the 1960s and 1970s through 1977 and after the cisco kill in August 1987. *D. pulicaria* dominated in 1976–77 and 1988–89, with population densities increasing earlier in the spring, causing a decrease in algal densities. *D. pulicaria* also was found to be relatively dense in sediment core depths corresponding to many decades prior to the late 1970s (Kitchell and Sanford, Ch. 4).

Water clarity during the early stratification period was also relatively poor in the early 1900s, when nutrient loadings and concentrations were low while planktivory was high. Water clarity was much greater during many years of the 1960s, early 1970s, and late 1980s when nutrient loadings and lake concentrations were much higher but planktivory was low. The much lower maximum Secchi disk readings recorded during the early 1900s suggest that planktivory did not allow *D. galeata mendotae* populations to clear spring algal populations or that a larger proportion of inedible algae occurred during those years. Since the 1960s, maximum Secchi disk readings were generally greater in years dominated by *D. pulicaria* than in the late 1970s and early 1980s, when *D. galeata mendotae* dominated.

Water clarity during the summer stagnation period also indicated that both nutrients and herbivory/planktivory were important in Lake Mendota. In the early 1900s, nutrients were low while planktivory was high. Secchi disk readings were similar to the long-term mean. In many years from the late 1930s through the early 1950s, planktivory probably was low due to the declining cisco population and yellow perch die-offs during the 1940s (Lathrop et al., unpubl. rep.; Magnuson and Lathrop, Ch. 11). Massive perch kills occurred in 1939 and 1946; summer water clarity was exceptional in both 1939 and 1947. This unusually good water clarity also occurred in the summer of 1988, the year after the massive cisco kill. Water clarity was high in the years immediately following the increases in P loadings and lake P concentrations in the mid-1940s, again indicating the importance of very low planktivory.

In the 1960s and early 1970s, summer Secchi disk readings were similar to the long-term mean at a time when nutrients were the highest and the cisco population was very low in Lake Mendota. These readings were similar to those readings taken during the early 1900s by Birge and Juday, a finding reported by Stewart (1976). However, by the late 1970s when P loadings and lake concentrations were declining while the cisco popula-

tion was high, the lowest summer Secchi disk readings reported for this century occurred. The combined effects of relatively high nutrients and high planktivory produced low water clarity. Better water clarity was observed in 1983, a year of a minor cisco kill. Secchi readings similar to the long-term average were reported after 1986, indicating the combined effects of decreasing nutrients and decreasing planktivory.

The relative importance of herbivory/planktivory during the destratification and fall turnover periods is more difficult to discern because *D. pulicaria* normally did not occur during the fall (Lathrop and Carpenter, Ch. 8). However, fall densities of *D. galeata mendotae* may have been affected by changes of planktivory. Fall peaks of *D. galeata mendotae* did not occur in 1977–83 when planktivory was high (Lathrop and Carpenter, Ch. 7; Rudstam et al., Ch. 12). In 1984–87 and 1989, fall peaks in *Daphnia* occurred at a time when planktivory was reduced after a cisco kill in 1983 and years of poor perch recruitment. Water clarity in the destratification and fall turnover periods from the late 1970s through the early 1980s was much poorer than after the mid-1980s, except for 1985 when the lowest Secchi disk readings were recorded in these periods during this century. Nutrient loadings were relatively high in 1985, and internal recycling may also have been enhanced because of reduced lake stability (Lathrop and Carpenter, Ch. 7). This improvement in water clarity throughout the 1980s also mirrored the decrease in lake P concentrations. Relatively high Secchi disk readings were recorded in the early 1900s, particularly in the 1920s, when nutrients were lower than in recent years.

These seasonal patterns in nutrients, herbivory, and planktivory for spring to fall and their effect on water clarity support the conceptual model presented by Carpenter (Ch. 23). This model depicts an elliptical probability distribution that contains 95% of the possible water clarity states (days of phytoplankton blooms or clear water) in Lake Mendota. The positioning of the ellipse is determined by both the level of planktivory (or herbivory) and the nutrient input. The model predicts that the same overall water clarity condition can be produced by different degrees of a “top-down” and a “bottom-up” effect.

This same conclusion—that periods of similar water clarity can be produced by different nutrient–herbivore–planktivore regimes—is also supported by a qualitative assessment of the historical record in Lake Mendota. While it is impossible to quantify the absolute levels of nutrients (either loadings or in-lake concentrations), herbivory, and planktivory since the early 1900s based on information presented in this chapter, I assigned relative levels (low, medium, or high) for different time periods that reflect generally stable conditions in the historical record (Table 6.6). For the same time periods, I also assigned relative levels of water clarity for the spring (spring turnover and early stratification), summer, and fall (destratification and fall turnover) seasons based on overall differences

**Table 6-6.** Seasonal water clarity responses to relative levels of nutrients, herbivory, and planktivory in Lake Mendota since the early 1900s.

Lake condition	Period					
	Late 1800s–1920s	1940s	1960s–1977	1978–summer 1983	Fall 1983–summer 1987	Fall 1987–1988
Nutrients <sup>a</sup>	Low	Medium	High	Medium–high	Medium	Medium
Herbivory	Low	High	Low	Low	Medium	High
Planktivory	High	Low	High	High	Medium	Low
Water clarity						
Spring	Low	Medium	Medium–high	Low	Low	High
Summer	Medium	High	Medium	Low	Low–medium	High
Fall	Medium–high	Medium	Medium–high	Low	Medium–high	Medium–high

<sup>a</sup> Loadings and/or in-lake concentrations.

from their respective long-term means (Figures 6.11–15). (Only in more recent years when detailed nutrient, zooplankton, and fish data were available could shorter time periods be used to detect water clarity responses.)

In summary, high water clarity during the spring months occurred when planktivory was low and herbivory was high because *D. pulicaria* dominated for much of the period. Low water clarity occurred when planktivory was high and herbivory was low because *D. galeata mendotae*, a less efficient filter-feeder, dominated for a shorter period in late spring. Because nutrients were usually elevated during the spring months, differences in their relative levels produced less impact on spring water clarity. In the fall months, planktivory/herbivory was also important, although apparently limited to determining the extent of *D. galeata mendotae* populations that reduced fall blooms of edible algae.

The summer water clarity, of central concern to the food web research presented in this volume, exhibited the most interesting responses to different levels of nutrients and planktivory/herbivory. Average water clarity occurred in both the early 1900s and the 1960s through 1977. Nutrients were low and planktivory was high in the earlier period, while the opposite conditions occurred in the latter period. When nutrients were average to high and planktivory was high during the 1978–83 period, the worst summer water clarity in Lake Mendota during this century occurred. The best water clarity occurred for brief periods during the 1940s and in the late 1980s when nutrients were medium but planktivory was low because of fish kills and/or poor recruitment. These data suggest that desirable improvements in summer water clarity in Lake Mendota can be achieved from management programs that promote both a bottom-up control of nutrients and a top-down control of planktivorous fish.

*Acknowledgments.* I thank D.E. Armstrong, S.R. Carpenter, and M.J. Vanni for critical reviews of this manuscript and S.H. Nehls for editorial assistance. I also thank B.G. Saley and W.C. Sonzogni for making available unpublished lake nutrient records and T.D. Brock, R.A. Ragotzkie, D.M. Robertson, W.C. Sonzogni, and K.W. Stewart for providing unpublished Secchi disk data. Finally, I thank the many people who assisted in the WDNR's lake sampling program since 1976. This data collection was supported principally by the WDNR.

## References

- American Public Health Association (1923) Standard methods for the examination of water and sewage. 5th edn. Am. Public Health Assn., New York

- American Public Health Association and American Water Works Association (1946) Standard methods for the examination of water and sewage. 9th edn. Am. Public Health Assn. and Am. Water Works Assn., New York
- Atkins WRG (1923) The phosphate content of fresh and salt waters in its relationship to the growth of algal plankton. J. Mar. Biol. Assn. 13:119–150
- Belter WG, Calabresa TA (1950) The origins and quantities of algal fertilizers tributary to Lake Mendota (1949). M.S. Thesis, University of Wisconsin, Madison
- Brock TD (1985) A eutrophic lake: Lake Mendota, Wisconsin, Springer-Verlag, New York
- Clesceri NL (1961) The Madison lakes before and after diversion. M.S. Thesis, University of Wisconsin, Madison
- Dane County Regional Planning Commission (1980) Baseflow water quality trends in Dane County, Wisconsin. Dane Cty. Reg. Plann. Comm., Madison
- Delfino JJ (1968) Aqueous environmental chemistry of manganese. Ph.D. Thesis, University of Wisconsin, Madison
- Domogalla BP (1926) Treatment of algae and weeds in lakes at Madison. Eng. Newsrecord 97:950–954
- Domogalla BP (1935) Eleven years of chemical treatment of the Madison lakes: Its effect on fish and fish foods. Trans. Am. Fish. Soc. 65:115–120
- Domogalla BP, Fred EB, Peterson WH (1926) Seasonal variations in the ammonia and nitrate content of lake waters. J. Am. Water Works Assn. 15:369–385
- Domogalla BP, Juday C, Peterson WH (1925) The forms of nitrogen found in certain lake waters. J. Biol. Chem. 63:269–285
- Elser JJ, Goldman CR (1991) Zooplankton effects on phytoplankton in lakes of contrasting trophic status. Limnol. Oceanogr. 36:64–90
- Frey DG (1940) Growth and ecology of the carp *Cyprinus carpio* Linnaeus in four lakes of the Madison region, Wisconsin. Ph.D. Thesis, University of Wisconsin, Madison
- Goering JJ (1963) Studies of nitrogen-fixation in natural fresh waters. Ph.D. Thesis, University of Wisconsin, Madison
- Gulati RD, Lammens EHRR, Meijer ML, Van Donk E (eds) (1990) Biomanipulation: Tool for water management. Kluwer Academic Publishers (Hydrobiologia 200/201), Dordrecht
- Hasler AD, Bardach JE (1949) Daily migrations of perch in Lake Mendota, Wisconsin. J. Wildl. Manage. 13:40–51
- Hasler AD, Wohlschlag DE (1951) Some quantitative aspects of algal growth in Lake Mendota. Ecology 32:581–593
- Juday C (1929) Limnological methods. Arch. Hydrobiol. 20:517–524
- Juday C, Birge EA (1933) The transparency, the color and the specific conductance of the lake waters of northeastern Wisconsin. Trans. Wis. Acad. Sci. Arts Lett. 28:205–259
- Juday C, Birge EA, Kemmerer GI, Robinson RJ (1928) Phosphorus content of lake waters of northeastern Wisconsin. Trans. Wis. Acad. Sci. Arts Lett. 23:233–248
- Lathrop RC (1979) Appendix H: Lake management. In Dane County Regional Planning Commission, Dane County water quality plan. Vol. 2. Dane Cty. Reg. Plann. Comm., Madison, pp H-1 to H-77

- Lathrop RC (1986) A simplified method for obtaining monitored phosphorus loadings. In Redfield G, Taggart JF, Moore LM (eds) Lake and reservoir management. Vol. 2. Proc. 5th Annu. Conf. Int. Symp. Appl. Lake and Watershed Manage. N. Am. Lake Manage. Soc., Washington, pp 20–26
- Lathrop RC (1990) Response of Lake Mendota (Wisconsin, U.S.A.) to decreased phosphorus loadings and the effect on downstream lakes. Verh. Int. Verein. Limnol. 24:457–463
- Lathrop RC, Nehls SH, Brynildson CL, Plass KR (1992) The fishery of the Yahara lakes. Technical Bulletin (in press), Wisconsin Department of Natural Resources, Madison
- Lueschow LA, Helm JM, Winter DR, Karl GW (1970) Trophic nature of selected Wisconsin lakes. Trans. Wis. Acad. Sci. Arts Lett. 58:237–264
- McQueen DJ (1990) Manipulating lake community structure: Where do we go from here? Freshwat. Biol. 23:613–620
- Robertson DM (1989) The use of lake water temperature and ice cover as climatic indicators. Ph.D. Thesis, University of Wisconsin, Madison
- Robinson RJ, Kemmerer G (1930) Determination of organic phosphorus in lake waters. Trans. Wis. Acad. Sci. Arts Lett. 25:117–121
- Sawyer CN, Lackey JB, Lenz AT (1945) Investigation of the odor nuisance occurring in the Madison lakes particularly Lakes Monona, Waubesa, and Kegonsa from July 1943 to July 1944. Rep. to Gov. Comm., Madison
- Schindler DW (1977) Evolution of phosphorus limitation in lakes. Science 195:260–262
- Sonzogni WC (1974) Effect of nutrient input reduction on the eutrophication of the Madison lakes. Ph.D. Thesis, University of Wisconsin, Madison
- Sonzogni WC, Lee GF (1974) Diversion of wastewaters from Madison lakes. Am. Soc. Civ. Eng. J. Environ. Eng. 100:153–70
- Stauffer RE (1974) Thermocline migration: Algal bloom relationships in stratified lakes. Ph.D. Thesis, University of Wisconsin, Madison
- Stewart KW (1976) Oxygen deficits, clarity, and eutrophication in some Madison lakes. Int. Rev. Ges. Hydrobiol. 61:563–579
- Torrey MLS (1972) Biological nitrogen fixation in Lake Mendota. Ph.D. Thesis, University of Wisconsin, Madison
- Vigon BW (1976) The role of silica and the vernal diatom bloom in controlling the growth of nuisance algal populations in lakes. M.S. Thesis, University of Wisconsin, Madison
- Vollenweider RA (1968) Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. Rep. No. DAS/CSI/68.27. Organization for Economic Cooperation and Development, Paris
- Wisconsin Committee on Water Pollution (1949) Report on Lake Mendota studies concerning conditions contributing to occurrence of aquatic nuisances 1945–1947. Wis. Comm. Water Pollut., Madison
- Zimmerman FR (1953) Waterfowl habitat surveys and food habit studies, 1940–1943. Final Rep., Pittman-Robertson Proj. No. 6-R. Wisconsin Conservation Department, Madison

# 7

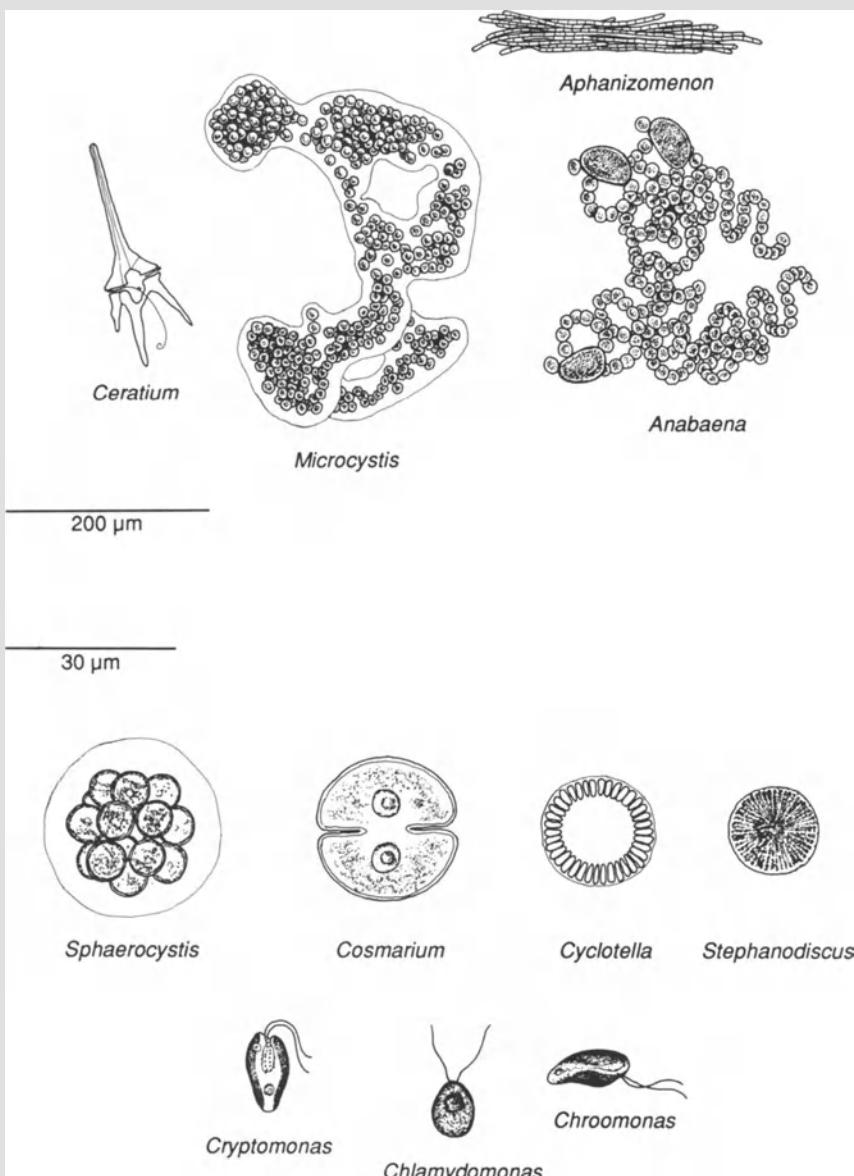
## Phytoplankton and Their Relationship to Nutrients

**Richard C. Lathrop and Stephen R. Carpenter**

### Introduction

The phytoplankton that commonly occur in Lake Mendota are the central focus of the food web research detailed in this volume (Figure 7.1). The role of nutrients, particularly phosphorus, in regulating algal biomass and stimulating blooms is well established (Vollenweider 1968; Schindler 1977, 1988). Herbivory by zooplankton has also been long recognized as an important influence on phytoplankton abundance and species composition (Hrbacek 1962; Brooks and Dodson 1965; Shapiro et al. 1975; Shapiro and Wright 1984; Carpenter and Kitchell 1988). While phosphorus reductions cause declines in blue-green algal densities (Schindler 1988), the effects of herbivory are more variable and complicated (Sterner 1989; Carpenter, Ch. 23). For example, increased herbivory has both stimulated (Lynch 1980; Andersson and Cronberg 1984) and suppressed (Shapiro and Wright 1984; Carpenter et al. 1987; Vanni et al. 1990) blue-green algae.

Lake Mendota offers an unusual opportunity to examine the joint effects of nutrients and herbivory on phytoplankton. A substantial range of nutrient concentrations and phytoplankton and zooplankton population densities is represented in the historical record. Wide seasonal fluctuations in nutrients (Sonzogni 1974) and phytoplankton and zooplankton (Brock 1985) have already been documented. Lathrop (1990) also documented long-term declines in loadings and in-lake concentrations of phosphorus and declines in algal biomass from the late 1970s through 1988.



**Figure 7-1.** The major phytoplankton genera of Lake Mendota.

The regular sampling program that has been sustained for many years allowed us to apply time series techniques that account explicitly for the effects of seasonality and autocorrelation (Jassby and Powell 1990). Our approach avoids the effects of temporal scale and autocorrelation that

impair many analyses of nutrient–alga–herbivore systems (Carpenter 1988; Carpenter and Kitchell 1988; Carpenter et al. 1991). Our presentation is observational and descriptive, in the sense that the range of variability analyzed derives from the natural fluctuations of the unmanipulated system (Carpenter 1988). In fact, most lakes are singular and do not offer the prospect of large-scale experimental manipulation. In this chapter, we demonstrate an approach that applies to such lakes and reveals the range of dynamic variability susceptible to manipulation by large-scale management actions.

This chapter presents a historical review of phytoplankton studies in Lake Mendota prior to 1976 and the highlights of a 14-year record of phytoplankton densities and nutrient concentrations from 1976 to 1989. We focus on total algal densities and the densities of functional groups most germane to the food web research. Time series models are developed for selected algal variates and are related to phosphorus and nitrogen concentrations. The relationships between algal time series and zooplankton time series are presented in the companion chapter on zooplankton (Lathrop and Carpenter, Ch. 8). Long-term trends in nutrient concentrations were discussed in the previous chapter on nutrient loadings and water quality (Lathrop, Ch. 6).

## Historical Background

Trelease (1889) was the first to record blue-green algal blooms in Lake Mendota. In 1882 noxious shore area scums occurred periodically from June to November. *Microcystis aeruginosa*, *Coelosphaerium* sp., and *Anabaena* spp. were the major species identified. Algal blooms also occurred during the summers of 1883–84, but blooms were not as severe as in 1882. In 1885–87, blue-green algal blooms were much less noticeable.

Subsequent reports of dense growths of blue-green algae and other phytoplankton species were made by Birge (1898) for 1894–97. However, samples were collected by a net and only qualitative descriptions were given. During the summer months of 1894, *Lyngbya* and *Aphanizomenon* were the dominant algae. Blue-greens predominated in the summer of 1896, but diatoms predominated in 1895 and in 1897, except for August and September when *Lyngbya* was abundant. *Ceratium* was very abundant during the summers of 1895–96, but it was not important during the summers of 1894 and 1897. *Aphanizomenon* was abundant during the fall months of 1894 and 1896, lasting through the following winter months.

The next algal records came from extensive sampling by Birge and Juday (1922) during 1911–17. Samples were collected by a pump in order to obtain large volumes of plankton for organic matter analysis, but

the phytoplankton were concentrated through a net used for sampling zooplankton. In so doing, the smaller nanoplankton were lost. Between April 1915 and May 1917, Birge and Juday also analyzed the nanoplankton that passed through the net. The nanoplankton averaged three to four times more organic matter than that contained in the net plankton. These smaller plankters were concentrated by centrifugation, but buoyant blue-green algae probably were lost (Brock 1985). In Birge and Juday's net plankton samples, *Ceratium* was abundant during the late summers of 1911–12 and 1916. Blue-green algae were important at different times during the summers of 1911–17. In the nanoplankton samples, a small diatom (*Stephanodiscus* sp.) followed by cryptomonads (especially *Chroomonas* sp.) were abundant during the springs of 1915–17.

The first study focusing on severe algal blooms in Lake Mendota did not occur until the mid-1940s. Between October 1945 and September 1947, the major nutrient sources to the lake and the dominant species composing the phytoplankton were documented (Wisconsin Committee on Water Pollution 1949). Diatoms were the major component of the spring plankton and, as a group, occurred throughout both years. Cryptomonads and *Ceratium hirundinella* were relatively unimportant during the study period. Blue-green algal blooms caused by *Gloeotrichia echinulata* and *Microcystis aeruginosa* were dense in August and September 1946 and to a lesser extent in July 1947. At other times during the summer of 1947, algal production was fairly low. A bloom of *Gloeotrichia* also occurred in late June 1948 (Bardach 1951).

Information is scanty on Lake Mendota's phytoplankton populations between the late 1940s and the early 1970s. The most comprehensive study was conducted by Sager (1967) during 1965. Other data which we believe were obtained during this period could not be located. Sager recorded numerical and volume densities for all species, but his samples were concentrated through a net, so the smaller organisms were lost. Total biovolumes of the blue-green algae and *C. hirundinella* for the months of July through October indicated the importance of *Ceratium* in the summer plankton in 1965. *Anabaena spiroides* and *G. echinulata* were the dominant species in early July when the blue-greens were the most abundant. *Oscillatoria* sp. and *M. aeruginosa* were the most prominent blue-greens in late July and August. Other algae were not abundant until late August when the diatoms *Fragilaria crotonensis* and *Melosira italica* were also abundant. *Fragilaria* was the dominant alga in late September/early October.

Other accounts of algal blooms during these years are incomplete. Torrey (1972) found *Aphanizomenon flos-aquae* to be the major N<sub>2</sub>-fixing species present during the summers of 1970–71. She noted that previous researchers documented blooms of *Gloeotrichia* in July of 1961 and 1967. *Ceratium* was also very abundant during the early fall of 1961 (McNaught 1965).

A major study of the phytoplankton of Lake Mendota was conducted during 1976–81 by Brock (1985) and his students. Whole-lake biovolumes of different groups of algae were calculated from discrete samples integrated over depth. In the Discussion section of this chapter, we compare Brock's findings to the results of our 1976–89 phytoplankton record.

## Methods

### Data Collection and Tabulation

Phytoplankton data for 1976–87 were collected as part of a long-term limnological research study of the four Yahara River lakes, including Lake Mendota, by the Wisconsin Department of Natural Resources (WDNR) Bureau of Research. Samples were taken at Lake Mendota's deepest spot from a 0- to 2-m composite. For most years, sampling was conducted approximately every 2 weeks from ice-out in the spring until late fall and at least once during the winter months. In 1977–78 samples were collected monthly, and in 1987 samples were collected every week during the spring and summer months and biweekly during the fall.

The phytoplankton samples were preserved with Lugol's solution and later identified and enumerated using an inverted microscope (Utermöhl technique). Different volumes of the preserved samples were settled for this analysis, depending on the amount of chlorophyll *a* (Chl *a*) contained in the sample. For every sampling date, cell measurements were taken and averaged for each species, and cell volumes were computed from the appropriate geometric formulas. Biovolumes were computed from the numerical density of each species and its cell volume.

Beginning in 1987, the University of Wisconsin Center for Limnology (CFL) began collecting and analyzing phytoplankton for Lake Mendota. Sampling was conducted approximately weekly during the spring and summer months and less frequently during the fall. Samples were collected at the Deep Hole region from a 0- to 10-m composite. The CFL determined biovolumes by a technique similar to that used by the WDNR. Further information on CFL methods for phytoplankton analyses is given by Vanni et al. (Ch. 13).

We chose four major groups of algae to illustrate long-term trends in Lake Mendota's phytoplankton: blue-green algae, edible algae, *C. hirundinella*, and total biovolume. Edible algae were considered to be those species with cell volumes less than the volume of a 30-µm diameter sphere ( $14,100 \mu\text{m}^3$ ). However, species with extremely elongated shapes (e.g., *Synedra*) were not considered edible regardless of cell volume. Species that formed colonies were also excluded if the colony size exceeded the criterion.

**Table 7-1.** Phytoplankton ratios for WDNR/CFL based on paired 1987 samples. CFL data for 1988–89 were multiplied by the mean ratio to convert them to WDNR equivalents.

Group	N	Mean	SD	SEM
Blue-greens	15	0.403	0.278	0.072
Edible algae	6	0.591	0.145	0.059
<i>Ceratium hirundinella</i>	12	1.057	0.826	0.239
Total algal biovolume	24	0.608	0.286	0.058

Because it was desirable to have a continuous phytoplankton record for 1976–89, the 1987 data collected by the WDNR and CFL were compared in order to check for possible differences in analysis methods. This comparison showed significant differences for some algal groups. While similar species were recorded by both groups in 1987, differences in time of sampling, sampling depth, microscopes, and technicians resulted in different total biovolumes. Because small differences or biases in cell measurements translate into large differences in cell volumes, the CFL biovolume data were converted to WDNR biovolume data by using the 1987 data to develop biovolume ratios for all major groups of organisms (Table 7.1). This allowed merger of the WDNR data for 1976–87 with the CFL data for 1988–89.

Chl-*a* data for 1976–89 were obtained from the same 0- to 2-m composite samples collected as part of the WDNR's lake sampling program. Chl-*a* was determined after filtration through glass fiber filters and extraction in 90% acetone, using the trichromatic technique (Kopp and McKee 1979).

After the long-term databases for phytoplankton biovolumes and Chl-*a* were compiled, it was evident that the data for the summer of 1977 were misleading. The only sampling dates that represented summer conditions were 28 July and 1 September. The Secchi disk readings recorded on these two dates were 1.9 and 1.4 m, respectively. Numerous readings taken by Brock and his students (unpubl. data) during July and August averaged 1.2 m (corrected for disk size as discussed in Lathrop, Ch. 6). This average indicated that algal blooms were significantly worse than the 28 July WDNR reading.

In order to provide a truer representation of summer phytoplankton conditions in 1977, we converted Brock's Secchi data from four summer dates (27 June, 11 July, 8 August, and 22 August) to Chl-*a* based on the regression of WDNR Chl-*a* and Secchi disk data for 1976–89:

$$\log \text{Chl-}a = 1.751 - 1.415 (\log_{10} \text{Secchi}) \quad (1)$$

$R^2 = 0.64$ ; S.E.  $\hat{Y} = 0.253$ ;  $N = 220$ . Chl-*a* and Secchi disk (black/white 20-cm) units are  $\mu\text{g L}^{-1}$  and m, respectively. Phytoplankton total bio-

volumes ( $\mu\text{L L}^{-1}$ ) were computed for the four additional dates based on the regression of WDNR phytoplankton data for 1976–87:

$$\begin{aligned}\log \text{TotBiov} = & 1.154 - 1.665 (\log_{10} \text{Secchi}) - 0.00409 (\% \text{Edbl}) \\ & - 0.00239 (\% \text{BG})\end{aligned}\quad (2)$$

$R^2 = 0.56$ ; S.E.  $\hat{Y} = 0.339$ ;  $N = 190$ . Data on percent edible algae (%Edbl) and percent blue-green algae (%BG) were obtained from appendices in Brock (1985) that summarized phytoplankton species bio-volumes in integrated water column samples for the four dates. *Ceratium* was not recorded on those dates.

Concentration data for phosphorus (P), nitrogen (N), and silica (Si) were also obtained by the WDNR during their regular sampling program. Water samples were collected in a 2.2-L Plexiglas Kemmerer at discrete depths. Surface concentration data presented in this chapter are averages of samples obtained at 0 and 4 m for most years during the open-water period. During the ice-covered period, data are from samples collected at 1–5 m.

Water samples were analyzed for total phosphorus (TP) and total reactive phosphorus (TRP), and nitrate ( $\text{NO}_3\text{-N}$ ), nitrite ( $\text{NO}_2\text{-N}$ ), ammonium ( $\text{NH}_4\text{-N}$ ), and organic nitrogen (ON) at the WDNR Delafield Research Laboratory during 1976–79. Analytical methods followed commonly accepted procedures and were summarized by Lillie and Mason (1983). Beginning in 1980, water samples were analyzed at the State Laboratory of Hygiene (SLH) using U.S. Environmental Protection Agency prescribed procedures (Kopp and McKee 1979). Analyses performed were TP, dissolved reactive phosphorus (DRP), nitrite + nitrate (henceforth called  $\text{NO}_3\text{-N}$ ),  $\text{NH}_4\text{-N}$ , and ON (determined by subtracting  $\text{NH}_4\text{-N}$  from Kjeldahl nitrogen).

Because of differences between the earlier and later laboratory procedures, data from early years were excluded from time series analyses of certain nutrient constituents. For the 1976–79 Delafield lab data, samples were refrigerated but were not preserved chemically. Holding times averaged about 1 week until the samples were analyzed. Because we were concerned about possible changes during storage, TRP,  $\text{NO}_3\text{-N}$ , and  $\text{NH}_4\text{-N}$  data from 1976–79 were excluded from time series analyses. TP and total nitrogen (TN) data were considered reliable because large changes in the dissolved components were not found in a study of the laboratory's holding times, and a year-long split sample check with the SLH resulted in good correspondence for both TP and TN (R. Lathrop, unpubl. data). SLH laboratory detection limits for TP were lowered from  $<0.01$  to  $<0.004 \text{ mg PL}^{-1}$  in April 1983, but the early data from both labs were precise enough for the time series analyses.

A check was also made to determine differences between TRP and DRP in the earlier lab data. Paired analyses during 1978–79 from Lake Monona indicated that TRP averaged slightly higher (ca.  $0.010 \text{ mg PL}^{-1}$ ) than DRP, which was filtered within 6 h after sample collection. After

1980, when the water analyses were performed at the SLH, holding times for DRP have been less than 24 h. Sample filtration usually was done the morning after sampling. Beginning in 1981, all nitrogen constituents and TP were preserved with sulfuric acid in the field, which allowed for longer laboratory holding times. Because of possible biases in the earlier data, DRP, NH<sub>4</sub>-N, and NO<sub>3</sub>-N data are only presented for 1980–89. Detection limits were <0.004, <0.02, and <0.02 mg L<sup>-1</sup>, respectively.

Dissolved reactive silica (DRSi) values are also presented for surface water samples analyzed in 1985–89 at the SLH. DRSi data were available for 1979–84, but the detection limits were not low enough to detect periods of Si depletion in the lake. Consequently, no time series analyses were performed on the DRSi data.

Temperature profiles for 1976–89 were used to calculate the Schmidt stability factor,  $S$ , as an index of the susceptibility of the water column to mixing by the wind.  $S$  is proportional to the amount of work required to mix the lake and also to how far the center of mass of the lake has been lowered by thermal stratification.  $S$  is zero when the lake is isothermal and reaches maximum values during summer stratification. Temperature profiles for 1976–88 were compiled by Robertson (1989) at 1-m intervals from data collected by the WDNR. We compiled profiles for 1989 from data collected by the WDNR and CFL at the same intervals. Computation of stability from these profiles followed the formula given by Likens (1985):

$$S = A(0)^{-1} \sum (z - z^*) ((z) - \rho^*) A(z) \Delta Z \quad (3)$$

where the summation is taken over all depths ( $z$ ) at interval  $\Delta z = 1$  m.  $A(z)$  is the lake area at depth  $z$ ,  $\rho(z)$  is density as calculated from temperature at depth  $z$ ,  $\rho^*$  is the lake's mean density, and  $z^*$  is the depth at which the mean density is found.

### Statistical Analysis

Each of our observed time series is a mixture of trend, seasonal, auto-correlational, and residual components (Brockwell and Davis 1987). The purpose of time series analysis is to separate these components and use them to examine relationships among variates (Jassby and Powell 1990). From the many analyses that might be informative, we have chosen a select few that pertain to the objectives of this book. We regard these results as the first steps in a more extensive analysis to be developed elsewhere.

To facilitate time series analysis, equispaced series were constructed. For each variate, each year was divided into 13 4-week “months.” In this chapter, “month” refers to this 4-week interval, not to a calendar month. The value for a month was taken as the mean of all observations of the variate during that month. For some months in some years (correspond-

ing to the calendar months December, January, and February), no data were available. In such cases, the mean for that month over all years was substituted for the missing value. This substitution is an ecologically reasonable way of approximating missing observations that makes it possible to analyze the data by conventional time series techniques. Substitutions contributed to the seasonal component of the time series models. Our approach is conservative in the sense that the substitutions made it more difficult to detect shifts in the series or relationships among the series. However, significant shifts or relationships were still detectable despite our protocol used for missing values.

Time series analyses presented here test for relationships between the stability and phosphorus time series and selected algal time series. They also examine the statistical significance of apparent shifts in the nutrient and blue-green algal time series. Computations were performed using the ARIMA procedure of the Statistical Analysis System (SAS Institute 1988), Systat (Wilkinson 1988), the programs provided with Brockwell and Davis (1987), and original programs written at the CFL.

Forecasting equations were developed by fitting autoregressive, integrated, moving-average (ARIMA) models following the guidelines of Box and Jenkins (1976), Brockwell and Davis (1987), and Wei (1990). For each variate, we examined several alternative models. All time series could be fit by the seasonal autoregressive model:

$$(1 - \phi_1 B_1 - \phi_2 B_2)(1 - \phi_{13} B_{13})Z(t) = a(t) \quad (4)$$

where  $Z(t)$  is the observed time series and  $a(t)$  is a series of residuals. Models were selected and fit so that residuals were distributed approximately normally with nonsignificant autocorrelation and partial autocorrelation functions.  $B$  is the backshift operator;  $B_x Z(t) = Z(t - X)$ . The model for autocorrelation involves the autoregressive parameters  $\phi_1$  and  $\phi_2$ , and seasonality is accounted for by the parameter  $\phi_{13}$ . In most cases reported here, the lag 2 autoregressive term ( $\phi_2 B_2$ ) was nonsignificant and was removed from the model.

Intervention analysis tests for a shift in a time series following a perturbation or manipulation (Box and Tiao 1975; Wei 1990). A model is fit that accounts for the seasonality and autocorrelation in the time series and includes coefficients for the effects of the intervention. If the intervention coefficients appear significant statistically, then the analysis implies that a nonrandom change occurred after the intervention. Our intervention analyses employed the model:

$$(1 - \phi_1 B_1 - \phi_2 B_2)(1 - \phi_{13} B_{13})Z(t) = a(t) + aS_1 \quad (5)$$

where  $Z(t)$  is the time series of the response variable and  $a(t)$  is the residual time series. The left-hand side of the equation is the same seasonal autoregressive model described above. The intervention par-

ameter is  $\alpha$ . The dummy variable  $S_1$  is zero prior to the intervention and one afterwards. Thus  $\alpha$  represents the magnitude of the step-change shift in level of the response variable following the intervention.

Relationships among time series were examined using cross-correlation functions and transfer functions. Cross-correlation functions of the raw series are strongly influenced by the phenological sequence of seasonal events. They are useful for illustrating the correlations and lags implicit in the seasonal sequence, but do not necessarily show how two variates affect each other.

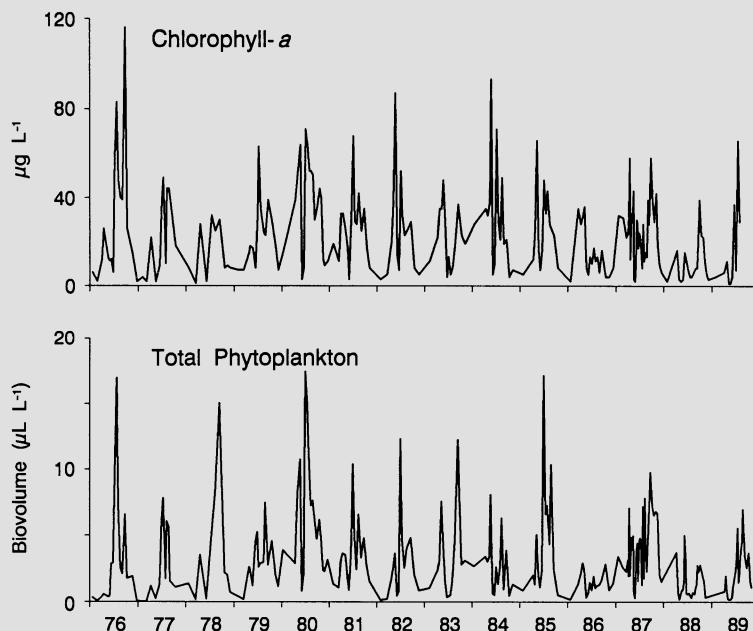
Predictive links among variates can be demonstrated by showing that anomalies (i.e., deviations from typical seasonal patterns) in one variate are followed by anomalies in the other variate. The procedures used to identify transfer functions can be used to test for such predictive links (Box and Jenkins 1976). Briefly, an ARIMA model is fit to the series for the predictor variate, and the residuals are calculated. Then the same ARIMA model, or filter, is applied to the series for the response variate, and the residuals are calculated. The cross-correlation function for the two sets of residuals is then computed. Significant cross-correlations at positive lags indicate that the predictor variate is a leading indicator of the response variate. Therefore a forecasting model for the response variate that includes terms for the predictor variate will have significantly smaller errors than a forecasting model based on the response variate alone.

To study the relationships of phosphorus and Schmidt stability to algal concentrations, we examined cross-correlation and transfer functions for DRP, TP, total nitrogen to total phosphorus (N:P) ratio, and algal variates. We recognize that correlations involving TP are potentially circular because, in summer, all phosphorus is in algae or soon will be, so TP and algal biomass measure the same thing (Carpenter et al. 1991). Phosphorus concentrations shortly after ice-out, however, can be a reasonable surrogate for loading rates (Carpenter et al. 1991). Sterner (1991) argues that DRP concentrations are monotonically related to phosphorus supply rates.

Our transfer functions used the model:

$$(1 - \phi_1 B_1 - \phi_2 B_2) (1 - \phi_{13} B_{13}) Y(t) = [(\omega_0 - \omega_2 B_2) X(t - S)/(1 + \delta)] + a(t) \quad (6)$$

where  $Y(t)$  is the time series for the response variable,  $X(t - S)$  is the time series for the input variable, and  $a(t)$  is the time series of the residual.  $S$  is the shift (in months) of the predictor series relative to the response series. The left-hand side of the equation is an autoregressive model for seasonality and autocorrelation. The bracketed terms on the right-hand side account for the effect of the input on the response variable. In most cases, satisfactory fits could be achieved using fewer parameters than we have listed in equation 6.



**Figure 7-2.** Chl-*a* concentrations and total phytoplankton biovolumes in the surface waters of Lake Mendota during 1976–89.

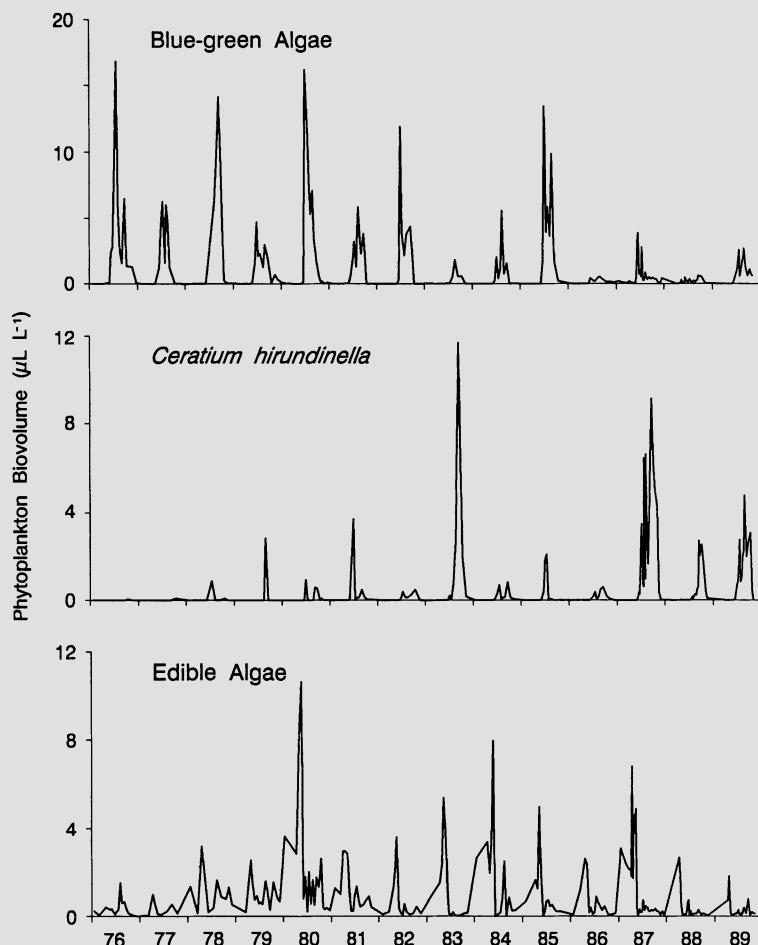
## Results

### Interyear Patterns

Chl-*a* and total phytoplankton biovolume data indicate widely variable seasonal patterns (Figure 7.2). Seasonal minima usually occurred during the winter months and briefly sometime during late spring (May–June), a period referred to as the spring clear-water phase. Peaks of Chl-*a* or total biovolume occurred in early spring and mid- to late summer of most years.

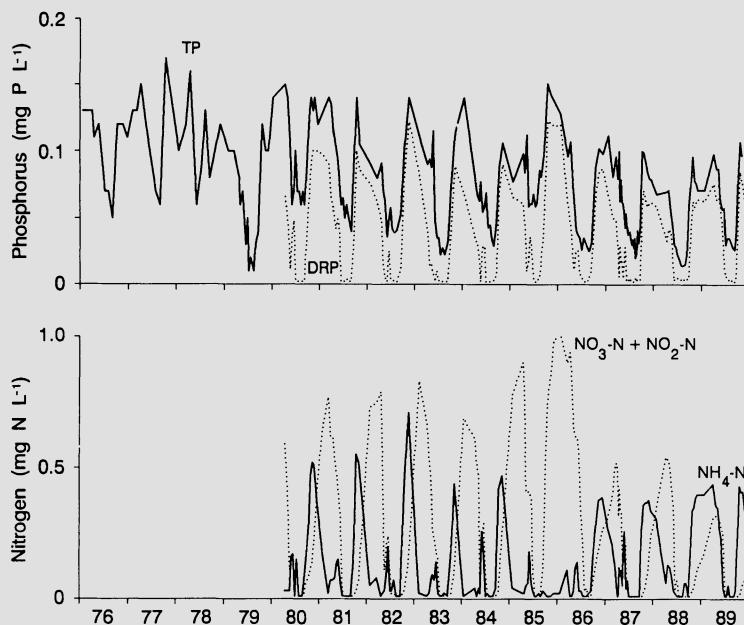
Blue-green algae were abundant during the summers of 1976–85, except for 1983 (Figure 7.3). Blue-green algae were unimportant during the summers of 1986 and 1988 and late summer 1987. *Ceratium hirundinella* exhibited short-term population increases in most years during late summer/early fall. Populations were notably large in 1983 and 1987. Biovolumes of edible algae were greatest in the early spring before the clear-water phase.

Surface water concentrations of TP and DRP exhibited regular seasonal patterns (Figure 7.4). Concentrations were lowest during the summer months, with DRP often below analytical detection ( $<0.004 \mu\text{g L}^{-1}$ ). TP



**Figure 7-3.** Biovolumes of blue-green algae, *Ceratium hirundinella*, and edible algae in the surface waters of Lake Mendota during 1976–89.

and DRP increased dramatically by early October after thermal stratification ended, because large concentrations of hypolimnetic DRP were mixed throughout the entire water column (Sonzogni 1974; Lathrop, Ch. 6). TP and DRP remained high until the following spring, when DRP began declining because of algal uptake. TP declined through direct sedimentation of larger algal species and through herbivore grazing, particularly by *Daphnia*, on smaller edible species (Vanni et al., Ch. 13). This grazing resulted in the sedimentation of fecal material as evidenced by degraded algal pigments in sedimentation traps (Hurley et al., Ch. 5). While the decline in DRP from early spring to summer was rapid, a minor increase occurred during the time of peak *Daphnia* abundance in

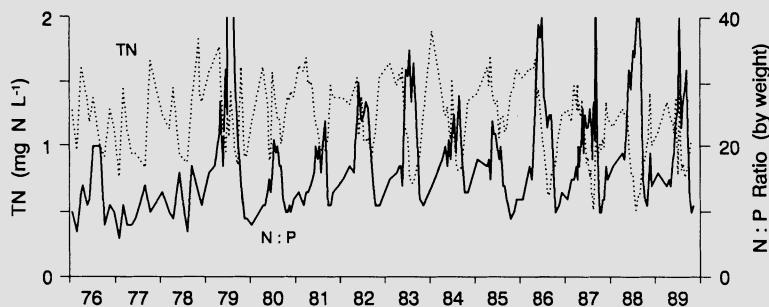


**Figure 7-4.** TP, DRP,  $\text{NH}_4\text{-N}$ , and  $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$  concentrations in the surface waters of Lake Mendota during 1976–89.

May–June. DRP concentrations in 1980–89 normally were lower by early April than during the previous fall or winter months, except in 1989 when spring runoff loadings increased concentrations in the lake (Lathrop, Ch. 6).

Long-term trends in phosphorus were discussed by Lathrop (Ch. 6). Unusually low TP in Lake Mendota's surface waters in the summer of 1979 may have been the result of a double thermocline restricting internal recycling to those waters. While these conditions were also noted by R.E. Stauffer (pers. comm.), Brock (1985) did not report low TP surface concentrations. Chl-*a* and algal biovolume data during the summer of 1979 were also not unusually low (Figure 7.2), which indicated that the overall lake trophic status that summer was not improved.

Inorganic N concentrations in Lake Mendota's surface waters also exhibited regular patterns (Figure 7.4). Both  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  were near or below analytical detection ( $<0.02 \mu\text{g L}^{-1}$ ) during the summer months.  $\text{NH}_4\text{-N}$  increased after destratification because of high concentrations that accumulated in the hypolimnion prior to mixing. Surface water  $\text{NO}_3\text{-N}$  concentrations began increasing by late fall and early winter as  $\text{NH}_4\text{-N}$  declined, which was probably the result of nitrification. Algal uptake also most likely contributed to the decline of  $\text{NH}_4\text{-N}$  as well as causing the spring decline of  $\text{NO}_3\text{-N}$  before the low summer concen-

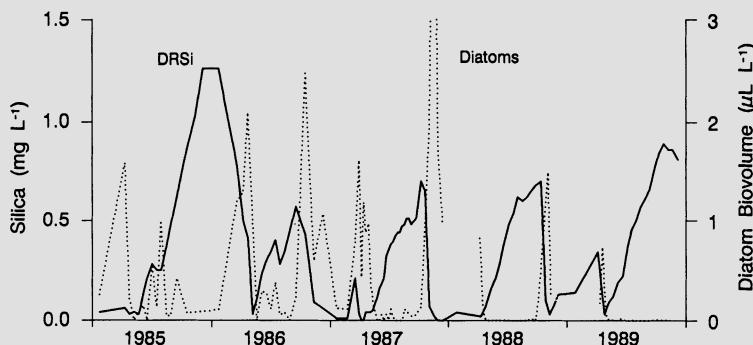


**Figure 7-5.** TN concentrations and total N:P ratios (by weight) in the surface waters of Lake Mendota during 1976–89.

trations were achieved. Coinciding with peak *Daphnia* densities in May–June, a noticeable increase of NH<sub>4</sub>-N occurred, which was probably the result of excretion.

Although these inorganic N patterns were consistent in 1980–89, some differences also occurred. In the fall of 1985, NH<sub>4</sub>-N did not increase in the surface waters, while NO<sub>3</sub>-N increased earlier than normal and to much higher concentrations, indicating that nitrification must have occurred rapidly during destratification. Hypolimnetic temperatures were very high that summer, and blue-green algal blooms persisted later than normal into the fall. Other noteworthy differences occurred during the winter and spring months of 1987–89. NH<sub>4</sub>-N concentrations were not depleted as rapidly in early spring as in earlier years, particularly in 1988–89, and winter maximum NO<sub>3</sub>-N concentrations were not as high. In 1989, NH<sub>4</sub>-N was higher in early spring than in winter, which may have been the result of spring runoff that year. The much longer duration of NH<sub>4</sub>-N in the springs of 1988–89 could have been caused by: (1) less NH<sub>4</sub>-N uptake because of reduced algal biomass, and (2) more excretion of NH<sub>4</sub>-N because of the longer duration of the *Daphnia pulicaria* population peak.

TN also exhibited a seasonal pattern, with highest concentrations occurring from late fall through early spring (Figure 7.5). A slight decrease in TN was observed in 1987–89 as compared to 1976–86. Total N:P ratios were highly seasonal, with the highest ratios usually occurring during the summer months when TP was at its seasonal minimum. The highest summer ratios (>30:1) occurred in 1983 and 1986–89 during periods when algal biomass was low. The high ratios in the summer of 1979 were the result of the abnormally low surface TP concentrations, which were not characteristic of the whole epilimnion that year. Consequently total N:P ratios were heavily influenced by the seasonal cycles of DRP. The lowest ratios were not associated with blue-green algal



**Figure 7-6.** DRSi concentrations and diatom biovolumes in the surface waters of Lake Mendota during 1985–89.

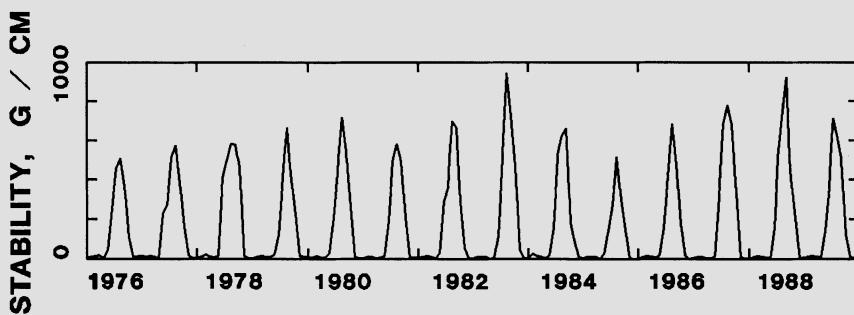
blooms. A more thorough analysis of nitrogen and phosphorus nutrient dynamics for 1987–89 is given in Vanni et al. (Ch. 13).

DRSi concentrations and diatom biovolumes each exhibited wide fluctuations during 1985–89 (Figure 7.6). After a seasonal minimum in the spring, DRSi increased steadily throughout the summer in the surface waters even before destratification could have augmented concentrations from the hypolimnetic buildup. In the falls of 1986–88, diatom blooms rapidly depleted DRSi before ice cover. In the falls of 1985 and 1989, diatom blooms did not occur, and DRSi remained high into the winter months. In 1985–89, early spring diatom blooms occurred and rapidly depleted DRSi concentrations. In some years, these blooms began during late winter under the ice, so that DRSi concentrations were already low by the time the lake was sampled soon after ice-out. Concentrations normally increase under the ice in waters near the bottom sediments, providing additional DRSi for the development of an early spring diatom bloom.

Schmidt stability ( $S$ ) varied by a factor of 2 among the 14 summers studied (Figure 7.7). The years with highest Schmidt stability (1983 and 1988) had very low blue-green algal biovolume and no blooms. The year with lowest Schmidt stability (1985) had relatively high blue-green algal biovolume and a series of intensive blooms. Although years of extremes in stability were years with extremes of blue-green algal biovolume, the simple correlation of mean summer stability with mean summer blue-green algal biovolume was marginal ( $r = -0.517$ ,  $df = 12$ ,  $p = 0.058$ ).

### Intrayear Patterns

Algal populations in 1980 followed a seasonal pattern that was very common in Lake Mendota (Figure 7.8). The spring algae were dominated by cryptophytes and chrysophytes (almost exclusively diatoms). The



**Figure 7-7.** Schmidt stability ( $\text{g cm}^{-1}$ ) of Lake Mendota, 1976–89.

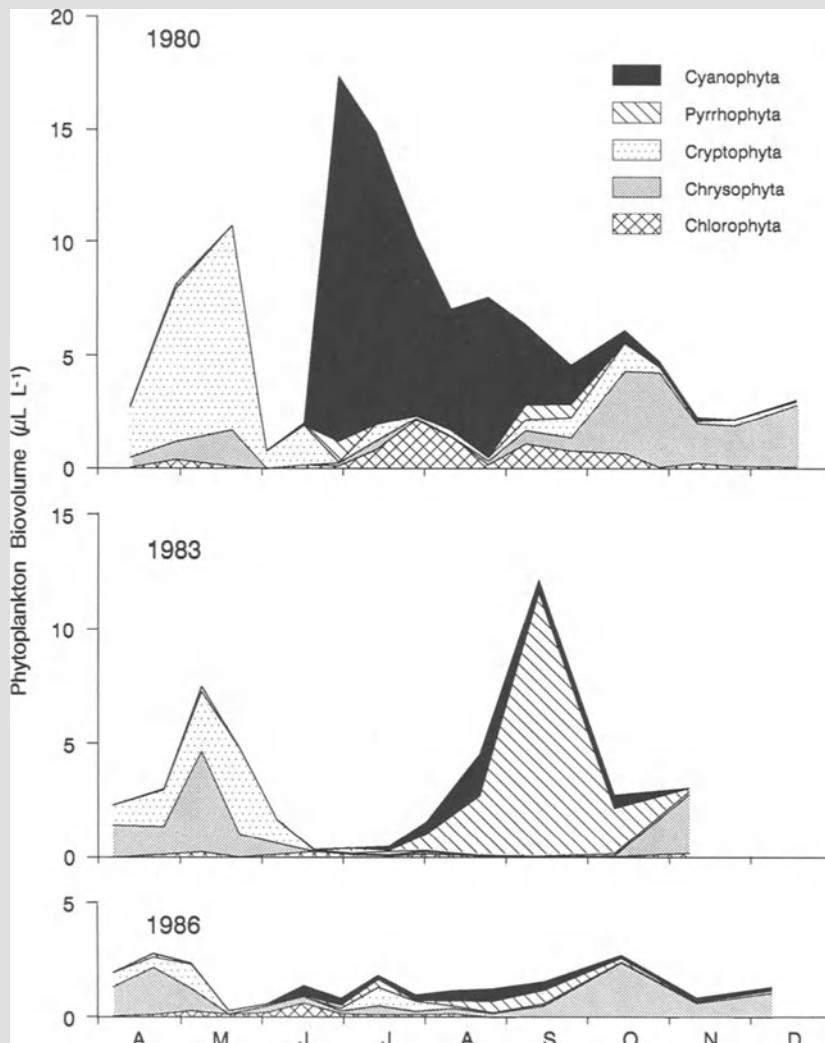
clear-water phase occurred in early June before a massive blue-green algal bloom developed in early July. This bloom declined by late July, but blue-green algae still dominated the plankton into September. By mid-October, diatoms predominated. This pattern of cryptophytes and diatoms in the early spring, followed by a late spring clear-water phase, followed by a summer blue-green algal bloom, followed by a fall increase in diatoms was typical for many years, among them 1976–82, 1984–85, and 1989.

In 1983, spring and fall algal populations were similar to that in most years (Figure 7.8). However, this was the first summer since the records began in 1976 that did not experience a large bloom of blue-green algae. By August, a bloom of *C. hirundinella* (Pyrrhophyta) began, which lasted into October. A similar large bloom of *Ceratium* also occurred during the late summer of 1987 (Figure 7.3).

In 1986, the spring and fall succession of phytoplankton was typical of that in other years, but no single group of algae (including blue-green algae) dominated throughout the summer months. Total biovolumes were low. This lack of any significant blue-green algal bloom also was characteristic of the summer of 1988, when water clarity was the greatest for all summers during 1976–89 (Lathrop, Ch. 6).

### Bloom Species

Numerous species were recorded during 1976–89 with biovolumes  $>0.5 \mu\text{L L}^{-1}$  (Tables 7.2 and 7.3). As a group, the Chlorophyta were least important, with only *Sphaerocystis* sp. occurring once throughout the study period with a biovolume  $>2 \mu\text{L L}^{-1}$ . The Chrysophyta, represented mostly by diatoms, had two species (*Stephanodiscus niagarae* and *S. tenuis*) that occurred almost every year in the plankton. Their biovolumes rarely exceeded  $2 \mu\text{L L}^{-1}$ . The smaller *S. tenuis* was part of the edible fraction, whereas the much larger *S. niagarae* was inedible by



**Figure 7-8.** Biovolumes of major phytoplankton groups in 0- to 2-m water depth of Lake Mendota during 1980, 1983, and 1986.

the biovolume size criterion. Two species of Cryptophyta, *Cryptomonas ovata* and *Chroomonas acuta*, were important in the plankton throughout the study and occasionally occurred with biovolumes  $>2 \mu\text{L L}^{-1}$ . They were particularly important in the spring plankton and to a lesser extent in the fall plankton. Both species were edible.

The Cyanophyta as a group were the most important bloom-forming species in 1976–89 during the summer months. Only in 1983, 1986, and 1988 were blue-green algal species not recorded  $>2 \mu\text{L L}^{-1}$ . Because

**Table 7-2.** Species composition and yearly maximum biovolume of phytoplankton blooms occurring in Lake Mendota during 1976-89.

Species	Maximum biovolume for each year <sup>a</sup>									
	1976	77	78	79	80	81	82	83	84	85
Chlorophyta										
<i>Actinastrum hantzschii</i>	-	-								
<i>Chlamydomonas</i> sp.										-
<i>Closterium aciculare</i>					-					
<i>Coelastrum microporum</i>					-	-				
<i>Cosmarium</i> spp.					-	-				
<i>Dityosphaerium pulchellum</i>					-					
<i>Sphaerocystis</i> spp.					-					
<i>Oocystis</i> spp.					-					
<i>Staurastrum</i> sp.					-					
Chrysophyta										
<i>Cyclorella</i> spp.					-					
<i>Erkenia subaequiciliata</i>					+					
<i>Fragilaria</i> spp.					-	-				
<i>Melosira</i> spp.					-	+	-			
<i>Stephanodiscus niagarae</i>					-	-	-	-		
<i>Stephanodiscus tenuis</i>					-	-	-	-		

Table 7.2. Continued

Species	Maximum biovolume for each year <sup>a</sup>							
	1976	77	78	79	80	81	82	83
Cryptophyta	—	—	*	+	—	+	—	+
<i>Cryptomonas</i> spp. <sup>b</sup>	—	—	*	+	—	+	—	—
<i>Chroomonas</i> spp. <sup>c</sup>	—	—	*	+	—	+	—	—
Cyanophyta	—	—	+	—	+	—	—	—
<i>Anabaena spiroides</i>	—	—	+	—	*	—	+	*
<i>Aphanizomenon flos-aquae</i>	*	—	+	—	*	—	+	+
<i>Chroococcus</i> spp.	—	—	+	—	*	—	+	—
<i>Coelosphaerium naegelianum</i>	—	—	+	—	+	—	—	—
<i>Microcystis aeruginosa</i>	—	—	*	+	+	—	*	+
<i>Oscillatoria</i> spp. <sup>d</sup>	—	—	*	+	+	+	—	—
Pyrrophyta	—	—	+	—	+	—	+	—
<i>Ceratium hirundinella</i>	—	—	+	—	+	—	+	—
<i>Glenodinium gymnodinium</i>	—	—	—	—	*	—	—	*
Number of sampling dates	20	8	10	14	18	16	14	15
							14	17
							15	33
							17	33
							28	17

<sup>a</sup> Biovolumes ( $\mu\text{L L}^{-1}$ ) are categorized as: (—) 0.50–1.99; (+) 2.00–4.99; (×) 5.00–7.99; (\*)  $\geq 8.00$ .<sup>b</sup> Mostly *Cryptomonas ovata*, also *C. erosa* and *C. marsamii*.<sup>c</sup> Mostly *Chroomonas acuta*.<sup>d</sup> Mostly *Oscillatoria agardhii*.

**Table 7-3.** Species composition and frequency of occurrence of major phytoplankton blooms occurring in Lake Mendota during 1976–89.

Species	Bloom frequency expressed as number of sampling dates with biovolumes ( $\mu\text{L L}^{-1}$ ) <sup>a</sup> in the ranges:		
	2–5	5–8	>8
Chlorophyta			
<i>Sphaerocystis</i> sp.	0	1	0
Chrysophyta			
<i>Cyclotella</i> sp.	2	0	0
<i>Fragilaria</i> sp.	1	0	0
<i>Stephanodiscus niagarae</i>	2	1	0
<i>Stephanodiscus tenuis</i>	2	0	0
Cryptophyta			
<i>Cryptomonas ovata</i>	5	1	1
<i>Chroomonas acuta</i>	3	0	1
Cyanophyta			
<i>Anabaena spiroides</i>	2	0	0
<i>Aphanizomenon flos-aquae</i>	8	3	6
<i>Chroococcus</i> sp.	1	0	0
<i>Microcystis aeruginosa</i>	9	0	1
<i>Oscillatoria agardhii</i>	8	0	1
Pyrrhophyta			
<i>Ceratium hirundinella</i>	18	4	2

<sup>a</sup>Total number of sampling dates = 238.

sampling was only conducted monthly during the summer of 1977, major blooms were apparently missed. Brock (1985) reported extensive blue-green algal blooms throughout that summer. Blooms  $>5 \mu\text{L L}^{-1}$  were recorded in 1976, 1978, 1980, 1982, 1985, and 1989; blooms  $>8 \mu\text{L L}^{-1}$  were recorded in all of those years except for 1989. *Aphanizomenon flos-aquae* was the species found most frequently in massive bloom densities; it was found on nine occasions with biovolumes  $>5 \mu\text{L L}^{-1}$ . It was also very abundant during the summer of 1977 (Brock 1985). *Microcystis aeruginosa* and *Oscillatoria agardhii* were the next most important bloom-forming species, but each of them was found only once at massive densities. *Microcystis* was also abundant during 1977 (Brock 1985). Other blue-green algae were much less important contributors to summer blooms. All species of blue-green algae were considered inedible, except for some species of *Chroococcus*. While most dense growths of blue-green algae occurred during the summer months of 1976–89, blooms during other seasons were rare. *Microcystis* continued blooming into October of 1985. However, beginning in late October 1989, at the end of the period covered in this volume, a bloom of *Aphanizomenon* began and

**Table 7-4.** Results of intervention analysis for shifts in 1986 of the time series for dissolved reactive phosphorus (DRP), total P (TP), total (N:P) ratio nitrogen to phosphorus, and blue-green algal biovolume (BGA). Parameter estimates, asymptotic standard errors, and *t*-ratios are presented. Because of the large number of degrees of freedom, *t*-ratios larger than 1.96 indicate that the parameter is significantly different from zero at the 5% level.

Variate	Parameter	Estimate	SE	<i>t</i> -ratio
DRP	$\phi_1$	0.434	0.069	6.25
	$\phi_{13}$	-0.480	0.068	7.05
	$\alpha$	-14.48	7.40	1.96
TP	$\alpha$	-0.108	0.171	0.63
N:P	$\phi_1$	0.614	0.059	10.42
	$\phi_{13}$	0.292	0.073	3.98
	$\alpha$	0.973	3.349	0.29
BGA	$\phi_1$	0.481	0.065	7.36
	$\phi_{13}$	0.373	0.069	5.42
	$\alpha$	-525.2	742.6	0.71

remained viable under the ice before developing into a massive bloom that continued through the entire spring season of 1990.

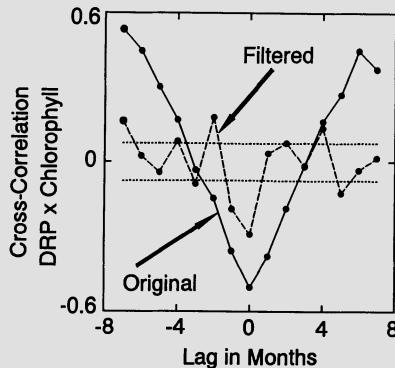
The last group of significant bloom-forming algae was the Pyrrhophyta, particularly *Ceratium hirundinella*. As previously discussed, it occurred in the summer or early fall plankton in most years and had massive blooms during 1983 and 1987. Only *Aphanizomenon* was found with biovolumes  $>5\text{ }\mu\text{L L}^{-1}$  more frequently than *Ceratium*. *Ceratium* was found more frequently than any other species with biovolumes  $>2\text{ }\mu\text{L L}^{-1}$ . *Ceratium* was considered inedible because of its large cell size and irregular shape.

### Time Series Analysis

The apparent shifts that occurred in some of the time series after 1986 are not substantially larger than the noise in the data (Table 7.4). The decline in DRP was marginally significant. Changes in TP, N:P ratio, and blue-green algal biovolume were not detectable statistically.

Cross-correlations of physical-chemical and algal variates were dominated by the seasonal cycle. For example, consider the cross-correlations of DRP with Chl-*a* (Figure 7.9). Correlations are negative at small lags, because DRP is low when algae are abundant and high when algal concentrations are low. At lags of about 6 months, correlations are positive: high DRP concentrations are followed by high algal concentrations in about 6 months. These seasonal patterns are strongly developed in the dataset.

To determine whether anomalies in DRP are followed by anomalies in Chl-*a*, the DRP series and the Chl-*a* series were filtered using the same



**Figure 7.9.** Cross-correlations versus lag in months for dissolved reactive phosphorus (DRP) and Chl-*a* concentrations. The original cross-correlation function (solid line) was calculated using the untransformed series. The filtered cross-correlation function (dashed line) was calculated from the residuals of both series filtered using the ARIMA model for DRP. Horizontal dashed lines indicate one standard error above and below zero. Significant correlations at positive lags indicate that DRP is a leading indicator of Chl-*a*.

time series model, and cross-correlation functions were computed for the residuals. Significant negative correlations occurred at lag zero, indicating that high algal biovolume was accompanied by low DRP, and low algal biovolume was accompanied by high DRP (Figure 7.9). Significant correlations at positive lags would indicate that DRP was a leading indicator of Chl-*a* concentration. Cross-correlations at positive lags are only slightly larger than the standard errors and include both positive and negative values.

Cross-correlations of physical-chemical variates with algal variates were examined to search for possible predictive relationships. In all cases, time series filters were used to remove seasonal patterns. Transfer functions were fit to evaluate the predictive value of relationships evident in the cross-correlations.

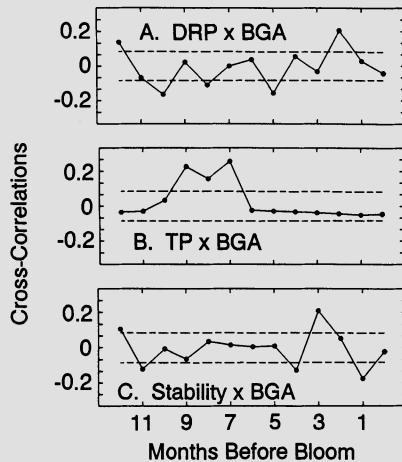
The transfer function for effects of DRP on Chl-*a* has a significant negative parameter at lag 0 (Table 7.5). To be useful in forecasting, a leading indicator should have significant parameters at positive lags. Even though DRP and Chl-*a* are significantly related, there is no evidence that DRP concentration is useful for forecasting future Chl-*a* concentrations in Lake Mendota.

The relationship between DRP and edible algal biomass is similar to that for Chl-*a* (Table 7.5). Because edible algae are efficient at taking up DRP, the variates are negatively related at lag 0 and are unrelated at other lags. The relationship between edible algae and total P is not significant. N:P ratio had no significant cross-correlations with edible biovolume, so no attempt was made to estimate a transfer function.

**Table 7-5.** Transfer functions for effects of dissolved reactive phosphorus (DRP) on Chl- $a$ , DRP on edible biovolume (Ed), total phosphorus (TP) on Ed, DRP on blue-green algal biovolume (BGA), TP on BGA, and Schmidt stability on BGA. For each independent (predictor) variate, the magnitude of the shift,  $S$  (in months), is given in parentheses. Because of the large number of degrees of freedom,  $t$ -ratios larger than 1.96 indicate that the parameter is significantly different from zero at the 5% level.

Indep. variate	Dependent variate	Parameter	Estimate	SE	$t$ -ratio
DRP ( $S = 0$ )	Chl- $a$	$\phi_1$	0.172	0.076	2.27
		$\phi_2$	0.243	0.077	3.15
		$\phi_{13}$	-0.512	0.068	7.57
		$\omega_0$	-0.280	0.061	4.60
DRP ( $S = 0$ )	Ed	$\phi_1$	0.391	0.072	5.46
		$\phi_{13}$	-0.454	0.068	6.64
		$\omega_0$	-10.7	4.50	2.39
TP ( $S = 5$ )	Ed	$\phi_1$	0.405	0.069	5.88
		$\phi_{13}$	0.451	0.067	6.73
		$\omega_0$	0.110	0.061	1.81
DRP ( $S = 0$ )	BGA	$\phi_1$	0.368	0.073	5.04
		$\phi_{13}$	-0.564	0.063	8.91
		$\omega_0$	-9.05	8.05	1.12
		$\omega_2$	-23.9	8.11	2.94
TP ( $S = 7$ )	BGA	$\phi_1$	0.475	0.068	7.03
		$\phi_{13}$	0.345	0.072	4.82
		$\omega_0$	0.561	0.117	4.78
		$\delta$	0.629	0.141	4.47
Stability ( $S = 1$ )	BGA	$\phi_1$	0.383	0.074	5.20
		$\phi_{13}$	-0.538	0.066	8.16
		$\omega_0$	-4.01	1.55	2.58
		$\omega_2$	-4.05	1.56	2.60

DRP, TP, and Schmidt stability have significant relationships with blue-green algal biomass that are useful in forecasting (Table 7.5). These relationships are illustrated by correlations of the time series after filtering to remove seasonal and autoregressive components (Figure 7.10). Anomalies in DRP are positively related to anomalies in blue-green algal biovolume 2 months later. Conversely, anomalies in N:P ratio were negatively related to anomalies in blue-green biovolume two months later. This correlation was due to the dynamics of phosphorus rather than nitrogen. Therefore, we did not attempt to fit a transfer function using N:P ratio. Schmidt stability tended to be unusually low 1 month before blue-green algal blooms, but unusually high 3 months before blooms. Anomalously high TP occurred 7 to 9 months before blue-green algal blooms. Concentrations of TP during winter are thus a harbinger of summer blooms of blue-green algae. Transfer functions for effects of



**Figure 7-10.** Cross-correlations versus months before blue-green algal blooms in Lake Mendota. All time series were filtered using ARIMA models. Significant correlations in months before the blooms indicate leading indicators useful for forecasting. Horizontal dotted lines indicate one standard error above and below zero. A. Dissolved reactive phosphorus (DRP) versus blue-green algal biomass (BGA). B. Total phosphorus (TP) versus blue-green algal biomass (BGA). C. Schmidt stability versus BGA.

DRP, TP, and Schmidt stability on blue-green algal biovolume all have significant terms at positive lags useful for forecasting (Table 7.5).

## Discussion

### Phytoplankton Community Dynamics

Blue-green algal blooms have been reported for Lake Mendota for many years dating back to at least 1882, when the first observations were made. However, while massive blooms occurred in some years, blue-green algal populations were relatively minor in other years immediately preceding or following the blooms. Reasons for these varying bloom densities could not be deduced from information contained in past studies. The lack of extensive sampling and quantitative data collection prevents any determination of frequency of bloom years for the period prior to 1976. However, an increase in phosphorus concentrations in Lake Mendota after the mid-1940s and an initiation of a study focusing on nuisance algal blooms in the lake after that time suggest that blooms may have been more severe or more frequent in recent decades (Lathrop, Ch. 6).

Many species of blue-green algae have formed blooms in past years. *Aphanizomenon flos-aquae*, *Microcystis aeruginosa*, *Anabaena* spp., *Gloeotrichia echinulata*, and *Lyngbya* spp. were most often mentioned, as

well as *Oscillatoria* spp. and *Coelosphaerium* sp. During 1976–89, *Aphanizomenon* reached heavy bloom densities most frequently, followed by *Microcystis* and *Oscillatoria*.

Brock (1985) also listed *Aphanizomenon* as forming the most massive blooms in Lake Mendota, based on an extensive sampling program during 1976–81. He also listed *Anabaena* and *Microcystis* as common genera responsible for algal blooms in the lake. While he found occasional blooms of *Gloeotrichia*, it was never recorded at bloom densities in the 1976–89 data we analyzed. It was most noticeable during the early summer of 1989, but biovolumes were not large. *Oscillatoria* did not form blooms in Lake Mendota according to Brock, whereas we found bloom densities at certain times during 1978–82. Another difference between Brock's data and those presented here is the relative severity of blooms in different years. In Brock's data, there was a distinct ranking of years (from lowest to highest summer total biovolumes): 1981, 1980, 1979, 1976, 1978, and 1977. Differences between years were less apparent in our data.

Some of these differences between Brock's results and ours can be attributed to more extensive sampling in 1977–78 by Brock and to different sampling methods. He integrated discrete vertical-profile samples into whole-lake algal biovolumes, whereas the results we presented were based on samples taken in 0–2 m of water depth. These differences between the two data bases show that consistent methodology is essential for obtaining a detailed plankton record representing both seasonal and yearly variations for the lake over an extended number of years. Differences between the WDNR and CFL phytoplankton data for 1987 further confirm this point. Consistent methods are extremely important for sustaining an interpretable long-term record (Likens 1989).

While the blue-green algae were the most important bloom-forming group in our study, *Ceratium hirundinella* was also an important late summer bloom species during many years dating back to the late 1800s. *Ceratium* biovolume sometimes greatly exceeded that of blue-green algae. High *Ceratium* biovolume was associated with relatively high stability of the water column. In the summers of 1983 and 1987, water clarity was better than in years dominated by blue-greens (Lathrop, Ch. 6). The reason for the improvement in water clarity when *Ceratium* biovolume predominates is that the large cells do not attenuate light as much as smaller cells (Edmondson 1980). Predominance of *C. hirundinella* over blue-green algae during the summer months occurs occasionally in other eutrophic lakes (Lund 1979; Harris 1986).

Stauffer and Lee (1973) argued that blue-green algal blooms in Lake Mendota were associated with summer storms that entrained nutrient-rich hypolimnetic water into the epilimnion. This hypothesis implies that summers with low water column stability should have high blue-green biovolumes. Our data do not contradict this hypothesis. However, the

rather loose correlation of Schmidt stability and blue-green biovolume indicates that factors other than mixing are involved in the algal blooms of Lake Mendota.

The much larger biovolumes that were recorded for blue-green algae and *Ceratium* as opposed to many of the smaller-sized spring and fall plankton reflect the importance of edibility in phytoplankton succession (Sterner 1989). Apparently when nutrients are available to stimulate algal growth during the summer months, the inedible forms will predominate. The clearing of the early spring plankton that are mostly of an edible size suggests the role that *Daphnia* and other grazers play in selectively removing these species when they are in abundance. The statistical analyses in this chapter and that on zooplankton (Lathrop and Carpenter, Ch. 8) are designed to investigate these successional mechanisms quantitatively.

The generalized seasonal succession of phytoplankton in Lake Mendota closely follows the PEG (Plankton Ecology Group) model for eutrophic lakes (Sommer et al. 1986) with only minor exceptions. In the early spring, the growth of cryptophytes and small centric diatoms provides a rich food source for herbivore grazers (*Daphnia*) to develop. Eventually the *Daphnia* population becomes too large, overgrazes the phytoplankton, and establishes a clear-water phase by late spring. A minor increase in green algae may occur. Contrary to the PEG model, large diatoms do not develop in early summer, probably because DRSi is depleted early in the spring and silica recycling does not increase concentrations enough to support large diatoms. Meanwhile, an extensive bloom of relatively inedible blue-green algae usually develops, responding to DRP that is rapidly recycled in Lake Mendota because of low iron to phosphorus ratios in anoxic waters (interstitial and hypolimnetic). Blooms of both nitrogen-fixing and non-nitrogen-fixing species occur during the summer, but the most severe blooms are usually related to *Aphanizomenon flos-aquae*, a nitrogen-fixing species. The dominance of this species over *Microcystis aeruginosa*, a non-nitrogen-fixing species that has a low nitrogen requirement for growth (Horne 1978), suggests that nitrogen fixation may become important if phosphorus supplies are high enough to support more growth. The PEG model also recognized that *Ceratium hirundinella* can develop into large blooms during late summer and early fall in some lakes, a condition that occurs to varying degrees almost every year in Lake Mendota. The development of both inedible and edible diatoms and other algae during the fall months as nutrient concentrations increase occurs in both the PEG model and Lake Mendota.

### Patterns in the Time Series

Our analyses revealed several relationships that are useful predictors of blue-green algal biovolume. Unusually high blue-green biovolumes occur simultaneously with unusually low DRP concentrations. When the algae

are abundant, then the phosphorus is in algal biomass rather than the DRP pool. A more interesting relationship is the positive correlation at a lag of 2 months. This correlation means that high DRP concentrations forecast high blue-green algal biomass 2 months later.

The negative relationship between Schmidt stability and blue-green biovolume at lag 1 indicates that months with anomalously high stability are followed by months with anomalously low blue-green algae biomass. When the water column is very stable, vertical mixing and regeneration of nutrients from the hypolimnion are reduced. For example, relatively low levels of blue-green algae in 1983 and 1988, the years with highest Schmidt stability during summer, may be partially explained by low rates of nutrient mixing from the hypolimnion. Conversely, months with anomalously low stability are followed by months with anomalously high blue-green algae biomass. When the water column is unstable, vertical mixing regenerates nutrients and stimulates algal blooms (Stauffer and Lee 1973). Low stability may partly explain the high blue-green algal biomass that occurred in the summer of 1985. It is more difficult to explain the positive relationship between Schmidt stability and blue-green algal biovolume at a lag of 3 months. This relationship has predictive value: anomalously high stability is associated with anomalously high blue-green algal biomass 3 months later. During summer periods of high stability, nutrients may build up in the hypolimnion and support high blue-green algal biomass in fall as stratification breaks down.

Unusually high TP concentrations during winter are followed by unusually high blue-green algal biovolumes the next summer. This relationship underscores the importance of winter sampling for anticipating summer water quality conditions in Lake Mendota.

Despite these useful relationships, it remains very difficult to forecast blue-green algal biomass in Lake Mendota. The forecasting model with minimal errors is the transfer function that forecasts blue-green algal biomass from its past values and the time series of Schmidt stabilities (Table 7.5). This equation's forecasts for the summer of 1990 have standard errors of about  $1.5 \mu\text{L L}^{-1}$ . The standard error is comparable to the maximum blue-green algal biovolume in some summers! There is much room for improvement in our capacity to forecast blue-green algal biomass. Nitrogen is not likely to improve our predictive capacity because its dynamics tend to track those of phosphorus and are controlled to some extent by nitrogen-fixing blue-green algae (Schindler 1977; Carpenter et al. 1991; Lathrop, Ch. 6). Variates related to nutrient input are a promising possibility (Jassby et al. 1990) which we are currently researching. Effects of grazing on algae are another potential predictor of central importance to this book. We consider the relationships of grazer and algal dynamics in the next chapter.

*Acknowledgments.* We thank P.R. Leavitt and M.J. Vanni for critical reviews of this chapter and S.H. Nehls for editorial assistance. Data

collection was supported by the WDNR and the Federal Aid in Sport Fish Restoration Act under Project F-95-P. Phytoplankton enumerations were conducted by P.K. Montz, R.E. Last, and T.L. Brasino (WDNR) and J. Temte and R. Dodds (CFL). Time series analyses were supported by a grant from the Andrew Mellon Foundation.

## References

- Andersson G, Cronberg G (1984) *Aphanizomenon flos-aquae* and large *Daphnia*—an interesting plankton association in hypertrophic water. In Bosheim S, Nicholls M (eds) Nordisk limnologysymposium, Interactions between trophic levels in freshwaters, Norsk Limnologforening, Oslo
- Bardach JE (1951) Changes in the yellow perch population of Lake Mendota, 1916–1948. *Ecology* 32:719–728
- Birge EA (1898) Plankton studies on Lake Mendota: II. The Crustacea of the plankton from July, 1894, to December, 1896. *Trans. Wis. Acad. Sci. Arts Lett.* 11:274–448
- Birge EA, Juday C (1922) The inland lakes of Wisconsin: The plankton I. Its quantity and chemical composition. *Wis. Geol. Nat. Hist. Surv. Bull.* No. 64, Sci. Ser. No. 13
- Box GEP, Jenkins GJ (1976) Time series analysis: Forecasting and control. Holden-Day, San Francisco
- Box GEP, Tiao GC (1975) Intervention analysis with applications to economic and environmental problems. *J. Am. Stat. Assoc.* 70:70–79
- Brock TD (1985) A eutrophic lake: Lake Mendota, Wisconsin. Springer-Verlag, New York
- Brockwell PJ, Davis RA (1987) Time series: Theory and methods. Springer-Verlag, New York
- Brooks JL, Dodson SI (1965) Predation, body size, and composition of plankton. *Science* 150:28–35
- Carpenter SR (1988) Transmission of variance through lake food webs. In Carpenter SR (ed) Complex interactions in lake communities, Springer-Verlag, New York, pp 119–135
- Carpenter SR, Frost TM, Kitchell JF, Kratz TK, Schindler DW, Shearer J, Sprules WG, Vanni MJ, Zimmerman AP (1991) Patterns of primary production and herbivory in 25 North American lake ecosystems. In Cole J, Findlay S, Lovett G (eds) Comparative analyses of ecosystems: Patterns, mechanisms, and theories. Springer-Verlag, New York, pp 67–96
- Carpenter SR, Kitchell JF (1988) Consumer control of lake productivity. *BioScience* 38:764–769
- Carpenter SR, Kitchell JF, Hodgson JR, Cochran PA, Elser JJ, Elser MM, Lodge DM, Kretchmer D, He X, von Ende C (1987) Regulation of lake primary productivity by food-web structure. *Ecology* 68:1863–1876
- Edmondson WT (1980) Secchi disk and chlorophyll. *Limnol. Oceanogr.* 25:378–379
- Harris GP (1986) Phytoplankton ecology: Structure, function and fluctuation. Chapman and Hall, New York

- Horne AJ (1978) Nitrogen fixation in eutrophic lakes. In Mitchell R (ed) Water pollution microbiology, Vol. 2, John Wiley & Sons, New York, pp 1–30
- Hrbacek J (1962) Species composition and the amount of zooplankton in relation to the fish stock. Rozpr. Cesk. Akad. Ved Rada Mat. Prir. Ved 72:1–116
- Jassby AD, Powell TM (1990) Detecting change in ecological time series. Ecology 71:2044–2052
- Jassby AD, Powell TM, Goldman CR (1990) Interannual fluctuations in primary production: Direct physical effects and the trophic cascade at Castle Lake, California. Limnol. Oceanogr. 35:1021–1038
- Kopp JF, McKee GD (1979) Methods for chemical analyses of water and wastes, 1978. 3rd edn. EPA-600/4-79-020. Environmental Monitoring and Support Laboratory, Cincinnati, Ohio
- Lathrop RC (1990) Response of Lake Mendota (Wisconsin, U.S.A.) to decreased phosphorus loadings and their effect on downstream lakes. Verh. Internat. Verein. Limnol. 24:457–463
- Likens GE (ed) (1985) An ecosystem approach to aquatic ecology: Mirror Lake and its environment. Springer-Verlag, New York
- Likens GE (ed) (1989) Long-term studies in ecology. Springer-Verlag, New York
- Lillie RA, Mason JW (1983) Limnological characteristics of Wisconsin lakes. Wis. Dep. Nat. Resour. Tech. Bull. No. 138
- Lund JWG (1979) Changes in phytoplankton of an English lake, 1945–1947. Hydrobiol. J. 14:6–21
- Lynch M (1980) *Aphanizomenon* blooms: Alternate control and cultivation by *Daphnia pulex*. In Kerfoot WC (ed) Evolution and ecology of zooplankton communities, University Press of New England, Hanover, New Hampshire, pp 299–304
- McNaught DC (1965) A study of some ecological relationships and the role of vision in the diel migrations of *Daphnia*. Ph.D. Thesis, University of Wisconsin, Madison
- Robertson DM (1989) The use of lake water temperature and ice cover as climatic indicators. Ph.D. Thesis, University of Wisconsin, Madison
- Sager PE (1967) Species diversity and community structure in lacustrine phytoplankton. Ph.D. Thesis, University of Wisconsin, Madison
- SAS Institute, Inc. (1988) SAS/ETS User's Guide, Version 6. 1st edn. Cary, North Carolina
- Schindler DW (1977) Evolution of phosphorus limitation in lakes. Science 195:260–262
- Schindler DW (1988) Experimental studies of chemical stressors on whole-lake ecosystems. Verh. Internat. Verein. Limn. 23:11–41
- Shapiro J, Lamarra V, Lynch M (1975) Biomanipulation: An ecosystem approach to lake restoration. In Brezonik PL, Fox JL (eds) Proceedings of a symposium on water quality management through biological control, University of Florida, Gainesville
- Shapiro J, Wright DI (1984) Lake restoration by biomanipulation: Round Lake, Minnesota the first two years. Freshwat. Biol. 14:371–383
- Sommer U, Gliwicz ZM, Lampert W, Duncan A (1986) The PEG\*-model of seasonal succession of planktonic events in fresh waters. Archiv. Hydrobiol. 106:433–471

- Sonzogni WC (1974) Effect of nutrient input reduction on the eutrophication of the Madison lakes. Ph.D. Thesis, University of Wisconsin, Madison
- Stauffer RE, Lee GF (1973) The role of thermocline migration in regulating algal blooms. In Middlebrooks EJ (ed) Modelling the eutrophication process, Ann Arbor Science, Ann Arbor, Michigan, pp 73–81
- Sterner RW (1989) The role of grazers in phytoplankton succession. In Sommer U (ed) Plankton ecology: Succession in plankton communities, Springer-Verlag, Berlin, pp 107–170
- Sterner RW (1991) The ratio of nitrogen to phosphorus resupplied by zooplankton: Grazers and the algal competitive arena. Am. Nat. 136:209–229
- Torrey MLS (1972) Biological nitrogen fixation in Lake Mendota. Ph.D. Thesis, University of Wisconsin, Madison
- Trelease W (1889) The “working” of the Madison lakes. Trans. Wis. Acad. Sci. Arts Lett. 7:121–129
- Vanni MJ, Luecke C, Kitchell JF, Rentmeester Y, Temte J, Magnuson JJ (1990) Cascading trophic interactions and phytoplankton abundance in a eutrophic lake: Effects of massive fish mortality. Nature 344:333–335
- Vollenweider RA (1968) Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. Organization for Economic Cooperation and Development Rep. No. DAS/CSI/68.27
- Wei WWS (1990) Time series analysis. Addison-Wesley, New York
- Wilkinson L (1988) SYSTAT: The system for statistics. Systat Inc., Evanston, Illinois
- Wisconsin Committee on Water Pollution (1949) Report on Lake Mendota studies concerning conditions contributing to occurrence of aquatic nuisances 1945–1947. Wis. Comm. Water Poll.

# 8

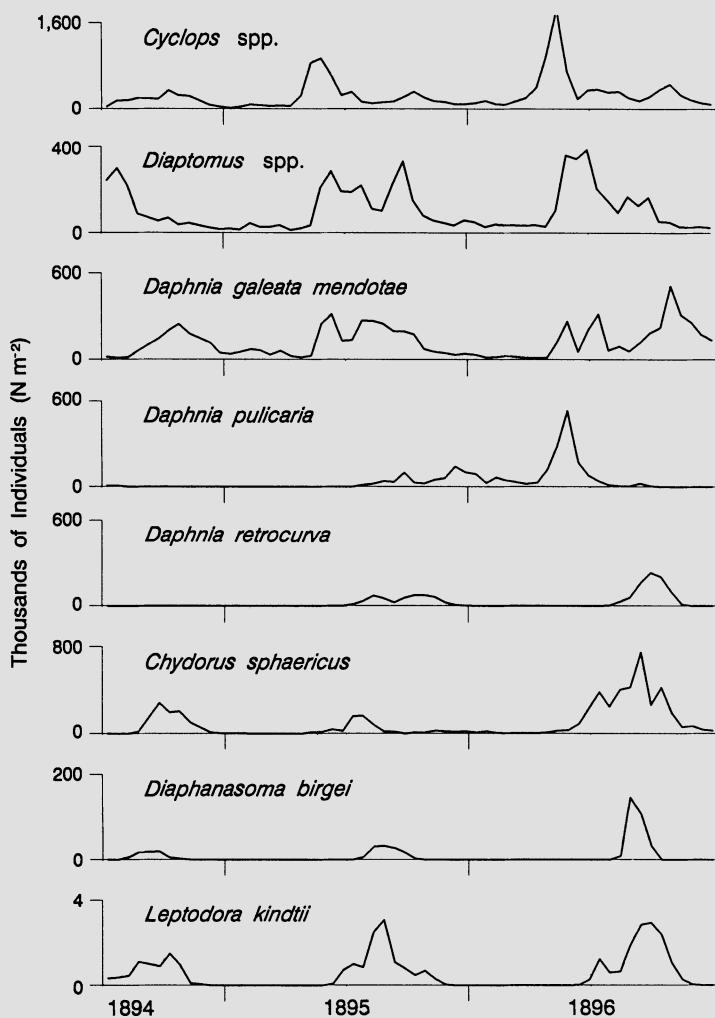
## Zooplankton and Their Relationship to Phytoplankton

**Richard C. Lathrop and Stephen R. Carpenter**

### Introduction

The limnetic zooplankton that commonly occur in Lake Mendota are important both as grazers of phytoplankton and as food for fish and large invertebrate predators. Because of their central role in the food web, they are a key ecosystem component from the standpoint of the food web research summarized in this book. *Daphnia* are of particular interest because they are subject to intensively selective predation by fishes and because they exert substantial grazing pressure on algal populations (Hrbacek 1962; Brooks and Dodson 1965; Shapiro et al. 1975; Carpenter et al. 1987; Sterner 1989; Vanni et al., Ch. 13; Luecke et al., Ch. 14). This chapter describes the zooplankton of Lake Mendota and, building on results from the preceding chapter on phytoplankton, evaluates patterns of herbivory in Lake Mendota.

This chapter addresses two major questions. First, what is the range of variability exhibited by *Daphnia* in the past? Past extremes in grazer biomass indicate the conditions that might be attainable by manipulation of the system. We evaluate past variability via a historical review of zooplankton studies in Lake Mendota prior to 1976 and analysis of selected data from a 14-year record for 1976–89. Second, have past fluctuations in *Daphnia* influenced the phytoplankton? Historical linkages between grazer and producer components indicate the magnitude and variance of a key interaction for the food web research. We evaluate plant–herbivore interactions by the time series and transfer function methods used in the previous chapter on phytoplankton.



**Figure 8-1.** Densities of major zooplankton species found in Lake Mendota from July 1894 to December 1896 (from Birge 1898).

## Historical Review

### Early Work of E.A. Birge

Birge (1898), using a small tow net, conducted the first survey of annual zooplankton abundances in Lake Mendota between July 1894 and December 1896. (We converted Birge's species names to current nomenclature.) While the copepod data did not distinguish between different species of *Cyclops* and *Diaptomus*, the cladoceran data were given for

each major species. *Daphnia galeata mendotae*, *D. pulicaria*, *D. retrocurva*, *Chydorus sphaericus*, and *Diaphanosoma birgei* were the most numerous cladocerans. Birge also reported abundances of the large predaceous cladoceran *Leptodora kindtii*.

*Cyclops* spp. (both adults and copepodites) were numerically the most important zooplankters during Birge's study (Figure 8.1). Populations peaked in May of both 1895 and 1896 and were much less abundant during the rest of the study. *Diaptomus* spp. were generally the most abundant during the months of May–July, but densities were lower during the other months except for September 1895.

*Daphnia galeata mendotae* was found in the plankton in all three study years, while *D. pulicaria* and *D. retrocurva* were absent for much of the period (Figure 8.1). *D. galeata mendotae* exhibited fall density increases in 1894–96 and late spring increases in both sampling years (1895–96). Densities were also relatively high during the late summer/early fall of 1895 and during July 1896. *D. galeata mendotae* densities were low during the winter and early spring of both 1895 and 1896. *D. pulicaria* was virtually absent from the plankton until the fall of 1895 when a minor population increase was noted. Populations were low again during the following winter, but by late April 1896 *D. pulicaria* began increasing to a major peak in late May. Densities declined during June, and by late July it was scarce for the remainder of 1896. *D. retrocurva* was the least abundant of the three *Daphnia* species during the study period. It was not found in the plankton prior to a minor population increase in late summer and fall of 1895. *D. retrocurva* was absent in samples from January through early July of 1896, before exhibiting a moderate density peak around late September of that year. Densities declined rapidly in October and it was absent for the rest of the year.

*Chydorus sphaericus*, one of the smaller zooplankters enumerated in Birge's study, exhibited seasonally cyclic densities (Figure 8.1). In 1894, *Chydorus* was scarce in late summer but increased to a peak in late September and then declined by the year's end. In 1895, it was absent through the spring months but exhibited a minor population increase in July. *Chydorus* was scarce in the plankton between the fall of 1895 and the spring of 1896. Densities increased rapidly in June 1896 and continued increasing to a peak density in early September before declining by late fall of that year.

*Diaphanosoma birgei* was not an important component of the zooplankton of Lake Mendota in Birge's study (Figure 8.1). Densities were highest in September–October in all three years. *Diaphanosoma* was not recorded in the plankton from late October through late June/early July during the study years.

The only other species enumerated by Birge (1898) was *Leptodora kindtii*, which was present in much smaller densities (Figure 8.1). It first appeared in the plankton in late May of both 1895 and 1896 and began

increasing by late June. Peak densities were recorded in early October 1894, late August 1895, and late September 1896. *Leptodora* was not found in the plankton after early December in any of the years.

### Other Studies

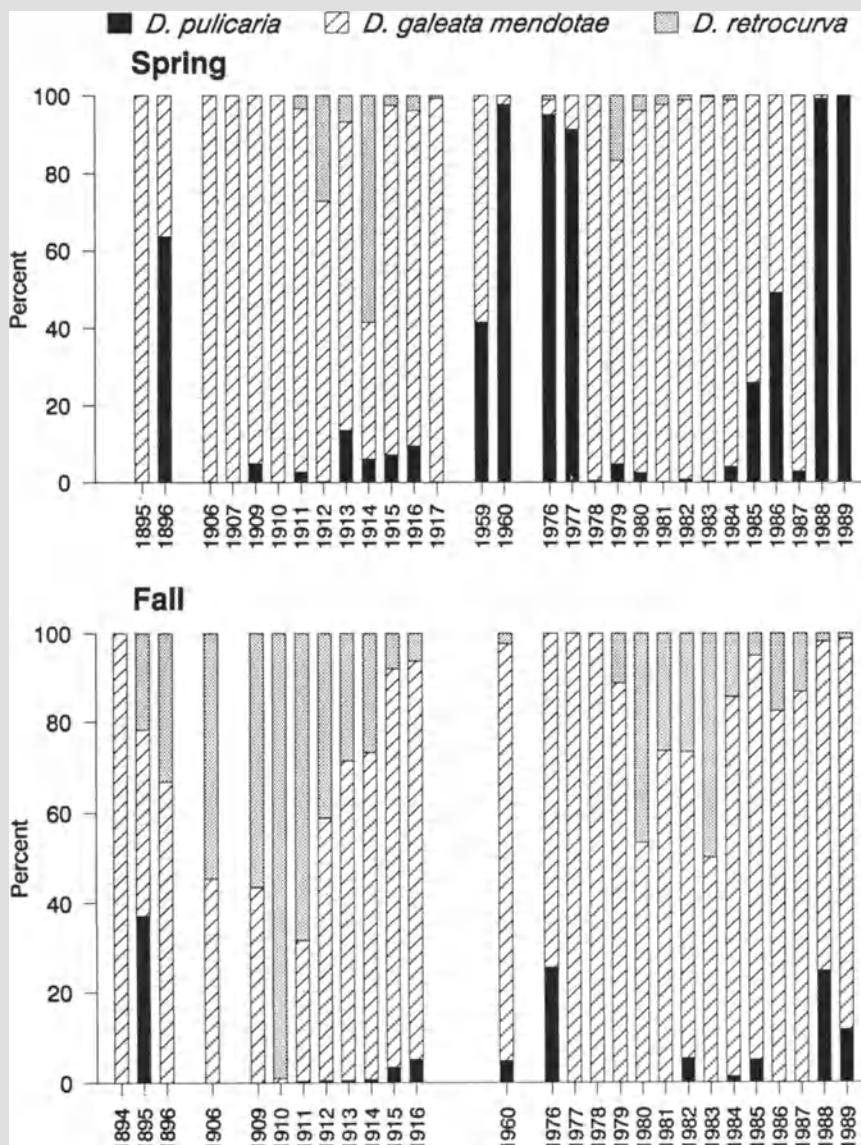
No other study prior to 1976 documented the seasonal dynamics of individual zooplankton species as completely as Birge's 1898 monograph summarized above. Birge and Juday (1922) reported on their extensive net plankton sampling in Lake Mendota during 1911–17, but the published results focused on total organic matter in the samples and the phytoplankton. Little information was given on densities of zooplankton species. *Cyclops* spp. were the most abundant crustaceans, with peak densities recorded in April and May. *Daphnia* spp. exhibited population increases in late spring and fall months.

We summarized the *Daphnia* species data from the voluminous unpublished raw records that were collected by Birge and Juday for 1906–17 (excluding 1908). During those years, *D. galeata mendotae* dominated the spring plankton, and both *D. galeata mendotae* and *D. retrocurva* dominated the fall plankton (Figure 8.2). *D. pulicaria* was not abundant in either season. Spring peak *Daphnia* densities were always greater than fall peak densities.

Further information on zooplankton species abundances in Lake Mendota prior to 1976 is scanty except for a few brief notations on *Daphnia* populations. Both Neess (1949) and Bardach (1949) gave densities of *Daphnia* spp. during the summer of 1947, a season of unusually high water transparency. Using a Clarke–Bumpus sampler towed through surface waters, Neess found *Daphnia longispina* (= *D. galeata mendotae* + *D. retrocurva* according to McNaught and Hasler 1964) averaging  $36\text{ L}^{-1}$  on an unspecified date in the summer, and Bardach found *Daphnia* spp. averaging 22 and  $5\text{ L}^{-1}$  on 8 July and 6 August, respectively.

Ragotzkie (1953) studied the effect of wind-induced, horizontal density differences in *D. pulicaria* (reported as *D. pulex*) during the summer of 1952. In the top 0–6 m of water, densities averaged about 4, 8, and  $15\text{ L}^{-1}$ , at upwind, center lake, and downwind stations on 25 June. On 8 August, *D. pulicaria* densities averaged 6, 9, and  $17\text{ L}^{-1}$  for upwind, center lake, and downwind sites in the open lake. Ragotzkie found that *Daphnia* densities could change greatly within a 24-h period if wind conditions changed.

McNaught and Hasler (1964), reporting on the vertical movement of *Daphnia* in relation to changes in light intensity, gave information on the relative abundances of *D. pulicaria* (reported as *D. schödleri*), *D. galeata mendotae*, and *D. retrocurva* in Lake Mendota during the summer of 1959 and the open-water period of 1960. Horizontal tows were collected with a



**Figure 8-2.** Spring and fall relative abundances of the major *Daphnia* species in Lake Mendota for selected years between 1894 and 1989 [from Birge (1898) for 1894–96, unpubl. raw data partly summarized in Birge and Juday (1922) for 1906–17, McNaught and Hasler (1964) for 1959–60, and WDNR unpubl. data for 1976–89].

Clarke-Bumpus sampler in the top 4.5 m of water near the south shore. In late June 1959, *D. pulicaria* represented about 42% of the population and *D. galeata mendotae* the remainder. Throughout that summer, *Daphnia* spp. densities were relatively high, averaging  $9\text{ L}^{-1}$  (range  $5\text{--}24\text{ L}^{-1}$ ). By late August, *D. retrocurva* became important, constituting 49% of the total, followed by *D. pulicaria* (32%) and *D. galeata mendotae* (19%).

In 1960, *D. pulicaria* represented about 98% of the total *Daphnia* population during a late spring period when abundances were greatest. Densities averaged about  $30\text{--}39\text{ L}^{-1}$  from late May through early July. Densities were about  $5\text{ L}^{-1}$  in late April and in early August before and after the period of high densities. However, in August when *D. pulicaria* was declining, *D. galeata mendotae* began increasing. By late October, *D. galeata mendotae* comprised about 94% of the *Daphnia* population, but peak densities were only about  $11\text{ L}^{-1}$  that fall. *D. retrocurva* was rare in April–November 1960.

A further set of observations on Lake Mendota's *Daphnia* populations was provided by Dr. Byron Torke (Ball State University, unpubl. data). In late July 1972, *D. pulicaria* (*D. pulex* + *D. schødleri*) densities were  $0.27\text{ L}^{-1}$  while *D. galeata mendotae* densities were only  $0.06\text{ L}^{-1}$ . In early July 1975, *D. pulicaria* was “abundant” while *D. galeata* was not found. In late November of that year, both species were “common.”

The zooplankton of Lake Mendota were sampled throughout 1976–80 by University of Wisconsin researchers. Density information for the major species that were encountered was summarized in Brock (1985), Pedrós-Alió and Brock (1985), and Pedrós-Alió et al. (1985). In the Discussion section of this chapter, we compare their findings to our 1976–89 zooplankton record.

## Methods

### Sample Collection and Enumeration

The 1976–89 zooplankton data were part of a long-term limnological research study of Lake Mendota and the other three Yahara lakes conducted by the Wisconsin Department of Natural Resources (WDNR) Bureau of Research. Information on the frequency of sampling for each of the study years was given in Lathrop (Ch. 6) and Lathrop and Carpenter (Ch. 7). On most sampling dates, a vertical tow sample was taken near Lake Mendota's deepest point, in water depths of approximately 23–24 m, using a 15-cm diameter conical net. (On a few dates during high winds or during winter through the ice, tows were taken in slightly shallower water.) The net was made of #20 Nitex screening with a mesh size of 75–80  $\mu\text{m}$  and had a filtering area to opening area ratio of

11. The net was lowered to about 0.5 m off the bottom and then raised at the speed of ca.  $0.3 \text{ m s}^{-1}$ . After the net was raised and the sides rinsed, the sample (ca. 200–250 mL) was transferred to a bottle and preserved with formalin. Beginning in 1986, seltzer water was added to the samples before they were preserved with sugared formalin solution in order to prevent the *Daphnia* from expelling their eggs.

Zooplankton samples were later enumerated in the lab by taking a 1-mL subsample transferred by a Hensen–Stemple pipette to a Sedgewick–Rafter counting cell of the same volume. Three separate subsamples were counted using a compound microscope. Average body lengths were also recorded for each species by measuring the first 5–10 individuals encountered in each subsample, except for *Daphnia*, for which all individuals were measured. All measurements in the three subsamples were then averaged for each species. Immature calanoid and cyclopoid copepodites and nauplii (not separated) were each counted and measured, as were adult copepod species. *Daphnia* were also separated into juvenile and adult forms for each species based on size criteria (Luecke et al., Ch. 14), and averages were made for each form.

Because of experience gained in recent years about Lake Mendota's zooplankton, many of the earlier samples were recounted to verify identifications and enumerations. All *Daphnia* data for 1976–85 were recounted because of the University of Wisconsin-Madison Center for Limnology (CFL) size criteria for separating adults and juveniles. *Daphnia* species determinations were also rechecked for 1986, because our data contradicted earlier published conclusions about what *Daphnia* populations were probably like during the 1980s.

In order to calculate zooplankton densities based on the vertical tow samples, a net efficiency factor was determined. Uncorrected densities of the most abundant organisms were determined for 15-m net tows and compared to densities obtained by lowering to the same depth a 10-cm diameter flexible tube with a threaded iron collar. The tube was sealed by a scuba diver shortly after it was lowered and then was slowly raised while the contents were poured through the zooplankton net with its opening held just above the water line. On three separate dates, average organism densities from six net tows were compared to average densities from six tube samples. Secchi disk readings for the three dates were 1.1, 1.8, and 8.2 m, indicating widely varying algal populations that could have caused differential clogging of the net. The net efficiency determined for the three dates ranged between 0.42 and 0.58 for all major organisms counted, with no indication that algal blooms affected net efficiency, thus implying that hydraulic overload was the principal reason for loss in efficiency. Consequently, a net efficiency of 0.5 was used in calculating all WDNR zooplankton densities, expressed as individuals per square meter.

In addition, biomass data, expressed as grams dry weight per square meter, for both total zooplankton and total *Daphnia* spp. were computed

from species-specific regression equations using body length to predict individual dry weights. Equations used for all species except *Daphnia* were from Downing and Rigler (1984); equations used for *Daphnia* species were from Lynch et al. (1986). Both sets of equations are listed in Luecke et al. (Ch. 14).

All numerical and biomass density data computed on a square meter basis were converted to a standardized depth of 20.0 m. Because almost all vertical tow depths (TOW) were greater than 20 m (mean = 23.0 m for 1976–89), unconverted densities were multiplied by 20/TOW if the entire water column was oxygenated. (This conversion was also used in the few cases when TOW was <20 m and the thermal structure indicated that the deeper waters were oxygenated.) The oxygenated depth (DO) was determined to be where dissolved oxygen concentrations were  $1.0 \text{ mg L}^{-1}$ , based on vertical profile data collected at the same time. In cases where TOW was >20 m, and  $20 \text{ m} < \text{DO} < \text{TOW}$ , densities were multiplied by  $20/\text{DO}$ . In cases where DO was <20 m, no density conversions were necessary because all organisms were located in depths shallower than 20 m.

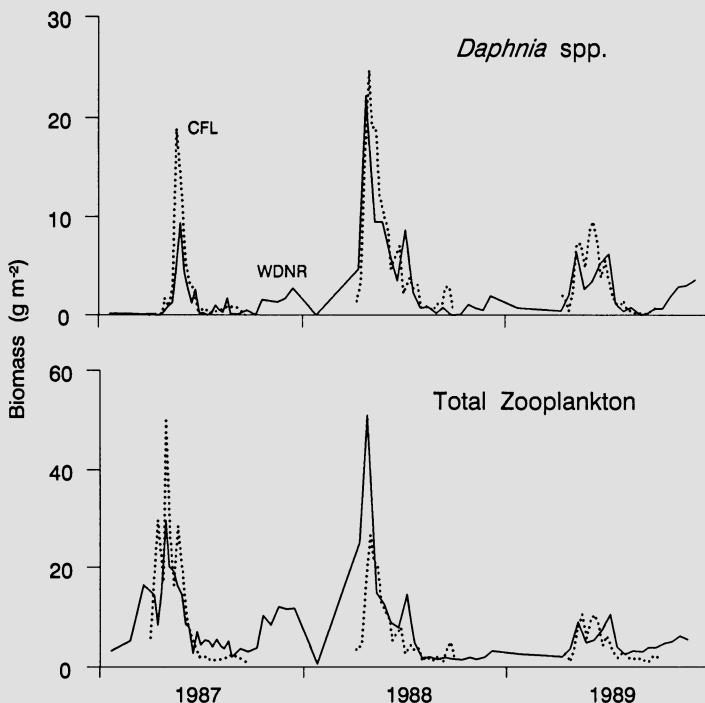
Numerical densities of all major crustacean zooplankton species found during 1976–89 in Lake Mendota are presented in time course graphs. Copepod data are presented for only calanoids and cyclopoids (adults + copepodites) and total nauplii. Biomass densities of total *Daphnia* species and total zooplankton are also given for 1976–89.

In addition to the WDNR 1976–89 zooplankton data, CFL zooplankton samples were also collected during 1987–89 with a metered Clarke–Bumpus sampler (13-cm diameter, 130- $\mu\text{m}$  mesh net) towed behind a boat (see Luecke et al., Ch. 14). We compared these data with the WDNR data for the same years in order to verify that the vertical tow net data represented actual zooplankton densities in Lake Mendota. Because WDNR and CFL sampling dates were different during the 3 years, the data are compared using time course graphs for *Daphnia* spp. and total zooplankton biomass densities. Both sampling methods produced remarkably similar seasonal patterns and biomasses for the 3 years (Figure 8.3). (Clarke–Bumpus samples were not collected between early fall and early spring.)

Finally, we computed percent relative abundances of the different *Daphnia* species found in various studies since 1894. Spring percentages were based on weighted mean densities for April–June. Fall percentages were based on weighted mean densities for September–December.

### Statistical Analysis

Time series analyses all were performed on dry weight biomass density data for 1976–89. The procedures used were the same as those in the chapter on phytoplankton (Lathrop and Carpenter, Ch. 7). We will

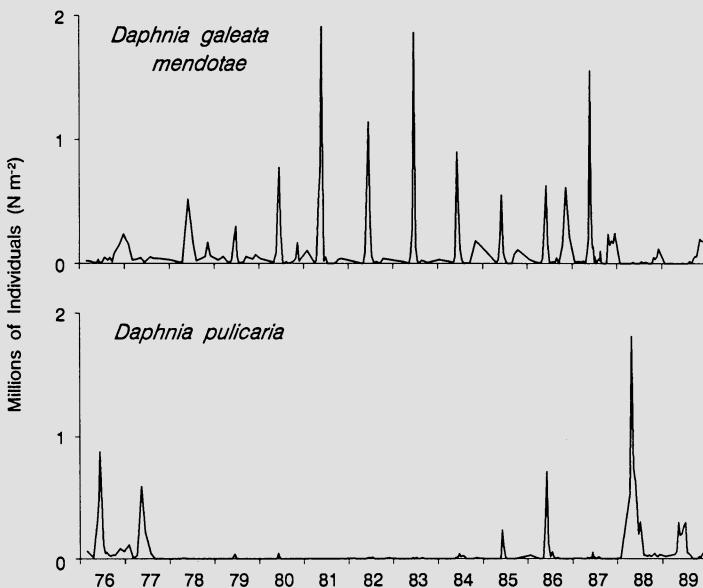


**Figure 8-3.** Comparison of biomasses of total *Daphnia* and total zooplankton from samples collected in Lake Mendota by the WDNR and CFL for 1987–89.

recount them briefly here. Equispaced series of 13 4-week “months” per year were constructed for each variate, using the mean of all observations in each month. In this chapter, “month” refers to a 4-week interval, not a calendar month. Missing values were replaced with the mean of the appropriate month over all available years. This convention added to the seasonal components of the models (see below) and makes results conservative in the sense that it is more difficult to detect shifts in the time series or nonseasonal relationships among them.

Time series analyses were performed to examine three questions: (1) Were there shifts in the relative density of *D. pulicaria* following the cisco year class of 1978 and the cisco die-off of 1987? (2) Were there shifts in algal biomass associated with shifts in relative density of *D. pulicaria*? (3) Are there significant dynamic relationships between *Daphnia* biomass and algal biomass? Intervention analyses were applied to the first two questions and transfer functions were calculated to address the third question. As these were explained in some detail in the previous chapter, we will provide only a brief summary here.

Intervention analysis tests for a shift in a time series following a perturbation or manipulation (Box and Tiao 1975; Wei 1990). A model is fit



**Figure 8-4.** Numerical densities of *Daphnia galeata mendotae* and *D. pulicaria* in Lake Mendota for 1976–89.

that accounts for the seasonality and autocorrelation in the time series and includes coefficients for the effects of the intervention. If the intervention coefficients appear significant statistically, then the analysis implies that a nonrandom change occurred after the intervention. Our intervention analyses employed the model:

$$(1 - \phi B)(1 - \phi_{13} B_{13})Z(t) = a(t) + \alpha S_1 + \beta S_2 \quad (1)$$

where  $Z(t)$  is the time series of the response variable and  $a(t)$  is the residual time series.  $B$  is the backshift operator;  $B_x Z(t) = Z(t - X)$ . The model for autocorrelation and seasonality involves the autoregressive parameter  $\phi$  and the seasonal parameter  $\phi_{13}$ . The intervention parameters are  $\alpha$  and  $\beta$ . The dummy variables  $S_1$  and  $S_2$  are zero prior to the intervention and one afterwards. Thus  $\alpha$  and  $\beta$  represent the magnitude of the step-change shift in level of the response variable following interventions 1 and 2, respectively.

Transfer functions are used to quantify forecasting relationships between a response time series and an input time series. Seasonality and autocorrelation in ecological time series preclude the use of conventional correlation and regression to study dynamic relationships (Carpenter and Kitchell 1988; Carpenter et al. 1991). In constructing transfer functions, a time series model removes the effects of seasonality and autocorrelation prior to analysis for a causal relationship between input and response

(Wei 1990). The transfer function thus accounts for seasonality and autocorrelation as well as the relationship between input and response. Our transfer functions used the model:

$$(1 - \phi B)(1 - \phi_{13}B_{13})Y(t) = [(\omega_0 - \omega_2 B_2)X(t)/(1 - \delta_1 B_1 - \delta_2 B_2)] + a(t) \quad (2)$$

where  $Y(t)$  is the time series for the response variable,  $X(t)$  is the time series for the input variable, and  $a(t)$  is the time series of the residual. The left-hand side of the equation is an autoregressive model for seasonality and autocorrelation. The bracketed terms on the right-hand side account for the effect of the input on the response variable. The  $\omega$  and  $\delta$  coefficients can be used to calculate impulse weights as a function of time after shift in the input variable (Wei 1990). A plot of impulse weights versus time therefore illustrates the effects of the input on the response.

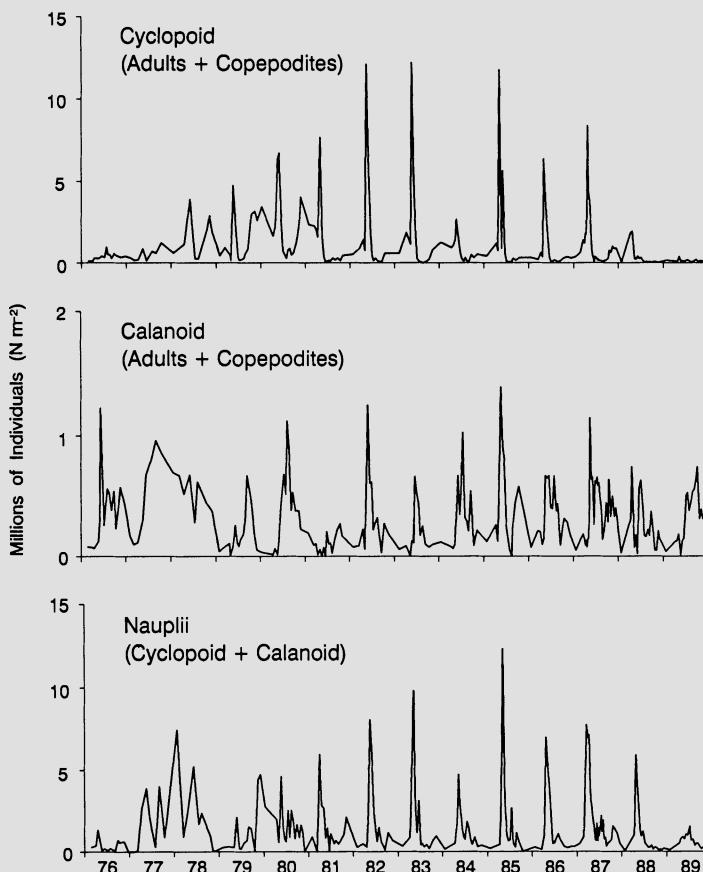
## Results

### 1976–89 Trends

Two main species of *Daphnia* were found during 1976–89: *D. galeata mendotae* and *D. pulicaria* (Figures 8.2 and 8.4). *D. galeata mendotae* had a pronounced spring peak in all years except 1976–77 and 1988–89. It also exhibited a smaller population increase in the late fall of 1976, 1978, 1984–87, and 1989. *D. pulicaria* had a pronounced spring peak in 1976–77 and then was virtually absent from the plankton until the spring of 1985, when it appeared again in measurable numbers. Densities increased in the spring of 1986, when it codominated with *D. galeata mendotae*, but *D. pulicaria* was virtually absent from the plankton in 1987. However, soon after ice-out in the spring of 1988, *D. pulicaria* began increasing; densities remained large until midsummer. Densities also increased in the spring of 1989 and remained high until summer, although peak densities were much less than in 1988. In general, *D. pulicaria* populations began increasing earlier in the spring (when water temperatures were colder) than *D. galeata mendotae*.

Other *Daphnia* species found during 1976–89 were *D. retrocurva* and *D. parvula*. *D. retrocurva* occurred in low densities in most years during late summer, while *D. parvula* was only sporadically recorded in very low densities in the early years of the study period.

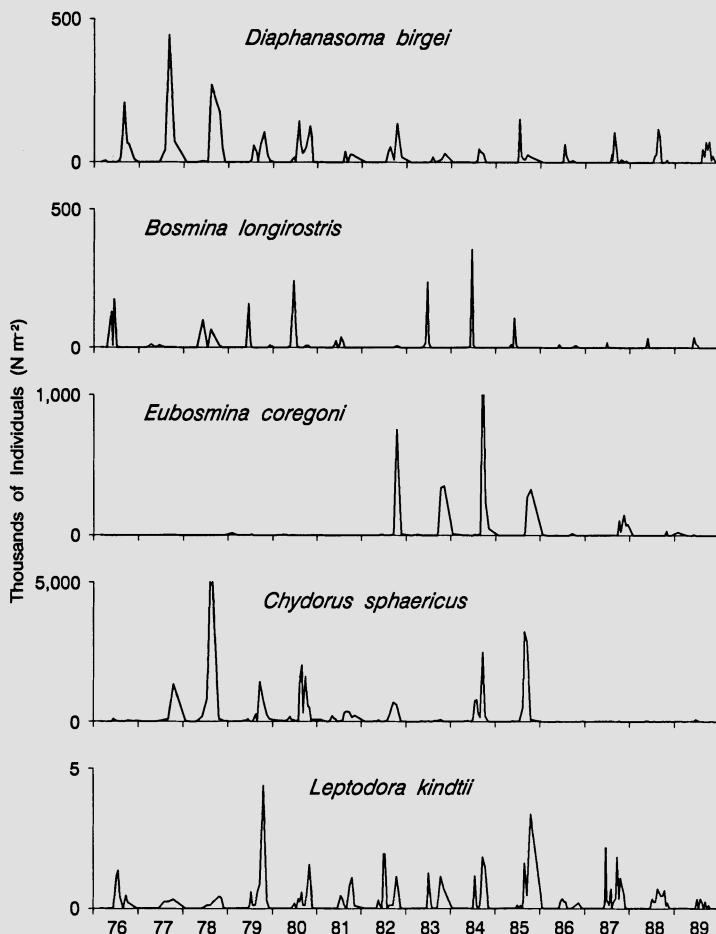
Only a few other crustacean zooplankton species were regularly important in the pelagic waters of Lake Mendota during 1976–89. (Rotifers were not abundant during 1976–89.) The cyclopoid copepod *Diacyclops biscutipatus thomasi* was the most abundant species found, particularly during the early spring when numerical densities of cyclopoid copepods



**Figure 8-5.** Numerical densities of cyclopoids (adults + copepodites) and calanoids (adults + copepodites) and total nauplii in Lake Mendota for 1976–89.

(almost exclusively this species) and total nauplii far exceeded all other crustacean maximum densities for the entire year (Figure 8.5). During the summer, it was not found because immature copepodites of this species undergo a diapause state in the lake sediments (Hutchinson 1967). Other cyclopoid copepods found, but in much lower densities, were *Mesocyclops edax*, which was moderately abundant in some summers, *Acanthocyclops vernalis*, and *Tropocyclops prasinus*, which was only rarely recorded.

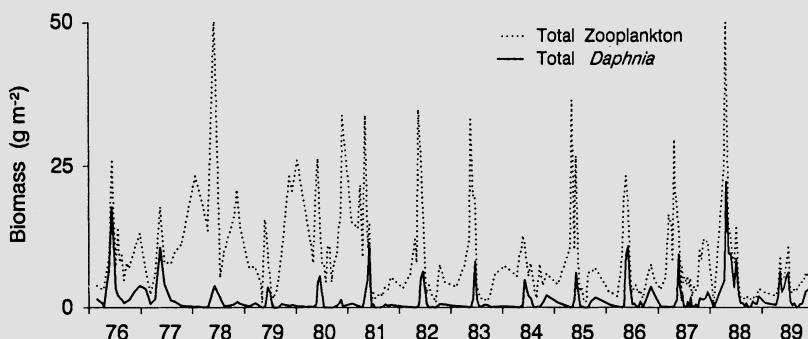
The most abundant calanoid copepod was *Leptodiaptomus siciloides*, which generally occurred in moderate densities from late spring through early fall. Other calanoid copepods, which were mostly found in low abundances, were *Aglodiaptomus clavipes*, *Leptodiaptomus sicilis*, and *Skistodiaptomus oregonensis*. The copepods as a group exhibited regular seasonal patterns in Lake Mendota during 1976–89, although annual



**Figure 8-6.** Numerical densities of other major cladocerans (excluding *Daphnia*) in Lake Mendota for 1976–89.

differences also occurred. Densities of cyclopoid copepods apparently did not exhibit the same seasonal cycle in 1977–78 as in other years, although less frequent sampling in those 2 years may have masked their actual population fluctuations. Further discussion of this dynamic group of organisms is beyond the scope of this chapter.

Other cladocerans that occurred in the plankton during 1976–89, in order of their maximum recorded densities, were *Chydorus sphaericus*, *Eubosmina coregoni*, *Diaphanasoma birgei*, and *Bosmina longirostris* (Figure 8.6). They each exhibited their own regular seasonal cycles but did not occur in all years. *Chydorus* was found between late summer and late fall in 1977–82 and 1984–85. Densities were very low in other seasons and years. *Eubosmina* was important only in the fall of 1982–85



**Figure 8-7.** Biomass densities of total *Daphnia* and total zooplankton in Lake Mendota for 1976–89.

and 1987. *Diaphana* occurred every year between midsummer and fall; somewhat higher densities were recorded in 1976–78 than in later years. *Bosmina* was found briefly in the plankton during early summer. Peak densities in many years prior to 1986 were higher than those in 1986–89.

*Leptodora kindtii*, the large predacious cladoceran, was also found regularly in the summer and fall plankton. Because of the small net used by the WDNR in sampling the zooplankton, *Leptodora* densities are less accurate than densities for the other smaller, but more numerous, crustacean species. A special large net was used in 1987–89 by the CFL to provide a better estimate of the true density of *Leptodora* (Lunte and Luecke 1990; Luecke et al., Ch. 14).

Both total *Daphnia* and total zooplankton biomasses exhibited wide seasonal fluctuations that were repeated annually (Figure 8.7). Peak zooplankton biomasses for each year occurred during the spring months and generally ranged between 20 and 40 g dry weight  $m^{-2}$ . A pronounced peak in *Daphnia* biomass also occurred during the spring months, but it reached only about one-half of the peak zooplankton biomass. Almost all of this difference between the two groups was attributed to the large populations of *Diacyclops biscuspisidatus thomasi* that occurred between late fall and early spring. Annual differences in peak biomasses for *Daphnia* and total zooplankton may have been caused by infrequent sampling during the spring period when population fluctuations were so pronounced. Minor fall increases in *Daphnia* biomasses also occurred during many years.

While the time course data for *D. pulicaria* and *D. galeata mendotae* depict their numerical densities in Figure 8.4, it is noteworthy that these species have different relative biomass characteristics. *D. pulicaria* weighs almost twice as much and has a much greater filtering or clearing rate

**Table 8-1.** Results of time series intervention analyses for effects of the shifts in cisco density on relative density of *D. pulicaria* (i.e., *D. pulicaria* density/total *Daphnia* density) and total *Daphnia* biomass. The shift parameters  $\alpha$  and  $\beta$  test for changes after the cisco year class of 1978 and the cisco summer kill of 1987, respectively. Because of the large number of degrees of freedom, *t*-ratios greater than 1.96 are significant at the 5% level.

Response variable	Parameter	Estimate	SE	<i>t</i> -ratio
Relative density of <i>D. pulicaria</i>	$\phi$	0.383	0.071	5.42
	$\phi_{13}$	-0.197	0.084	2.33
	$\alpha$	-0.299	0.080	3.72
	$\beta$	0.312	0.074	4.24
<i>Daphnia</i> biomass	$\phi$	0.264	0.072	3.69
	$\phi_{13}$	0.476	0.065	7.34
	$\alpha$	2.04	0.518	3.94
	$\beta$	1.08	0.508	2.12

capacity than *D. galeata mendotae* for the same body length (Lynch et al. 1986).

Minimum seasonal biomasses for total zooplankton were also recorded during most summers. Much of this summer depression was caused by the restriction of the zooplankton to oxygenated epilimnetic waters. In the central region where the net tow samples were taken, the anoxic bottom water represented as much as two-thirds of the total water column. During turnover and early summer when the entire water column was oxygenated, zooplankton were not restricted. Consequently, differences were greater between spring and summer biomasses (or densities) when expressed on a lake area basis as compared to biomasses when expressed on an oxygenated water volume basis.

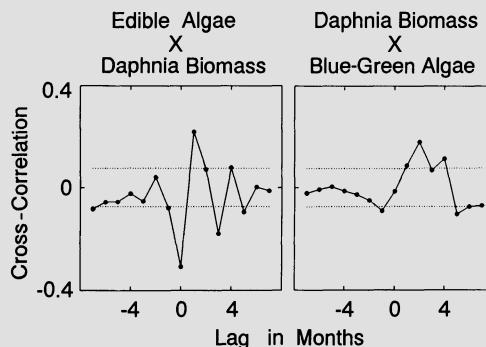
### Time Series Analysis

Fish population records for Lake Mendota indicate two changes in planktivory during 1976–89: increased planktivory in 1978 and decreased planktivory in 1987. The first change was followed by a sizeable year class of cisco in 1978, and the second one was preceded by a cisco summer kill in 1987 (Magnuson and Lathrop, Ch. 11; Rudstam et al., Ch. 12). Intervention analyses indicate that both events had significant effects on the *Daphnia* population (Table 8.1). After the cisco year class of 1978, biomass of *Daphnia* decreased by about  $2\text{ g m}^{-2}$  and the relative density of *D. pulicaria* decreased by about 30%. After the cisco die-off, biomass of *Daphnia* increased about  $1.1\text{ g m}^{-2}$  and relative density of *D. pulicaria* increased about 30%.

Intervention analyses detected increases in algal biovolume following the cisco year class of 1978 and decreases in algal biovolume following the

**Table 8-2.** Results of intervention analyses for the effects of the shifts in *Daphnia* species composition on edible and blue-green algal biovolumes. The shift parameters  $\alpha$  and  $\beta$  test for changes after the cisco year class of 1978 and the cisco summer kill of 1987, respectively. Because of the large number of degrees of freedom,  $t$ -ratios greater than 1.96 are significant at the 5% level.

Response variable	Parameter	Estimate	SE	$t$ -ratio
Edible algae	$\phi$	0.318	0.071	4.48
	$\phi_{13}$	0.426	0.068	6.30
	$\alpha$	609	345	1.77
	$\beta$	-573	343	1.67
Blue-green algae	$\phi$	0.479	0.066	7.30
	$\phi_{13}$	0.373	0.069	5.41
	$\alpha$	287	806	0.36
	$\beta$	-572	801	0.71



**Figure 8-8.** Cross-correlation vs. lag in months for filtered time series: edible algal biovolume  $\times$  *Daphnia* biomass and *Daphnia* biomass  $\times$  blue-green algal biovolume. Dashed lines denote the standard error around zero for the correlation coefficients. At positive lags, the first-named series antedates the second-named series; at negative lags, the second-named series antedates the first-named.

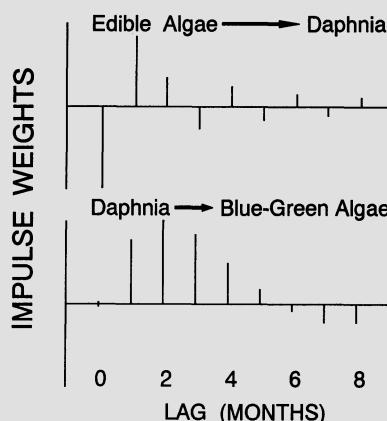
cisco summer kill of 1987, but the shifts were not significant at the 5% level (Table 8.2). Following the cisco year class, edible algal biovolume increased more than blue-green algal biovolume. Following the cisco die-off, both algal groups decreased by similar amounts.

Cross-correlations of edible algae with *Daphnia* biomass and of *Daphnia* biomass with blue-green algae were computed after using time series models to remove seasonal and autoregressive components of the variance (Figure 8.8). At lag 0, anomalies in edible algae and *Daphnia* biomass are negatively correlated. In early spring when edible algae are abundant, *Daphnia* biomass is relatively low. At lag 1 month, the

**Table 8-3.** Results of transfer function analysis for effects of edible biovolume on *Daphnia* biomass and effects of *Daphnia* biomass on blue-green algal biovolume. Because of the large number of degrees of freedom, *t*-ratios greater than 1.96 are significant at the 5% level.

Response variable	Parameter	Estimate	SE	<i>t</i> -ratio
<i>Daphnia</i> biomass	$\phi$	0.274	0.074	3.70
	$\phi_{13}$	0.301	0.076	3.98
	$\omega_0$	-6.95 <sup>a</sup>	1.55 <sup>a</sup>	4.50
	$\omega_2$	-6.84 <sup>a</sup>	1.71 <sup>a</sup>	3.99
	$\delta_1$	-0.823	0.167	4.91
Blue-green biomass	$\phi$	0.474	0.067	7.11
	$\phi_{13}$	0.266	0.075	3.53
	$\omega_0$	110	45.1	2.44
	$\delta_1$	1.27	0.230	5.51
	$\delta_2$	-0.585	0.220	2.66

<sup>a</sup>  $\times 10^{-4}$



**Figure 8-9.** Impulse weights vs. lag in months for transfer functions modeling effect of edible algae on *Daphnia* biomass and effect of *Daphnia* biomass on blue-green alga. Horizontal line denotes zero effect. Lengths of bars above or below the horizontal line show the relative magnitude of positive or negative effects. The bar at lag  $k$  months shows the effect of the input variable on the response variable  $k$  months in the future.

anomalies are positively correlated. An unusual bloom of edible algae leads to unusually high biomass of *Daphnia* a month later. At lag 3 months, the correlations are negative, indicating that the unusually high peak in *Daphnia* biomass leads to unusually low concentrations of edible algae 2 months later.

The pattern of correlations between *Daphnia* biomass and blue-green algae is quite different. Positive correlations occur at lags of 1 to 4 months. These indicate that unusually large peaks in *Daphnia* biomass are followed 1 to 4 months later by unusually high biomass of blue-green algae.

Transfer functions for effects of edible algae on *Daphnia* biomass and effects of *Daphnia* biomass on blue-green algae showed statistically significant effects (Table 8.3). Because the coefficients of the transfer functions are hard to understand intuitively, they are converted to impulse response functions (Wei 1990). Impulse weights (standardized to a maximum of one) are plotted against lag in months (Figure 8.9). The impulse weight at lag  $k$  shows the effect of the input variable on the response variable  $k$  months later. The impulse response function for edible algae effects on *Daphnia* biomass shows a predator-prey oscillation with decreasing amplitude at increasing lag. The impulse response function for *Daphnia* effects on blue-green algae shows that *Daphnia* have positive effects on blue-green algae several months later.

## Discussion

### Community Dynamics

The zooplankton community during 1976–89 was dominated by large spring and fall populations of *Diacyclops biscuspisidatus thomasi*. Either *D. galeata mendotae* or *D. pulicaria* was also important each year for a brief period in late spring, although their biomass and density were usually much less than that of *Diacyclops*. When *Daphnia* were at their peak abundance, they were able to graze the edible algae to very low levels, thus causing a clear-water phase. *D. galeata mendotae* also occurred during the fall months of some years, but in lower densities than during the spring. Other species of zooplankton were seasonally abundant during many years, but we did not evaluate their ecological role in Lake Mendota. The large invertebrate predator *Leptodora kindtii* was also found every year during the summer and fall months. Its ecological role is discussed by Luecke et al. (Ch. 14). *Eubosmina coregoni*, a recent invader of Wisconsin lakes, was abundant during the fall months of 1982–85. Kitchell and Sanford (Ch. 4) discuss its presence.

Zooplankton community dynamics during 1976–89 were not very different from conditions recorded for 1894–96 by Birge (1898). The same cladoceran species dominated and exhibited similar seasonal density changes. Brock (1985), Pedrós-Alió and Brock (1985), and Pedrós-Alió et al. (1985) summarized zooplankton densities for 1976–80 and also concluded that past and present community dynamics were similar.

### Long-term Trends in *Daphnia* Species

Historic records of *Daphnia* populations are of interest to the food web research detailed in this book, particularly because these data may indicate differences in planktivory and herbivory. The small *D. galeata mendotae* should dominate over the large *D. pulicaria* in periods of high planktivory by fishes; *D. pulicaria* should dominate over *D. galeata mendotae* when planktivory by fishes is low (Brooks and Dodson 1965).

In Birge's (1898) records for July 1894 to December 1896, *D. galeata mendotae* was abundant during the two spring and all three fall periods. *D. pulicaria* was only abundant during one spring season. Based on our analysis of the extensive unpublished data of Birge and Juday for 1906–17, *D. galeata mendotae* dominated the spring plankton except for one year when *D. retrocurva*, also a small species, was important. The fall plankton was dominated by both species, but in much lower total densities. The larger-sized *D. pulicaria* was relatively important for those years. We interpret these years to be a period of high planktivory, which corresponds to past observations about cisco and yellow perch populations during the early 1900s (Lathrop et al. 1992; Magnuson and Lathrop, Ch. 11).

More recent accounts indicate that *D. pulicaria* was abundant during the springs of 1952 (Ragotzkie 1953), 1959–60 (McNaught and Hasler 1964), and 1975 (B. Torke, unpubl. data). *D. galeata mendotae* was not abundant during the springs of 1960 and 1975 and presumably not in 1952. Also, zooplankton remains found in a sediment core suggest that *D. pulicaria* was abundant through recent decades (Kitchell and Sanford, Ch. 4). In the 1976–89 database that we analyzed in this chapter, *D. pulicaria* dominated the spring plankton in 1976–77. The cisco population was not abundant during much of the 1940s through 1977 (Magnuson and Lathrop, Ch. 11), until a major year class occurred in 1977 (Rudstam et al., Ch. 12). We interpret many of these years prior to the return of the cisco as being a period of low planktivory during the spring months. Because *D. galeata mendotae* was generally the dominant species during the fall months of 1976–89, and because the sediment core also contained a significant proportion of *D. galeata mendotae* remains, we suggest that planktivory from all fish species is normally high enough during the fall to prevent *D. pulicaria* from increasing.

Beginning in 1978 when the cisco population increased, the dominance of *D. galeata mendotae* in the spring suggests a return to a period of high planktivory. A decrease in planktivory may have occurred after the partial cisco kill in 1983 (Rudstam et al., Ch. 12), but it was not enough to allow *D. pulicaria* to again dominate. The increase in proportion of *D. pulicaria* in the springs of 1985 and 1986 suggests that planktivory was further decreasing, a finding consistent with planktivory data presented in Luecke et al. (Ch. 14), but this does not explain the almost complete

dominance of *D. galeata mendotae* in the spring of 1987. The return to dominance of *D. pulicaria* in 1988–89 after the massive cisco kill in the summer of 1987 is consistent with previous *Daphnia* trends. The dominance of the smaller-sized *D. galeata mendotae* in the fall months of 1976–89 follows our earlier observation about higher planktivory by other fish.

### Herbivore–Algae Interactions

Grazer density and biomass in Lake Mendota span an enormous range, from very high levels that likely have substantial grazing effects to very low levels that likely have scant impact on algae. However, most of the variation is expressed as intraannual seasonal fluctuations. Sustained multiyear shifts in grazing intensity have not occurred in the historical record we analyzed, although such changes may have occurred prior to initiation of the record studied (Kitchell and Sanford, Ch. 4).

Our analyses support the conclusion that significant decreases in *Daphnia* biomass, specifically *D. pulicaria*, followed the 1978 year class of cisco (Rudstam et al., Ch. 12). Changes in blue-green algal biovolume following this event were nonsignificant, both ecologically and statistically. Nutrient inputs and concentrations were relatively high during this period, and blue-green algae may have already been near their maximum attainable biomass before the decrease in grazing pressure. Modeling studies (Carpenter, Ch. 23) and empirical analyses (Benndorf 1990) suggest that grazing has little effect on blue-green algae if nutrient levels are sufficiently high. In contrast, the increase in edible algal biovolume after the cisco year class was large from an ecological standpoint, though not quite significant at the conventional 5% level of statistics.

Our analyses support the conclusion that the biomass of *Daphnia*, specifically *D. pulicaria*, increased after the 1987 summer kill of cisco. The shift in edible algal biomass was similar in magnitude (but opposite in direction) to the shift that occurred after 1978. The decrease in blue-green algal biovolume after the cisco summer kill was large from an ecological standpoint but smaller than its standard error. Vanni et al. (Ch. 13) show convincingly that increased grazing accounts for the events of 1988. Relatively high algal biomass in 1989 caused our intervention analyses to be nonsignificant. This variability appears consistent with the model of Carpenter (Ch. 23), although data from several more years at low cisco density are needed for a satisfactory test of the model.

The seasonal succession of plankton in Lake Mendota parallels that known from many eutrophic lakes (Sommer et al. 1986). The spring bloom of edible algae is followed by rapid growth of populations of grazers, especially *Daphnia*. Heavy grazing is followed by a clear-water phase of low algal densities. *Daphnia* decline in density later in the clear-

water phase, which gives way to summer conditions of algal blooms and low grazer densities.

Time series analysis shows that this sequence is not merely a seasonal correlation. It is actually driven by the coupled dynamics of herbivores and their algal prey. Anomalies (i.e., departures from typical seasonal patterns) in edible algal densities are positively related to anomalies in *Daphnia* densities a month later. In other words, the pulse of *Daphnia* in spring is controlled by algal resources. Anomalies in *Daphnia* density have strong negative relationship with subsequent anomalies in edible algal biovolume. We infer that grazing causes the clear-water phase, a conclusion consistent with the experimental studies of Lampert et al. (1986). Anomalies in *Daphnia* density also have positive relationships with anomalies in blue-green algal density 1–4 months later. Facilitation of colonial blue-green algae by grazing has been analyzed by Lynch (1980) and Andersson and Cronberg (1984) and modeled by Carpenter (Ch. 23). Blue-green algae benefit from nutrients recycled by *Daphnia* but suffer relatively low grazing losses.

The time series analyses presented in this chapter and the previous one corroborate the theoretical analysis of blue-green algal blooms offered by Carpenter (Ch. 23). Carpenter's model and the long-term record are consistent in several respects:

1. Edible algal resources determine the magnitude of the *Daphnia* pulse;
2. Grazing leads to the clear-water phase;
3. Resource limitation causes the subsequent collapse of *Daphnia* (Vanni et al., Ch. 13; Luecke et al., Ch. 14);
4. The predator-prey oscillation of *Daphnia* and edible algae fosters the establishment and growth of blue-green algae, which dominate the system for the remainder of the summer.

In summary, these data support the view of blue-green algal blooms as an ecosystem syndrome linked to destabilization of the interaction between edible algae and *Daphnia*.

Stern (1989) points out that abundant *Daphnia* do not always direct succession toward colonial blue-green algae. Large *Daphnia* populations induced by whole-lake fish manipulations have suppressed colonial blue-greens (Shapiro and Wright 1984; Carpenter et al. 1987). In pond experiments, absence of *Daphnia* in spring led to low transparency which favored the development of buoyant blue-green algae (Spencer and King 1984). On the other hand, high densities of *D. pulex* and *Aphanizomenon flos-aquae* often co-occur in eutrophic lakes (Lynch 1980; Andersson and Cronberg 1984). Our time series analyses indicate that peaks in *Daphnia* abundance do set the stage for dominance of blue-green algae in Lake Mendota.

Our finding has important management implications. *Daphnia* in Lake Mendota can certainly attain densities sufficient to suppress phyto-

plankton and improve water clarity. However, grazer control of the algae is sustained for only a few weeks during most years. A predator-prey cycle of *Daphnia* and edible algae in spring leads to dominance by blue-green algae, possibly through the mechanisms modeled by Carpenter (Ch. 23). If we are to sustain *Daphnia* populations through the summer and maintain the phytoplankton at low biovolumes through grazing, it may be essential to stabilize the interaction of *Daphnia* and edible algae during spring and early summer.

This chapter and the previous one show the enormous value of long-term records for both basic research and management. The database has allowed us to test fundamental ideas about interactions of three trophic levels and nutrients. Patterns in the time series are a benchmark for testing the simulation models developed in later chapters of this volume. Ecosystem states potentially attainable by management are illustrated by the historical record. Potentially causal relationships, revealed by time series analysis, help forecast the consequences of management actions.

The Lake Mendota time series is long enough to reveal some exciting patterns, such as the linkage between herbivore-alga oscillations and blue-green algal blooms. Other intriguing patterns are not yet clearly resolved because of the high variability of the time series. For example, the standard errors of the models for blue-green algal biomass are still too large to provide reliable forecasts or yield a satisfactory assessment of responses to zooplankton and nutrient dynamics (Lathrop and Carpenter, Ch. 7). The precision of our time series models will improve as more data are collected, and the decline in the standard errors with time should accelerate because of the massive reconfiguration of the fish community (Carpenter 1988). Sustained monitoring of Lake Mendota is likely to yield remarkable insights about physical, chemical, and biotic effects on water quality during the next decade.

*Acknowledgments.* We thank C. Luecke and L.G. Rudstam for critical reviews of this chapter and S.H. Nehls for editorial assistance. Data collection was supported by the WDNR and the Federal Aid in Sport Fish Restoration Act under Project F-95-P. Zooplankton enumerations were conducted by K.J. Kramer, T.L. Brasino, J.W. Ihrig, E.R. Deppe, and B.A. Kaplin. Modeling and time series analyses were supported by a grant from the Andrew Mellon Foundation.

## References

- Andersson G, Cronberg G (1984) *Aphanizomenon flos-aquae* and large *Daphnia*—An interesting plankton association in hypertrophic water. In Bosheim S, Nicholls M (eds) Nordisk limnologsymposium, Interactions between trophic levels in freshwaters, Norsk Limnologforening, Oslo

- Bardach JE (1949) Contribution to the ecology of the yellow perch (*Perca flavescens* Mitchell) in Lake Mendota, Wisconsin. Ph.D. Thesis, University of Wisconsin, Madison
- Benndorf J (1990) Conditions for effective biomanipulation: Conclusions derived from whole-lake experiments in Europe. *Hydrobiologia* 200/201:187–203
- Birge EA (1898) Plankton studies on Lake Mendota: II. The Crustacea of the plankton from July, 1894, to December, 1896. *Trans. Wis. Acad. Sci. Arts Lett.* 11:274–448
- Birge EA, Juday C (1922) The inland lakes of Wisconsin: The plankton I. Its quantity and chemical composition. *Wis. Geol. Nat. Hist. Surv. Bull.* No. 64, Sci. Ser. No. 13
- Box GEP, Tiao GC (1975) Intervention analysis with applications to economic and environmental problems. *J. Am. Stat. Assoc.* 70:70–79
- Brock TD (1985) A eutrophic lake: Lake Mendota, Wisconsin. Springer-Verlag, New York
- Brooks JL, Dodson SI (1965) Predation, body size, and composition of plankton. *Science* 150:28–35
- Carpenter SR (1988) Transmission of variance through lake food webs. In Carpenter SR (ed) Complex interactions in lake communities, Springer-Verlag, New York, pp 119–135
- Carpenter SR, Frost TM, Kitchell JF, Kratz TK, Schindler DW, Shearer J, Sprules WG, Vanni MJ, Zimmerman AP (1991) Patterns of primary production and herbivory in 25 North American lake ecosystems. In Cole J, Findlay S, Lovett G (eds) Comparative analyses of ecosystems: Patterns, mechanisms, and theories, Springer-Verlag, New York
- Carpenter SR, Kitchell JF (1988) Consumer control of lake productivity. *BioScience* 38:764–769
- Carpenter SR, Kitchell JF, Hodgson JR, Cochran PA, Elser JJ, Elser MM, Lodge DM, Kretchmer D, He X, von Ende C (1987) Regulation of lake primary productivity by food-web structure. *Ecology* 68:1863–1876
- Downing JA, Rigler FH (1984) A manual on methods for the assessment of secondary productivity in fresh waters. Blackwell, London
- Hrbacek J (1962) Species composition and the amount of zooplankton in relation to the fish stock. *Rozpr. Cesk. Akad. Ved Rada Mat. Prir. Ved* 72:1–116
- Hutchinson GE (1967) a treatise on limnology. Vol. 2: Introduction to lake biology and the limnoplankton. John Wiley & Sons, New York
- Lampert W, Fleckner W, Hakumat R, Taylor BE (1986) Phytoplankton control by grazing zooplankton: A study on the spring clear-water phase. *Limnol. Oceanogr.* 31:478–490
- Lathrop RC, Nehls SH, Brynildson CL, Plass KR (1992) The fishery of the Yahara lakes. Technical Bulletin (in press), Wisconsin Department of Natural Resources, Madison
- Lunte CC, Luecke C (1990) Trophic interactions of *Leptodora* in Lake Mendota. *Limnol. Oceanogr.* 35:1091–1100
- Lynch M (1980) *Aphanizomenon* blooms: Alternate control and cultivation by *Daphnia pulex*. In Kerfoot WC (ed) Evolution and ecology of zooplankton communities, University Press of New England, Hanover, New Hampshire, pp 299–304

- Lynch M, Weider LJ, Lampert W (1986) Measurement of the carbon balance in *Daphnia*. Limnol. Oceanogr. 31:17–33
- McNaught DC, Hasler AD (1964) Rate of movement of populations of *Daphnia* in relation to changes in light intensity. J. Fish. Res. Board Can. 21:291–318
- Neess J (1949) Development and status of pond fertilization in central Europe. Trans. Am. Fish. Soc. 76:335–358
- Pedrós-Alio C, Brock TD (1985) Zooplankton dynamics in Lake Mendota: Short-term versus long-term changes. Freshwat. Biol. 15:89–94
- Pedrós-Alio C, Woolsey E, Brock TD (1985) Zooplankton dynamics in Lake Mendota: Abundance and biomass of the metazooplankton from 1976 to 1980. Trans. Wis. Acad. Sci. Arts Lett. 73:167–185
- Ragotzkie RA (1953) The distribution of *Daphnia* in Lake Mendota and their mode of feeding. Ph.D. Thesis, University of Wisconsin, Madison
- Shapiro J, Lamarra V, Lynch M (1975) Biomanipulation: An ecosystem approach to lake restoration. In Brezonik PL, Fox JL (eds) Proceedings of a symposium on water quality management through biological control, University of Florida, Gainesville
- Shapiro J, Wright DI (1984) Lake restoration by biomanipulation: Round Lake, Minnesota the first two years. Freshwat. Biol. 14:371–383
- Sommer U, Gliwicz ZM, Lampert W, Duncan A (1986) The PEG model of seasonal succession of planktonic events in freshwaters. Arch. Hydrobiol. 106:433–471
- Spencer CN, King DL (1984) Role of fish in regulation of plant and animal communities in eutrophic ponds. Can. J. Fish. Aquat. Sci. 41:1851–1855
- Sterner RW (1989) The role of grazers in phytoplankton succession. In Sommer U (ed) Plankton ecology: Succession in plankton communities, Springer-Verlag, Berlin, pp 107–170
- Wei WWS (1990) Time series analysis. Addison-Wesley, New York

# **9**

## **Long-Term Vegetation Trends: A History**

**Stanley A. Nichols, Richard C. Lathrop, and  
Stephen R. Carpenter**

### **Introduction**

Littoral zone vegetation is integral to the fish productivity of lakes and their capacity to support waterfowl. The refuge for small fishes provided by macrophyte beds alters predator-prey interactions in ways that directly affect productivity of sport fish (Crowder and Cooper 1982; Savino and Stein 1982; Wiley et al. 1984). Different plant species support varying number of macroinvertebrates that are prey for fish and waterfowl (Lathrop, Ch. 10). Over the past century the vegetation of Lake Mendota has undergone substantial changes with significant implications for water quality and fish populations. Valuable clues to the potential consequences of future changes in the macrophyte community can be derived from an understanding of these historical changes.

The history of vegetation studies in Lake Mendota is long, and research interests and techniques have varied over the years. However, it is possible to piece together studies so that the vegetational history of the lake since the early 1900s can be described with reasonable accuracy. Elements that are common to many studies are (1) description of important plant species, (2) maximum depth of plant distribution, (3) standing crop estimates, and (4) nitrogen and phosphorus composition of plant tissue. The purpose of this chapter is to (1) reconstruct macrophyte community changes, including those of filamentous algae, (2) evaluate trends found in the data and relate them to other events in the lake and its watershed, and (3) offer some generalizations about what the future may hold.

Early accounts of dense plants in Lake Mendota date from the mid-1880s (Lathrop 1989). Research on the distribution (Denniston 1921) and biomass (Rickett 1921) of aquatic plants throughout Lake Mendota was initially conducted between 1910 and 1920. Early studies also described the chemical composition of large aquatic plants and filamentous algae (Schuette and Hoffman 1921; Schuette and Alder 1927, 1929).

During the early 1940s the relationship between macrophytes and macroinvertebrates was intensively studied (Andrews and Hasler 1943; Andrews 1946), and during the 1940s and 1950s field surveys of aquatic plants were done to assess their potential as fish and waterfowl habitat (Threinen 1949; Threinen and Helm 1952; Zimmerman 1953).

From the 1960s on, interest turned to the ecological impacts caused by the invasion and subsequent decline of Eurasian watermilfoil (*Myriophyllum spicatum* L.) (Lind and Cottam 1969; Carpenter 1980a; Vander Zouwen 1982) and strategies to manage the milfoil problem (Mossier 1968; Nichols and Cottam 1972; Nichols 1973; Andrews 1980).

Most research after the initial whole-lake studies by Denniston (1921) and Rickett (1921) was confined to limited locations on the lake, primarily University Bay, or concentrated on the ecophysiology of selected species (Gerloff and Krombholz 1966; Gustafson 1976; Titus 1977; Carpenter 1980b). Macrophyte studies continue on the lake in an effort to understand the dynamics of lake vegetation, to develop future

**Table 9-1.** Relative importance of aquatic plants in Lake Mendota.<sup>a</sup>

Species	1912	1920	1940s–50s	1989
<i>Vallisneria americana</i>	1	1	1	5
<i>Potamogeton richardsonii</i>	2	3	—	—
<i>Potamogeton zosteriformis</i>	3	7	6	10
<i>Potamogeton pectinatus</i>	4	4	5	3
<i>Ceratophyllum demersum</i>	5	9	3	1
<i>Chara</i> sp.	6	5	—	—
<i>Najas flexilis</i>	7	8	—	—
<i>Myriophyllum</i> spp.	8	6	2	2
<i>Potamogeton amplifolius</i>	9	2	7	—
<i>Potamogeton illinoensis</i>	10	—	—	—
<i>Nymphaea tuberosa</i>	—	—	10	9
<i>Elodea canadensis</i>	—	—	4	6
<i>Ranunculus trichophyllum</i>	—	10	—	—
<i>Heteranthera dubia</i>	—	—	—	4
<i>Nelumbo lutea</i>	—	—	—	8
<i>Potamogeton praelongus</i>	—	—	9	—
<i>Potamogeton crispus</i>	—	—	8	7

<sup>a</sup> Data sources: 1912 (Denniston 1921); 1920 (Rickett 1921); 1940s–50s (Threinen 1949; Threinen and Helm 1952; Zimmerman 1953); 1989 (Lathrop and Hartman 1990).

—, not in the top 10 most important species.

**Table 9-2.** Relative importance of aquatic plants in University Bay.<sup>a</sup>

Species	1912	1920	1966	1978	1979	1980	1984	1989
<i>Vallisneria americana</i>	1	1	2	3	3	3	8	3
<i>Potamogeton amplifolius</i>	2	2	—	—	—	—	—	—
<i>Myriophyllum</i> spp.	3	9	1	1	1	1	1	2
<i>Ceratophyllum demersum</i>	4	3	3	4	2	5	2	1
<i>Potamogeton richardsonii</i>	5	5	5	—	—	—	—	—
<i>Potamogeton zosteriformis</i>	6	—	—	—	—	—	—	—
<i>Potamogeton pectinatus</i>	7	7	8	5	9	2	6	8
<i>Lemna minor</i>	8	—	—	—	—	—	—	—
<i>Potamogeton illinoensis</i>	9	4	—	—	—	—	—	—
<i>Chara</i> sp.	10	—	—	—	—	—	—	—
<i>Najas flexilis</i>	—	6	—	9	—	—	—	—
<i>Elodea canadensis</i>	—	—	10	6	5	6	3	7
<i>Nymphaea tuberosa</i>	—	—	4	7	6	4	5	5
<i>Potamogeton filiformis</i>	—	—	—	10	4	—	—	—
<i>Potamogeton foliosus</i>	—	—	—	2	7	7	—	—
<i>Nelumbo lutea</i>	—	—	9	—	—	10	7	6
<i>Zannichellia palustris</i>	—	—	—	—	—	9	—	—
<i>Heteranthera dubia</i>	—	10	7	—	—	—	—	4
<i>Potamogeton nodosus</i>	—	—	—	—	8	—	—	—
<i>Ranunculus trichophyllus</i>	—	8	6	—	—	—	—	—
Unidentified spp.	—	—	—	—	—	—	4	—
<i>Potamogeton crispus</i>	—	—	—	8	—	8	—	—

<sup>a</sup> Data sources: 1912 (Denniston 1921), 1920 (Rickett 1921); 1966 (Lind and Cottam 1969); 1978–79 (raw data used by Andrews 1980); 1980 (Vander Zouwen 1982); 1984 (R. Lathrop, WDNR); 1989 (Lathrop and Hartman 1990).

—, not in the top 10 most important species.

management strategies for nuisance macrophyte growth, and to gain a better understanding of the relationship between the littoral and pelagic zones (Lathrop and Hartman 1990).

## Changes in the Plant Community

### Species Occurrence

To compare species occurrence between surveys that used different sampling techniques and different reporting methods, the 10 most important species found in each study were ranked. Importance was determined by comparing relative frequency, relative biomass, or relative abundance of plants in each survey. Results were compared for both the whole lake (Table 9.1) and for University Bay (Table 9.2). The importance estimates for the 1940s–50s in Table 9.1 are based on an average of data

**Table 9-3.** Relative frequency (%) of macrophyte species in University Bay, 1966–89.<sup>a</sup>

Species	1966	1978	1979	1980	1984	1989
<i>Ceratophyllum demersum</i>	13.6	10.3	25.4	3.7	26.4	48.7
<i>Myriophyllum spicatum</i>	55.6	39.4	29.6	45.4	38.4	27.8
<i>Vallisneria americana</i>	15.7	14.3	14.8	14.2	1.2	9.8
<i>Heteranthera dubia</i>	1.2	—	—	1.0	—	9.8
<i>Elodea canadensis</i>	0.3	5.1	9.2	2.5	18.0	0.4
<i>Nymphaea tuberosa</i>	7.1	4.6	4.9	5.3	3.6	1.0
<i>Nelumbo lutea</i>	0.4	—	—	1.2	1.2	0.8
<i>Potamogeton pectinatus</i>	1.1	6.3	1.4	19.6	2.4	0.4
<i>P. crispus</i>	—	2.3	—	1.5	—	—
<i>P. filiformis</i>	—	0.6	10.6	—	—	—
<i>P. foliosus</i>	<0.1	15.4	4.2	2.0	—	—
<i>P. nodosus</i>	—	—	1.4	—	—	—
<i>P. richardsonii</i>	1.7	—	—	0.9	—	—
<i>P. zosteriformis</i>	0.1	—	—	—	—	—
<i>Najas flexilis</i>	0.1	0.6	—	1.0	—	—
<i>Ranunculus trichophyllus</i>	1.5	—	—	—	—	—
<i>Zannichellia palustris</i>	<0.1	—	—	1.2	—	—
Unidentified spp.	—	—	—	—	7.2	—

<sup>a</sup>Data sources: 1966 (Lind and Cottam 1969); 1978–79 (raw data used by Andrews 1980); 1980 (Vander Zouwen 1982); 1984 (R. Lathrop, WDNR); 1989 (Lathrop and Hartman 1990).

All surveys conducted during July/August.

—, not reported.

from Zimmerman (1953), Threinen (1949), and Threinen and Helm (1952). Because sampling techniques were more consistent, it is possible to compare the relative frequency of important species in University Bay (Table 9.3) from 1966 through 1989. A comparison between Table 9.2 and Table 9.3 shows the difference in importance between the first-ranked species, which varied between a relative frequency of 28% and 56%, and the 10th-ranked species, which usually had a relative frequency of less than 1%.

*Vallisneria americana* Michx. dropped from being the most important species in Lake Mendota in 1912 to the fifth most important in 1989. Conversely, *Ceratophyllum demersum* L. changed from the fifth most important species in 1912 to the most important in 1989. *Potamogeton richardsonii* (Benn.) Rydb., *Chara* sp., *Najas flexilis* (Willd.) Rostk. & Schmidt., and *Potamogeton illinoensis* Morong. were not ranked in the top 10 species after the 1912 or 1920 surveys. *Potamogeton amplifolius* Tuckerm. was no longer ranked after the 1940s–50s survey. *Potamogeton crispus* L., *Heteranthera dubia* (Jacq.) MacM., and *Elodea canadensis* Michx. became more important and *Potamogeton zosteriformis* Fern. less

important in later surveys. *Myriophyllum* spp. also became more important in later surveys but the species changed. This was caused by the invasion of *M. spicatum* L., which will be discussed later. Examinations of old reports (Rickett 1921; Denniston 1921; Threinen and Helm 1952) and specimens in the University of Wisconsin-Madison herbarium indicate that the following members of the submersed flora have not been recorded since prior to 1960: *Myriophyllum alterniflorum* DC., *M. verticillatum* L., *Potamogeton alpinus* Balbis, *P. friesii* Rupr., *P. natans* L., *P. praelongus* Wulf., and *P. vaginatus* Turcz.

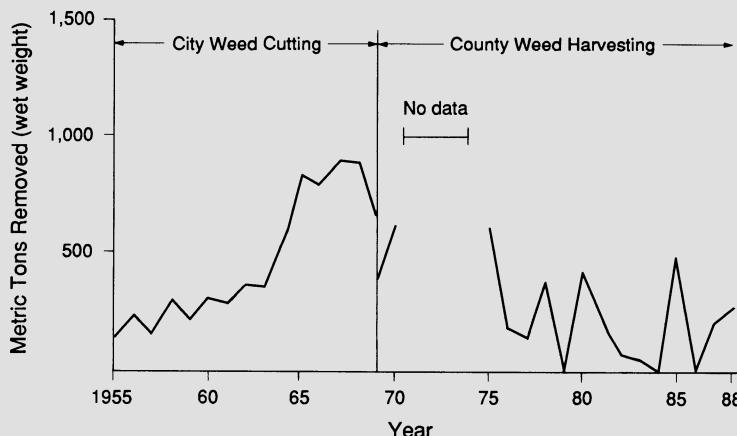
An examination of University Bay vegetation reflects similar trends. By 1966, *P. amplifolius*, *P. zosteriformis*, *P. illinoensis*, and *Chara* sp. were no longer important parts of the vegetation. *P. richardsonii* dropped out of importance after 1966. The predominance of *M. spicatum* between 1966 and 1984 is clearly seen, as is the gradual rise in importance of *C. demersum* and the decline in importance of *V. americana* over the years (Table 9.2).

### Invasion of Exotic Species

The first exotic macrophyte invader in Lake Mendota was reported by Andrews (1946). He found an abundance of *Potamogeton crispus* in University Bay in early June of 1946. At that time the plants had started flowering, and almost immediately they became detached from the bottom to form huge floating masses of plant material. Andrews had not found *P. crispus* in the 1939–41 era when his studies began, nor did Zimmerman (1953) find it in 1942.

*P. crispus* was reported as abundant in July 1948 (Threinen 1949) and common in late summer of 1951 (Threinen and Helm 1952). *P. crispus* was in the top 10 common species in 1989 (Table 9.1), but based on relative frequency it was an insignificant part of the vegetation (Table 9.3). *P. crispus* could have been more abundant earlier in the growing season than reported by these surveys. It typically blooms early in the spring and dies off by July (Nichols and Shaw 1986).

Dramatic changes in the Lake Mendota vegetation occurred with the invasion and subsequent decline of *M. spicatum*. The invasion probably occurred between 1962 and 1966. *M. spicatum* did not occur in collections made in 1962 (Nichols 1975). Macrophyte biomass removed by city weed-cutting crews doubled between 1963 and 1965 (Figure 9.1). Although this increase may be attributable to increased removal effort, the effort was probably needed because of nuisance-level growths of *M. spicatum*. Early weed cutting without immediate removal of cut plants may have spread the milfoil problem. Lind and Cottam (1969) found an abundance of *Myriophyllum exalbescens* Fern. in University Bay in 1966. Later examination of plant samples showed that the milfoil they recorded was *M. spicatum* (Nichols 1975). The importance of *Myriophyllum* spp.



**Figure 9-1.** Trends in macrophyte abundance in Lake Mendota based on City of Madison weed-cutting records and Dane County week-harvesting records. Although no data are available for the early 1970s, accounts by county personnel indicate that large amounts of weeds were removed (after Lathrop 1989).

increased from ninth in the 1920s to first in 1966 in University Bay (Table 9.2).

Denniston (1921) and Rickett (1921) reported *M. verticillatum* L. in Lake Mendota in 1912 and 1921. These collections could not be confirmed by herbarium specimens. *M. exalbescens* was found during the 1940s through the 1960s; *M. spicatum* was reported from the late 1960s onward. These three species are similar taxonomically, so interpreting *Myriophyllum* dynamics is difficult.

After invasion, a subsequent decline in *M. spicatum* is common (Carpenter 1980a). The beginning of the decline is not well documented for Lake Mendota, but there was a dramatic decline in *M. spicatum* biomass in neighboring Lake Wingra in 1977 (Carpenter 1980a). A major decrease in plant biomass harvested by Dane County weed removal crews occurred between 1975 and 1976 (Figure 9.1). By 1978 and 1979, Andrews (1980) reported a substantial decrease in the relative frequency of *M. spicatum* in University Bay (Table 9.3). He stated, “The most striking feature of the data is the precipitous general decline of species, predominant in 1978, to a lesser abundance in 1979.” There was a substantial increase in narrow-leaved *Potamogeton* spp. (*P. foliosus* Raf., *P. filiformis* Pers., and *P. pectinatus* L.) during the 1978–80 time period (Table 9.3). Vander Zouwen (1982) attributed the increase in *P. pectinatus* to an increase in water turbidity. However, plant populations may have changed because of the milfoil decline. A similar increase in *P. pectinatus* occurred after milfoil decline in Lake Wingra (Carpenter 1980a).

There are a number of hypotheses as to the cause of milfoil declines, including insects, disease, and pollution (Nichols and Shaw 1986). However, no single cause has been convincingly determined for Lake Mendota, and it is very likely to be multifactored (Carpenter 1980a). Andrews (1980), while investigating factors that may have caused the milfoil decline, recorded a major shift from *M. spicatum* to *M. exalbescens* (native milfoil) from 1978 to 1979 in University Bay. However, he noted that this shift may have actually been the occurrence of a less vigorous growth of Eurasian milfoil which had phenotypic characteristics similar to native milfoil. This interpretation seems more likely, particularly because of the difficulties with separating these two species. He noted that much of the milfoil displayed black, banded flecking of leaflets and nonuniform flecking of stems; elongate stem lesions; atrophied, malformed, darkened, and stiffened leaves; and general chlorosis and necrosis. These symptoms are similar to those found in other declining *M. spicatum* populations (Nichols and Shaw 1986).

In retrospect, it appears that Andrews (1980) and Vander Zouwen (1982) witnessed the end of the milfoil decline and subsequent community changes with their sampling efforts. For approximately 10 years before the decline, it appears that the plant community was stable but strongly dominated by *M. spicatum*. At least through 1969, *M. spicatum* constituted more than 90% of the vascular plant biomass in University Bay (Cottam and Nichols 1970). Between 1969 and 1978 the community was not sampled, but it appeared visually the same until the mid-1970s. Since the decline, Eurasian milfoil is still a significant part of the plant community, but its importance has decreased while the importance of *C. demersum* has increased (Table 9.3). The increase in narrow-leaved pondweeds was short-lived. By 1984, the relative frequency of *P. pectinatus* dropped below 2.5%.

### Shallow Bays

The 1920 plant community in shallow bays consisted of the emergent species *Zizania aquatica* L. and *Scirpus lacustris* L. (i.e., probably *Scirpus validus* Vahl.) along with *Nuphar advena* Ait., *Lemna minor* L., *Lemna trisulca* L., and a variety of submersed species (Rickett 1921). By 1974 the emergent species in University Bay was almost exclusively cattail (*Typha latifolia* L.) (Gustafson 1976). The distribution of emergent species was not mapped in detail by Rickett so it cannot be determined how much of the *Zizania–Scirpus* area has converted to cattail marsh; how much contains submersed and floating-leaved species, but no longer contains emergent species; and how much is now dry land caused by shoreline draining and filling. A number of shallow-water or emergent species, including *Acorus calamus* L., *Alisma plantago-aquatica* L., *Carex comosa* Boott., *Scirpus acutus* Muhl., *Scirpus fluviatilis* (Torr.) Gray, and

**Table 9-4.** Maximum water depth of macrophyte growth in Lake Mendota.<sup>a</sup>

Year	Average maximum depth (m)	Greatest depth (m)
1912	5.0–5.5	6.0
1920	5.0	6.5
1948	← 4.9 (?) →	
1951	← 4.8 (?) →	
1966	2.5–3.9	≤4.4
1978		≤3.8
1979		3.0
1980	1.5–2.4	≤2.9
1984		2.9
1989	3.5	5.0

<sup>a</sup> Data sources: 1912 (Denniston 1921); 1920 (Rickett 1921); 1948 (Threinen 1949); 1951 (Threinen and Helm 1952); 1966 (Lind and Cottam 1969); 1978–79 (Andrews 1980); 1980 (Vander Zouwen 1982); 1984 (R. Lathrop, WDNR, unpubl. data); 1989 (Lathrop and Hartmann 1990).

↔, bottom type undifferentiated.

*Zizania aquatica*, were noted in early reports or found as herbarium specimens but have not been recorded for at least the last 40 years.

### Changes in Depth of Plant Distribution

Indirectly, the maximum depth of plant growth indicates the extent of adequate light penetration through the water column during the parts of the year when light is critical to plant growth (Canfield et al. 1985; Chambers and Kalff 1985). A decrease in maximum plant growth depth decreases the total habitable area for plants and may indicate an increase in the turbidity of the water. Likewise, an increase in water clarity may allow macrophytes to expand into deeper water and increase the area of lake bottom inhabited by plants.

The average maximum depth of plant growth in Lake Mendota was 5 m or deeper in 1912 and 1920. This depth gradually decreased to 2.4 m or less in 1980 (Table 9.4). From 1986 through 1989, water clarity increased and the maximum depth of plant growth increased to 3.5 m (Lathrop and Hartman 1990).

How much of this change is cause and how much is effect? External loading of sediment and nutrients could increase turbidity and decrease the maximum depth of plant growth. Long-term trends of phosphorus and nitrogen concentrations did increase after the mid-1940s (Lathrop, Ch. 6). This is a possible explanation for the observed decline from 1912 to 1980. However, water clarity in late spring and early summer did not decrease during this time period, but water clarity during midsummer and late summer may have declined (Lathrop, Ch. 6). Vander Zouwen (1982)

**Table 9-5.** 1920 standing crop stratified by depth zone and bottom type ( $\text{g m}^{-2}$  dry weight).<sup>a</sup>

Depth (m)	Gravel	Mud
0–1	170	164
1–3	202	341
>3		↔ 181 ↔

<sup>a</sup> After Rickett (1921).

↔, bottom type undifferentiated.

attributed the shallow depth of plant growth he found in 1980 to turbidity and siltation from Willow Creek, which flows into University Bay. Since the 1978–80 era was probably part of the milfoil decline, plants may have died off from other causes. Increased turbidity may have been caused by sediment resuspension due to limited macrophyte cover and increased algal growth.

## Standing Crop Estimates

### Macrophytes

Rickett (1921) made the first and only standing crop estimates for the entire lake. He estimated the 1920 dry weight standing crop at  $2.1 \times 10^6 \text{ kg}$  for the whole lake or  $2.019 \times 10^3 \text{ kg ha}^{-1}$  for the littoral zone. He stratified his estimates by depth zone and bottom type. The highest standing crop was produced on mud bottoms in the 1- to 3-m depth zone (Table 9.5).

Rickett also separated out filamentous algal communities and shallow bays for special consideration. The 1920 standing crop estimate for shallow bays was  $383 \text{ g m}^{-2}$  (Rickett 1921). There were limited areas that supported  $670 \text{ g m}^{-2}$  of *Scirpus* sp., or  $501 \text{ g m}^{-2}$  of *Z. aquatica*, or  $290 \text{ g m}^{-2}$  of *N. advena*.

Gustafson (1976) conducted a detailed study of cattail growth in University Bay in 1974. He found a maximum above-ground standing crop of  $1,400 \text{ g m}^{-2}$  in early September and a maximum below-ground standing crop of  $686 \text{ g m}^{-2}$  in mid-October. A single sampling in September 1975 revealed an above-ground standing crop of  $1,207 \text{ g m}^{-2}$  and a below-ground standing crop of  $807 \text{ g m}^{-2}$ .

The cattail community sampled by Gustafson was nearly monotypic. The above-ground standing crop of cattail was around two to three times greater than the standing crop of emergents in 1920. In 1920 the standing crop of submersed species in shallow bays was considerably higher than the standing crop of submersed species in deeper water (Table 9.6).

**Table 9-6.** Average June–September standing crop for University Bay submersed macrophytes ( $\text{g m}^{-2}$  dry weight).<sup>a</sup>

Year	Area 1 <sup>b</sup>	Area 2	Area 3	Area 4
1920 <sup>c</sup>	← 289 →			383
1939 <sup>c</sup>	← 67 →			
1940 <sup>d</sup>	← 374 (94) →			
1941 <sup>d</sup>	← 146 →			
1966	74	99	85	113
1967	45	—	109	125
1968	—	204	103	—
1969	—	—	143	159
1978	9	—	—	—
1984	—	—	—	222

<sup>a</sup>Data sources: 1920 (Rickett 1921); 1939–41 (Andrews 1946); 1966 (Lind 1967); 1967 (Mossier 1968); 1968–69 (Nichols and Cottam 1972); 1978 (Carpenter 1980b); 1984 (R. Lathrop, WDNR).

<sup>b</sup>Sampling areas shown in Figure 9.2.

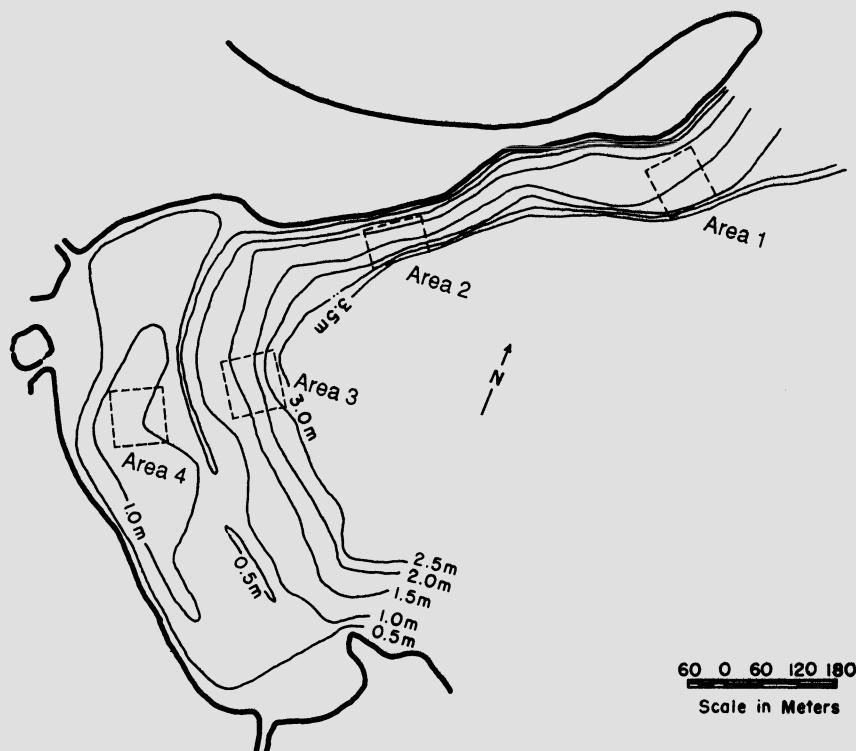
<sup>c</sup>Based only on one sampling per summer.

<sup>d</sup>Primarily *Chara* sp., mixed species bed reported in parentheses.

↔, specific sampling area unknown.

—, not reported.

All other standing crop estimates were confined to University Bay (Table 9.6). For descriptive purposes, the bay is divided roughly into four geographic areas (Figure 9.2). Areas 1 and 2 are along the south side of Picnic Point. Area 1 is near the eastern end of the point and area 2 is about half-way down the point. There is a north-south trending sandbar in the western end of the bay. Area 3 lies to the lakeward side of the bar and area 4 lies to the landward side. Area 1 has a sand bottom, areas 2 and 3 have a sand-silt bottom, and area 4 has a silt-ooze bottom. Depth contours are shown in Figure 9.2. Table 9.6 compares the standing crop found at these locations. Rickett (1921) reported the highest standing crop for the area behind the sandbar (i.e., the shallow bay area). Only the 1984 value comes within 50% of his estimates for this area. For the values outside the sandbar, Rickett's (1921) whole-lake value was used for comparison. Rickett considered anything to the lake side of the sandbar as part of the whole lake. The only value to exceed Rickett's whole-lake estimate was made by Andrews (1946) of the 1940 standing crop. This estimate was from a dense bed of *Chara* sp. which grew on both sides of the sandbar. Andrews was not specific about the location in the bay where samples were collected, so data were assigned to the whole bay.



**Figure 9-2.** Hydrographic map of University Bay showing stand locations.

Standing crops were also compared by month (Table 9.7). The maximum standing crop for areas 2, 3, and 4 occurred in July. This reflects the strong dominance of milfoil, which has a growth peak in late June to early July (Figure 9.3). The June standing crop in area 4 was a higher percentage of the maximum than in areas 2 or 3. Area 4 is more shallow and the sediments probably warm more quickly, so growth may begin earlier.

The maximum standing crop in area 1 occurred in August. This area is dominated by *Vallisneria americana*, which grows later in the summer (Carpenter 1980b). Baywide estimates by Andrews (1946) peaked in September. He thought this was unusual but attributed it to a strong late-season growth of *Chara* sp. Any standing crop after September is considered overwintering biomass. It was always less than  $50 \text{ g m}^{-2}$  except for  $62 \text{ g m}^{-2}$  found by Lind (1967) for 1966 in area 4.

Unfortunately, no standing crop estimates were made during the late 1940s or late 1970s, so the impact of the *P. crispus* invasion and of the milfoil decline on standing crop cannot be documented.

**Table 9-7.** Monthly variability of standing crop in University Bay ( $\text{g m}^{-2}$  dry weight).<sup>a</sup>

	June	July	August	September	After September
Area 1 <sup>b</sup>					
1966	20	100	115	43	45
1967	—	1.3	34	100	—
1978	2	8	18	8	0
Ave.	11	36	56	50	23
Area 2					
1966	85	174	45	23	23
Area 3					
1966	60	123	115	25	38
1967	75	98	178	87	—
1968	211	386	168	50	—
1969	45	172	191	117	—
Ave.	98	195	163	70	38
Area 4					
1966	175	137	60	75	62
1967	101	171	111	116	—
1968	127	123	103	57	—
1969	170	142	167	158	—
1984	—	222	—	—	—
Ave.	143	159	110	102	62
Bay-wide					
1940 <sup>c</sup>	288	159	423	580	—
1941 <sup>c</sup>	79	136	193	230	—
1946	—	—	—	—	33
Ave.	184	148	308	405	33

<sup>a</sup> Data sources: 1940, 1941, 1946 (Andrews 1946); 1966 (Lind 1967); 1967 (Mossier 1968); 1968–69 (Nichols and Cottam 1972); 1978 (Carpenter 1980b); 1984 (R. Lathrop, WDNR).

<sup>b</sup> Sampling areas shown in Figure 9.2.

<sup>c</sup> Primarily *Chara* sp.

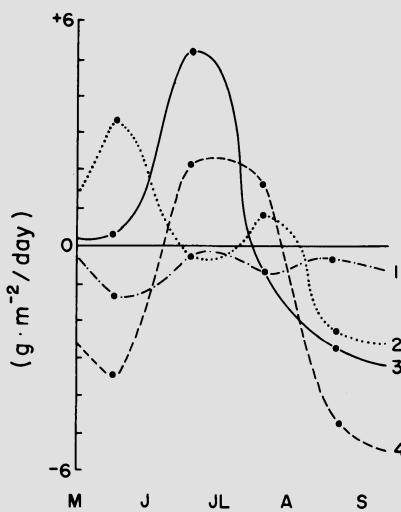
—, unreported.

### Filamentous Algae

Filamentous algae have been an important component of the littoral zone since at least 1912. Although freshwater filamentous algae are not usually considered macrophytes, we include them in this chapter because of their important interaction with other littoral vegetation.

Denniston (1921) noted that *Cladophora* sp. was present in most transects he sampled. Rickett (1921) found *Cladophora* sp. in shallow water, rocky shore areas. It grew luxuriantly in early June and then died back. He separated standing crop estimates by three bottom types. The highest standing crop of  $189 \text{ g m}^{-2}$  was found on tumbled masses of submerged or half-submerged rocks, an intermediate biomass of  $17 \text{ g m}^{-2}$

**Figure 9-3.** Production rates of *Myriophyllum spicatum* and filamentous algae in University Bay, 1969. 1—Area 4, algae. 2—Area 4, *M. spicatum*. 3—Area 3, algae. 4—Area 3, *M. spicatum*. M—May, J—June, JL—July, A—August, S—September. Letters indicate mid-month (after Nichols 1973).



**Table 9-8.** Biomass of filamentous algae in University Bay ( $\text{g m}^{-2}$  dry weight).<sup>a</sup>

	June	July	August	September
Area 3 <sup>b</sup>				
1967	0	0	55	65
1968	65	37	78	0.1
1969	39	99	154	0.1
Ave.	35	46	96	22

<sup>a</sup> Data sources: 1967 (Mossier 1968); 1968–69 (Nichols 1973).

<sup>b</sup> Sampling area shown in Figure 9.2.

on scattered rocks, and a scanty growth of  $4 \text{ g m}^{-2}$  on small pebbles or isolated large rocks. He also noted that there was an abundant growth of floating and attached filamentous algae, notably several species of *Spirogyra* on muddy shores and in bays. It was impossible to separate this algal mat from the larger plants, so no account of the algal growth in the lake, other than *Cladophora* sp., was given. Andrews (1946) noted that the periodic presence of large amounts of algae, chiefly *Spirogyra* and *Mougeotia*, caused sampling problems for him.

Nichols (1973) studied the relationship between the biomass of filamentous algae and macrophytes. Nichols found that area 3 (Figure 9.2) had filamentous algae biomasses up to  $154 \text{ g m}^{-2}$  depending on month and year (Table 9.8), but he found only trace amounts in area 4. However, when macrophyte biomass was removed from area 4 by 2 years of previous harvesting, the area supported a filamentous algae biomass of up to

**Table 9-9.** Nitrogen composition of plants from Lake Mendota—percent dry weight.<sup>a,b</sup>

Species	1920	June 1964	July 1964	Aug. 1964	Sept. 1964	July 1984	July 1989	July 1990
Filamentous algae	2.9 <sup>c</sup>	—	—	—	—	2.4 <sup>d</sup>	—	—
<i>Myriophyllum</i> spp.	3.0	2.7	2.4	2.6	2.8	1.9	2.2 <sup>e</sup>	—
<i>Vallisneria americana</i>	1.9	3.9	2.9	2.3	2.0	—	—	2.0
<i>Potamogeton</i> spp.	1.3	—	—	—	—	—	—	—
<i>Najas flexilis</i>	2.3	—	—	—	—	—	—	—
<i>Nymphaea odorata</i>	1.9	—	—	—	—	—	—	—
<i>Ceratophyllum demersum</i>	—	4.4	2.1	2.1	3.4	—	2.9	—
<i>Heteranthera dubia</i>	—	3.8	3.2	2.3	2.7	—	—	—
<i>Potamogeton richardsonii</i>	—	—	3.7	3.2	2.6	—	—	—
<i>Potamogeton zosteriformis</i>	—	3.7	3.7	3.7	3.4	—	—	—

<sup>a</sup> Data sources: 1920 (Schuette and Hoffman 1921; Schuette and Alder 1927, 1929); 1964 (Gerloff and Kromholz 1966); 1984, 1989, and 1990 (R. Lathrop, WDNR).

<sup>b</sup> Location of samples: 1920—lakewide; 1964—unknown; 1976, 1984, 1989—University Bay; 1990—Tenney Park.

<sup>c</sup> Primarily *Cladophora*.

<sup>d</sup> Primarily *Oedogonium*.

<sup>e</sup> Samples were acid washed but still averaged 20% Ca which may have been surface contamination and would lower N percentage.

—, unreported.

129 g m<sup>-2</sup>. *Mougeotia* and *Spirogyra* were common genera in the algae mats. The filamentous algae biomass averaged 149 g m<sup>-2</sup> in area 4 during July 1984 [R. Lathrop, Wisconsin Department of Natural Resources (WDNR), unpubl. data]. The algae were primarily *Oedogonium*.

The relationship between the productivity of algae and the macrophytes varied with site. In the shallow area 4, an inverse relationship was found between the production rate of filamentous algae and *M. spicatum*. In the deeper area 3, a maximum production rate of filamentous algae preceded the maximum production rate of milfoil (Figure 9.3).

### Nutrient Composition

Schuette and Hoffman (1921) and Schuette and Alder (1927, 1929) analyzed the nutrient content of plant material collected by Rickett (1921). They developed estimates for the annual demand of mineral matter to support the macrophyte crop in Lake Mendota. Gerloff and Kromholz (1966) used plant tissue analysis techniques to determine

**Table 9-10.** Phosphorus composition of plants from Lake Mendota—percent dry weight.<sup>a,b</sup>

Species	1920	June 1964	July 1964	Aug. 1964	Sept. 1964	July 1976	July 1984	July 1989	July 1990
Filamentous algae	0.07 <sup>c</sup>	—	—	—	—	—	0.41 <sup>d</sup>	—	—
<i>Myriophyllum</i> spp.	0.30	0.41	0.35	0.35	0.41	—	0.36	0.17 <sup>e</sup>	—
<i>Vallisneria americana</i>	0.23	0.42	0.42	0.43	0.37	0.52	—	—	0.31
<i>Potamogeton</i> spp.	0.13	—	—	—	—	—	—	—	—
<i>Najas flexilis</i>	0.27	—	—	—	—	—	—	—	—
<i>Nymphaea odorata</i>	0.30	—	—	—	—	—	—	—	—
<i>Ceratophyllum demersum</i>	—	0.75	0.51	0.56	0.71	—	—	0.36	—
<i>Heteranthera dubia</i>	—	0.55	0.69	0.51	0.58	—	—	—	—
<i>Potamogeton richardsonii</i>	—	—	0.45	0.32	0.23	—	—	—	—
<i>Potamogeton zosteriformis</i>	—	0.42	0.35	0.59	0.44	—	—	—	—

<sup>a</sup> Data sources: 1920 (Schuette and Hoffman 1921; Schuette and Alder 1927, 1929); 1964 (Gerloff and Krombholz 1966); 1976 (Titus 1977); 1984, 1989, and 1990 (R. Lathrop, WDNR).

<sup>b</sup> Location of samples: 1920—lakewide; 1964—unknown; 1976, 1984, and 1989—University Bay; 1990—Tenney Park.

<sup>c</sup> Primarily *Cladophora*.

<sup>d</sup> Primarily *Oedegonium*.

<sup>e</sup> Samples were acid washed but still averaged 20% Ca which may have been surface contamination and would lower the P percentage.

—, unreported.

nutrient availability for the growth of angiosperm aquatic plants. Collections from Lake Mendota were used as examples of plant tissue from a nutrient-rich lake. Titus (1977) studied the relationship between tissue phosphorus concentration and photosynthesis in *V. americana* plants from University Bay. Lathrop (WDNR, unpubl. data) measured tissue nutrient concentrations during the 1984, 1989, and 1990 growing seasons. Because there are numerous problems with comparing plant tissue analyses across different studies using different methods, no comparisons will be made (Gerloff and Krombholz 1966). Nutrient data are included because of possible value to future researchers (Tables 9.9 and 9.10).

## Discussion

Aquatic plants have been abundant in Lake Mendota for at least the last 100 years. Descriptions from the mid-1880s indicate that there were large areas of weedy shallows.

The present species composition of the Lake Mendota macrophyte community is markedly different from communities found during the early to mid-1900s. Up to the 1960s, the macrophyte community was dominated by *V. americana*. Pondweeds (*P. amplifolius*, *P. pectinatus*, *P. praelongus*, and *P. richardsonii*), coontail (*C. demersum*), and native milfoil were also significant community members. *Chara* sp. (Andrews 1946) and *Najas flexilis* were locally abundant in pre-1966 surveys (Tables 9.1 and 9.2). The diverse, shallow-bay communities found early in the century have been partially replaced by monotypic stands of cattail.

An invasion of *P. crispus* occurred in 1946 (Andrews 1946), but the impact to the plant community was not long-lasting. Today *P. crispus* is a minor part of the plant community. *P. crispus* typically dies back by early July, so that abundant growth does not cause as many problems as did the later milfoil invasion.

The invasion of *M. spicatum* appears to have started after 1962 and it was well established by 1966. Cutting records indicate it was a management problem by 1965 and the peak of the invasion lasted about 10 years (Figure 9.1). Records are not detailed enough to determine if heavy milfoil biomass occurred at the same location or different locations in the lake every year. That is, a single location in the lake may not have supported heavy milfoil growth for the entire 10 years.

The milfoil invasion was a serious nuisance for lake users. Previous plant communities stayed submersed; because *V. americana* was the predominant species, the maximum standing crop occurred late in the summer. *M. spicatum* grows early in the season and concentrates its biomass at the top of the plant. It produces long lax stems that float across the water surface in water depth up to 2.0m (Lind and Cottam 1969). This makes them more visible and more likely to entangle fishing gear, boating equipment, and swimmers.

By 1978 there was a definite decrease in the Lake Mendota milfoil harvest. No standing crop estimates were made during this time, so the impact of the milfoil decline on macrophyte biomass is not known. During this time the water was turbid (Andrews 1980; Vander Zouwen 1982) and the maximum depth of plant growth was at a minimum (Table 9.4).

The cause of the milfoil decline is not well known. Descriptions provided by Andrews (1980) indicate that the plants had symptoms similar to declining plants in other regions of North America (Nichols and Shaw 1986). It is not known whether increased turbidity triggered the decline, or whether limited plant cover caused increased turbidity by enhancing algal growth and resuspension of sediment.

Another littoral zone nuisance that appears annually on Lake Mendota is floating mats of filamentous algae. However, heavy algal growth was not found in shallow water during the years of heavy milfoil infestation

(Nichols 1973). Heavy algal growth reappeared in these areas after milfoil was removed by harvesting and after the milfoil decline (Nichols 1973; Lathrop, WDNR, unpubl. data).

The areal extent of plant growth decreased significantly between 1920 and 1980. During this time the average maximum depth and hence the area of plant growth decreased from more than 5 m to less than 2.5 m (Table 9.4). Recent data indicate that this trend has been reversed and the average maximum depth of plant growth is presently 3.5 m.

Data also indicate a decline in standing crop per square meter. Only the 1940 standing crop estimates exceed the 1920 estimate (Table 9.6). This estimate was for a dense bed of *Chara*, which can become heavily encrusted with marl. Only the 1984 estimate exceeded 50% of the 1920 estimate for the area behind the sandbar in University Bay. Although estimates of macrophyte standing crop are notoriously variable, the differences between 1920 standing crop estimates and later estimates are probably too great to be caused totally by sampling variability (Nichols 1982). None of the standing crops were reported as ash-free dry weight, which could be a cause of significant error. Schuette and Hoffman (1921) and Schuette and Alder (1927, 1929) indicate that Rickett's estimates should be reduced by 11–27%, depending on species, to correct for ash. However, more recent estimates should be corrected by a similar if not greater amount (Nichols 1971; Carpenter 1980b). Although plant densities in bays are higher than in the rest of the lake (Rickett 1921; Lathrop and Hartman 1990), the standing crop trends found in University Bay (Table 9.6) probably reflect trends in the whole lake. The combined effect of a decrease in plant growth depth, area of coverage, and standing crop per square meter indicates that the total macrophyte standing crop for Lake Mendota is less than it was in 1920.

How changes in the macrophyte community impacted the remainder of the Lake Mendota system is not well known. Carpenter (1980c), for instance, hypothesizes that the change in the plant community from a *Vallisneria–Potamogeton* community to a milfoil community could have a dramatic impact on nutrient cycling in the littoral zone. *Vallisneria* is late growing and conservative of nutrients. Most nutrients are recycled in the fall with death of the plants. Milfoil sloughs leaves during the entire growing season, so nutrients are being continually recycled.

Although individual plant species changed in importance, the plant community was stable and diverse from 1912 to the mid-1960s, except for a brief period in the mid-1940s when *P. crispus* invaded the lake. After the milfoil invasion in the mid-1960s, the plant community was stable but strongly dominated by milfoil until the mid-1970s. Presently, the direction of community change is uncertain (Tables 9.2 and 9.3). As the water becomes more clear, will plant biomass increase? Which species, if any, will invade deep water?

Rickett (1921) found the majority of the standing crop in water depth less than 3 m. If there is a significant increase in biomass, it will probably be restricted to water less than 3 m deep.

*C. demersum* is one of the species found consistently over the years of surveys. It is also the species found in the deepest water by Denniston (1921) and Lathrop and Hartman (1990). This species will probably continue to become more important.

Milfoil is still a significant part of the vegetation. Milfoil has been found growing in water up to 10 m deep in North America, but 1 to 4 m appears to be the typical range for milfoil growth (Nichols and Shaw 1986). Lind and Cottam (1969) found that milfoil did not reach the surface in water deeper than 2 m, and Lathrop and Hartman (1990) found most of the milfoil in less than 3 m water depths. Even in the relatively clear water of Devils Lake, Wisconsin, where milfoil was found at depths of 9 m, it did not grow to the surface in water deeper than 3 m (Lillie 1986). Milfoil will probably continue to be a significant part of the vegetation, but if it invades water deeper than 3 m it will not be a major nuisance because it will not reach the water surface.

*Chara* spp. and *Najas flexilis* could invade open areas in the littoral zone. Both species can grow in deep water (Nichols, Wisconsin Geological and Natural History Survey, unpubl. data), and both have revegetated other lakes where vegetation was drastically changed because of management practices (Engel and Nichols 1984). The community is usually short-lived until some other species become established.

The most desirable option would be for the open areas to be recolonized by *V. americana* and a variety of broad-leaved pondweeds such as *P. amplifolius*, *P. richardsonii*, and *P. illinoensis*. These species are not nuisances because the majority of their biomass is submersed. They are desirable habitat or food sources for fish, fish food organisms, or waterfowl (Nichols and Vennie 1991). *V. americana* has a growth cycle later in the summer and is conservative of nutrients. The probability of these species recolonizing the lake is unknown. They have lower reproductive capacities than *M. spicatum*, *C. demersum*, *E. canadensis*, and *P. crispus*, so they are at a competitive disadvantage with these species for rapidly colonizing open areas (Storch et al. 1986; Nichols and Shaw 1986). The possibility of replanting desirable species in Lake Mendota is being investigated by the WDNR (Lathrop and Hartman 1990).

Current trends in nutrient loading and water quality indicate that Lake Mendota is becoming clearer, though variability is high (Lathrop, Ch. 6; Lathrop and Carpenter, Ch. 7; Lathrop 1990). The ongoing biomanipulation project is intended to hasten this process. As the lake becomes clearer, we can expect macrophyte beds to expand. Community composition is likely to change but is difficult to forecast. The vegetation of shallow water is managed by localized spraying of herbicides and mechanical harvesting. Changes in water clarity and the macrophyte

management program present opportunities to alter the spatial structure of the littoral zone in ways that maximize benefits for fish management goals. How fish management and macrophyte management strategies can be effectively coordinated remains an open question. Fundamental research at whole-lake scales is needed to better understand the interactions between macrophyte beds and fish community dynamics (Carpenter and Lodge 1986). The changes underway in Lake Mendota make it a natural laboratory for studies of the interactions of macrophytes and fishes.

In summary, Lake Mendota has supported lush macrophyte growth for more than a century. The crop supported in recent years is less than that supported in earlier times. Recent plant communities are more noticeable and cause more lake use problems than earlier plant communities because of their growth form. Lake Mendota's littoral communities are changing. The water is becoming clearer, and maximum plant growth depth is increasing. It is uncertain how this will impact the plant community. The most desirable change would be for the open areas to be recolonized by species that were found there in 1920. It is hard to imagine, however, that *C. demersum* and *M. spicatum* will not be significant members of the future plant community.

*Acknowledgments.* We thank John Titus and John Barko for careful, helpful reviews of an early draft of this manuscript.

## References

- Andrews JD (1946) The macroscopic invertebrate population of the larger aquatic plants in Lake Mendota. Ph.D. Thesis, University of Wisconsin, Madison
- Andrews JD, Hasler AD (1943) Fluctuations in the animal population of the littoral zone in Lake Mendota. Trans. Wis. Acad. Sci. Arts Lett. 35:175–185
- Andrews JH (1980) Plant pathogens as agents for biological and integrated control of aquatic plants. Technical Report WIS WRC 80-01, Water Resources Center, University of Wisconsin, Madison
- Canfield DE, Langeland KA, Linda SB, Haller WT (1985) Relations between water transparency and maximum depth of macrophyte colonization in lakes. J. Aquat. Plant Manage. 23:25–28
- Carpenter SR (1980a) The decline of *Myriophyllum spicatum* in a eutrophic Wisconsin USA Lake. Can. J. Bot. 58:527–535
- Carpenter SR (1980b) Estimating net shoot production by a hierarchical cohort method of herbaceous plants subject to high mortality. Am. Midl. Nat. 104: 163–175
- Carpenter SR (1980c) Enrichment of Lake Wingra by submersed macrophyte decay. Ecology 61:1145–1155
- Carpenter SR, Lodge DM (1986) Effects of submersed macrophytes on ecosystem processes. Aquat. Bot. 26:341–370
- Chambers PA, Kalff J (1985) Depth distribution and biomass of submersed aquatic macrophyte communities in relation to Secchi depth. Can. J. Fish. Aquat. Sci. 42:701–709

- Cottam G, Nichols SA (1970) Changes in the water environment resulting from aquatic plant control. Technical Report OWRR B-019-Wis. Water Resources Center, University of Wisconsin, Madison
- Crowder LB, Cooper WE (1982) Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63:1802–1813
- Denniston RH (1921) A survey of large aquatic plants of Lake Mendota. *Trans. Wis. Acad. Sci. Arts Lett.* 20:495–500
- Engel S, Nichols SA (1984) Lake sediment alteration for macrophyte control. *J. Aquat. Plant Manage.* 22:38–41
- Gerloff GC, Krombholz PH (1966) Tissue analysis as a measure of nutrient availability for growth of angiosperm aquatic plants. *Limnol. Oceanogr.* 11:529–537
- Gustafson TD (1976) Production, photosynthesis, and the storage of reserves in a natural stand of *Typha latifolia L.* Ph.D. Thesis, University of Wisconsin, Madison
- Lathrop RC (1989) The abundance of aquatic macrophytes in the Yahara Lakes. *Res. Manage. Find.* No. 22, Wisconsin Department of Natural Resources, Madison
- Lathrop RC (1990) Response of Lake Mendota (Wisconsin, U.S.A.) to decreased phosphorus loading and the effects on downstream lakes. *Verh. Internat. Verein. Limnol.* 24:457–463
- Lathrop RC, Hartmann LN (1990) A 1989 survey of aquatic macrophytes in Lake Mendota. Wisconsin Department of Natural Resources, Madison
- Lillie, RA (1986) The spread of Eurasian watermilfoil *Myriophyllum spicatum* in Devils Lake, Sauk County, Wisconsin. In Redfield G, Taggart JF, Moore LM (eds) *Lake and reservoir management II. Proc. 5th Annu. Conf. Int. Symp. N. Am. Lake Manage. Soc.*, Washington, D.C., pp 64–68
- Lind CT (1967) The submerged vegetation of University Bay. M.A. Thesis, University of Wisconsin, Madison
- Lind CT, Cottam G (1969) The submerged aquatics of University Bay: A study in eutrophication. *Am. Midl. Nat.* 81:353–369
- Mossier JN (1968) Response of submergent macrophytes to harvesting. M.S. Thesis, University of Wisconsin, Madison
- Nichols SA (1971) The distribution and control of macrophyte biomass in Lake Wingra. Technical Report OWRR B-019-Wis. Water Resources Center, University of Wisconsin, Madison
- Nichols SA (1973) The effects of harvesting aquatic macrophytes on algae. *Trans. Wis. Acad. Sci. Arts Lett.* 61:165–172
- Nichols SA (1975) Identification and management of Eurasian watermilfoil in Wisconsin. *Trans. Wis. Acad. Sci. Arts Lett.* 63:116–128
- Nichols SA (1982) Sampling characteristics of macrophyte biomass. *Water Resour. Bull.* 18:521–523
- Nichols SA, Cottam G (1972) Harvesting as a control for aquatic plants. *Water Resour. Bull.* 8:1205–1210
- Nichols SA, Shaw BH (1986) Ecological life histories of the three aquatic nuisance plants, *Myriophyllum spicatum*, *Potamogeton crispus* and *Elodea canadensis*. *Hydrobiologia* 131:3–21
- Nichols SA, Vennie JG (1991) Attributes of Wisconsin lake plants. *Information Circular 73*, Wisconsin, Geological and Natural History Survey, Madison

- Rickett HW (1921) A quantitative study of the larger aquatic plants of Lake Mendota. *Trans. Wis. Acad. Sci. Arts Lett.* 20:501–527
- Savino JF, Stein RA (1982) Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Trans. Am. Fish. Soc.* 111:255–266
- Schuette HA, Alder H (1927) Notes on the chemical composition of some of the larger aquatic plants of Lake Mendota. II. *Vallisneria* and *Potamogeton*. *Trans. Wis. Acad. Sci. Arts Lett.* 23:249–254
- Schuette HA, Alder H (1929) Notes on the chemical composition of some of the larger aquatic plants of Lake Mendota. III. *Castalia odorata* and *Najas flexilis*. *Trans. Wis. Acad. Sci. Arts Lett.* 24:135–139
- Schuette HA, Hoffman AE (1921) Notes on the chemical composition of some of the larger aquatic plants of Lake Mendota. I. *Cladophora* and *Myriophyllum*. *Trans. Wis. Acad. Sci. Arts Lett.* 20:529–531
- Storch TA, Winter JD, Neff C (1986) The employment of macrophyte transplanting techniques to establish *Potamogeton amplifolius* beds in Chautauqua Lake, New York. In Redfield G, Taggart JF, Moore LM (eds) *Lake and reservoir management II*. Proc. 5th Annu. Conf. Int. Symp. N. Am. Lake Manage. Soc., Washington, D.C., pp 263–266
- Threinen CW (1949) The effects of carp upon the normal aquatic habitat. *Invest. Rep. No. 709*, Wisconsin Conservation Department, Madison
- Threinen CW, Helm WT (1952) A comparative summary of the vegetation surveys on important carp waters in southeastern Wisconsin. *Invest. Rep. No. 669*, Wisconsin Conservation Department, Madison
- Titus JE (1977) The comparative physiological ecology of three submerged macrophytes. Ph.D. Thesis, University of Wisconsin, Madison
- Vander Zouwen WJ (1982) Vegetational change in University Bay from 1966 to 1980. *Trans. Wis. Acad. Sci. Arts Lett.* 70:42–51
- Wiley MJ, Gorden RW, Waite SW, Powless T (1984) The relationship between aquatic macrophytes and sport fish production in Illinois ponds: A simple model. *No. Am. J. Fish. Manage.* 4:111–119
- Zimmerman FR (1953) Waterfowl habitat surveys and food habit studies, 1940–1943. Final Rep. Pittman-Robertson Proj. No. 6-R, Wisconsin Conservation Department, Madison

# 10

## Benthic Macroinvertebrates

**Richard C. Lathrop**

### Introduction

The benthic macroinvertebrates<sup>1</sup> of Lake Mendota are not central to the pelagic food web research presented in this volume, but they are important food organisms for many fish species inhabiting the lake (see Magnuson and Lathrop, Ch. 11). Macroinvertebrate density trends provide useful information for a recently initiated research project by the Wisconsin Department of Natural Resources (WDNR) and the University of Wisconsin (UW). This project deals with the ecology of the major fish species inhabiting Lake Mendota's littoral zone and the relationship of these fish to different species and densities of macrophytes. Understanding the linkage between the littoral and pelagic food webs is an objective of the new project.

Benthic macroinvertebrates can be divided into groups corresponding to three zones in the lake with markedly different environmental conditions: littoral (water depths of 0–4 m), sublittoral (4–10 m), and profundal (>10 m). The proportions of lake surface area that these zones represent are 23%, 24%, and 63%, respectively. The divisions between the three zones are not absolute. For example, during the early 1980s macrophytes did not grow in water deeper than 3 m, whereas from the early 1900s through the 1950s, macrophytes grew to 5 m or more (Lathrop 1989;

---

<sup>1</sup>“Benthic macroinvertebrates” in this chapter refers to organisms associated with a solid surface (both plant-dwelling and sediment-dwelling) to avoid confusion with planktonic macroinvertebrates. “Benthos” refers to sediment-dwelling macroinvertebrates only.

Nichols et al., Ch. 9). The demarcation between sublittoral and profundal is also imprecise; a gradual transition in sediment characteristics and benthic organisms is apparent, and the lower limit of the thermocline varies throughout the summer. Thermal stratification allows anoxia to extend to 8 m water depths during late July in many years prior to thermocline deepening during August.

Within these three depth zones, benthic macroinvertebrate density and species composition vary depending on the environmental limitations of the zone. The littoral zone includes both plant-dwelling and sediment-dwelling macroinvertebrate species. Littoral zone organisms do not have to be tolerant of anoxic conditions for prolonged periods, as do organisms in the profundal sediments during summer stratification and late winter. The complexity of the ecological niches within the macrophyte community supports a great diversity of organisms (Wetzel 1983). In contrast, the deep-water profundal sediments have fewer niches and hence are inhabited by only a few species tolerant of low oxygen. However, because the profundal zone collects more organic matter than the shallower zones, densities of benthos species utilizing this energy source can be very large (Brinkhurst 1974). The benthos of the sublittoral sediments are intermediate in complexity between inhabitants of the littoral and profundal zones. While the habitat is less complex because aquatic macrophytes are absent, the sediments are overlain by oxygenated water throughout most of the year, thus allowing a greater diversity of organisms to be present.

This chapter summarizes past studies on Lake Mendota's benthic macroinvertebrate populations. Because of the great difficulty in sampling littoral macroinvertebrates, few quantitative surveys have been done. Periodic surveys have been conducted on benthos densities in sublittoral and profundal zone sediments, particularly during either the winter or summer months. Long-term trends in densities of these organisms are presented in this chapter and related to other trends in Lake Mendota. Possible reasons for a major decline in profundal benthos densities that occurred in recent decades are also discussed.

## Data Sources

### Past Surveys

Benthic macroinvertebrate density data were available from numerous published and unpublished sources. Only three surveys systematically sampled the benthic macroinvertebrates in the littoral zone. In 1914–15, Muttkowski (1918) used a variety of nets and a clamshell dredge to sample both plants and bottom sediments in water depths of 0–7 m around the entire lake shoreline. Average densities at 1-m depth intervals for the open-water period were reported. In 1939–41, Andrews used a

specially designed bag to determine invertebrate densities on different macrophyte species in University Bay (Andrews and Hasler 1943; Andrews 1946). Bottom sediments were not sampled. In 1964–65, Sapkarev (1967–68) used an Ekman dredge to sample bottom sediments in the littoral zone as well as in deeper water, but organisms living on the macrophytes were not quantitatively sampled with this gear. He reported densities for leeches (Sapkarev 1967–68), but densities for other organisms were never published.

The benthos inhabiting the sublittoral and profundal sediments have been sampled in various years during the 1900s. Profundal sediments were sampled exclusively with Ekman dredges but of different sizes or weights. A large dredge ( $473\text{ cm}^2$ ) was used by Juday (1921) during his detailed survey from May 1916 to August 1918. Smaller dredges ( $225$ – $232\text{ cm}^2$ ) were used by most later researchers, although dredge sizes were not always recorded. Occasionally clam-style Petersen dredges were used in sublittoral depths where the sediments were sandier.

Juday's (1921) detailed survey data were not consistently summarized for all species. Monthly density data were given for the Deep Hole region in most cases, but only annual averages were reported at 1-m depth intervals throughout the profundal zone. Past surveys were also conducted by seven other investigators: D.G. Frey (unpubl. data) in August 1939, E. Jones (cited in Sawyer et al. 1945) in June/July 1944, Hasler (1945) in the winters of 1943 and 1944, Mackenthun and Cooley (1952) in the winter of 1951, Dugdale (1955) studying the chironomids between December 1953 and December 1954, K.M. Stewart (unpubl. data) in August 1961, and J.A. Sapkarev (unpubl. data) between September 1964 and August 1965. Methods and summarized results for the unpublished data were available in Frey (1940), Stewart (1965), and Sapkarev (1967–68), while the raw data were obtained from the authors. Because of the historical value of Sapkarev's extensive unpublished survey, his organism densities for the littoral, sublittoral, and profundal zones are summarized in this chapter.

### 1987–89 Surveys

Present-day abundances of benthos in sublittoral and profundal sediments were sampled by the WDNR Bureau of Research in January–February of 1987–89 (Lathrop, in press) and in August of 1987. Five Ekman dredge ( $232\text{ cm}^2$ ) samples were collected at each station located at depth contour intervals of 6, 9, 12, 15, 18, 21, and 24 m on a transect from the deepest location (25.3 m) northeast toward Warner Bay (Fig. 3.2). Additional stations were also located in University Bay and in the west end of the lake at 18–20 m for comparison to similar depths along the main transect.

Individual dredge samples were sieved through a  $300\text{-}\mu\text{m}$  screen by washing them with a gentle stream of water. The organisms (and debris)

collected on the screen were transferred to a jar and preserved with 95% ethanol for later identification and enumeration. Chironomids were identified only to genus, which corresponded to most earlier surveys and which reduced uncertainties about their taxonomy. *Chaoborus* was identified to species. Oligochaetes were not reported for 1987–89, because the sieving procedure and alcohol did not adequately preserve these fragile organisms for accurate enumeration.

### Interpretation of Data Sources

Detailed comparisons of benthic macroinvertebrate densities in the littoral zone before and after the 1960s invasion of Eurasian watermilfoil were not possible because of differences in sampling techniques used in past surveys. For the sublittoral and profundal zones, several factors complicate comparisons between data sources. First, some surveys did not report the size or height of the Ekman dredge used. Depth of dredge penetration into the sediments, which is a function of the weight of the dredge, has been shown to affect the number of organisms collected (Berg 1938; Dugdale 1955). Second, the screen mesh size used to sieve organisms from sediment samples differed. In most cases, mesh size was not recorded, but mesh sizes of 500–600 µm were commonly used (Welch 1948; Jónasson 1955; American Public Health Association et al. 1971). Smaller-sized chironomids may therefore have been under-represented in studies using these mesh sizes (Jónasson 1955). Third, the time of sample collection was not given. Stewart (1965) found differences in organism densities between morning and late afternoon sampling in sublittoral and profundal sediments to water depths of 14 m.

In addition to these differences or uncertainties in past sampling methods or sieving techniques, other potential interpretation problems were caused by the lack of multiyear sampling for many surveys and the inherent year-to-year variability in benthic invertebrate populations. For all of these reasons, I considered long-term trends in sublittoral and profundal benthos densities to be significant only if density differences between surveys were at least one order of magnitude. Smaller density changes were noted but not considered important due to the potential interpretation problems described above.

Because the emergence of dipteran midges during the summer months caused their densities to fluctuate greatly over a yearly cycle, I compared long-term density trends separately for winter and summer months, when the less extensive surveys were conducted. For these comparisons, January and February data were selected to compute winter densities (if unavailable, March was used). Likewise August data were selected to reflect summer densities (if unavailable, July was used). For fingernail clams (*Pisidium*) and oligochaetes that have no emergence cycles and are relatively sessile, I combined all density data representing winter,

**Table 10-1.** Average macroinvertebrate densities ( $\text{Nm}^{-2}$ ) in water depths of 0–7 m during the open-water period of 1914–15 in Lake Mendota (summarized from Muttkowsky 1918).

Animal group	Number of species	Depth ranges (m)				
		0–1	1–2	2–3	3–5	5–7
Turbellaria	4	65	4	10	54	19
Nematoda	2	3	<1	1	0	0
Oligochaeta	6	176	268	649	1,560	620
Hirudinea	—	11	2	1	14	<1
Mollusca	15	22	140	250	279	319
Amphipoda	2	173	77	89	287	83
Decapoda	1	1	0	0	0	0
Hydracarina	5	47	79	100	63	34
Ephemeridae	7	41	8	4	15	7
Odonata	5	2	1	2	1	0
Hemiptera	4	6	2	<1	0	0
Sialidae	1	0	0	0	0	5
Trichoptera	14	207	180	132	85	17
Chaoborinae	1	1	<1	<1	0	11
Chironomidae	19	99	156	104	144	97
Coleoptera	12	42	1	1	1	1
Total	98	896	918	1,343	2,503	1,213

summer, or annual averages and used these combinations for long-term comparisons.

## Results

### Littoral Zone

Densities of benthic macroinvertebrates recorded by Muttkowsky (1918) in 1914–15 indicated the importance of oligochaetes, molluscs, amphipods, water mites, caddisfly larvae, and chironomid midge larvae at various depths in the littoral zone throughout the lake (Table 10.1). Densities of numerous species were affected by bottom type as well as depth. The caddisfly *Leptocella* had the largest biomass, but small oligochaetes, a mollusc (*Amnicola*), and the amphipod *Hyalella azteca* all had larger numerical densities; oligochaetes were notably more abundant than any other group in 2- to 7-m depths. The total number of species (excluding leeches) recognized by Muttkowsky was 98. Chironomids, molluscs, and caddisflies were the groups containing the most species.

Andrews, in his 1939–41 study of macroinvertebrates associated with different macrophyte species, found higher densities of animals on plants

**Table 10-2.** Macroinvertebrate density in relation to leaf structure of macrophyte species in University Bay during 1939 (after Andrews 1946).

Leaf structure	Macrophyte species	Invertebrate density (N kg <sup>-1</sup> dry wt plant)
Highly dissected	<i>Ceratophyllum demersum</i>	45,300
	<i>Myriophyllum exalbescens</i>	29,200
Moderately dissected	<i>Potamogeton pectinatus</i>	24,400
	<i>Chara</i> sp.	18,300
Broad-leaved	<i>Potamogeton richardsonii</i>	11,100
	<i>P. nodosus</i>	5,400
	<i>P. amplifolius</i>	5,000
Ribbon-like	<i>Vallisneria americana</i>	2,400

with highly dissected structure than on plants with less dissected structure (Andrews and Hasler 1943; Andrews 1946). The highest macroinvertebrate densities were found on coontail (*Ceratophyllum demersum*) followed by native milfoil (*Myriophyllum exalbescens*) (Table 10.2). Neither plant species was very abundant prior to the 1960s (Lathrop 1989; Nichols et al., Ch. 9). Invertebrate densities were low on wild celery (*Vallisneria*) and the broad-leaved pondweeds (*Potamogeton* spp.) that dominated the littoral zone prior to the invasion of Eurasian watermilfoil (*M. spicatum*) in the 1960s. The most numerically abundant invertebrates on the plants, in decreasing order, were: *Hyalella*, chironomid larvae, mayfly nymphs, caddisfly larvae, annelids, leeches, hydrachnids, and snails.

Sapkarev's unpublished 1964–65 data on the littoral macroinvertebrates are summarized in Table 10.3. Average yearly densities of water mites, oligochaetes, chironomid larvae, hydras, and amphipods were much greater than corresponding densities of other organism groups. Water mites and oligochaetes were particularly abundant in late spring. Densities of turbellarians, leeches, amphipods, water mites, and chironomids were all notably greater than densities recorded by Muttkowski (1918). Other organisms that were recorded in both surveys had relatively similar densities except for caddisflies, which were more abundant in Muttkowski's survey. However, the plant-dwelling caddisflies may have been underrepresented in the 1964–65 survey because an Ekman dredge was used for sampling.

### Sublittoral Zone

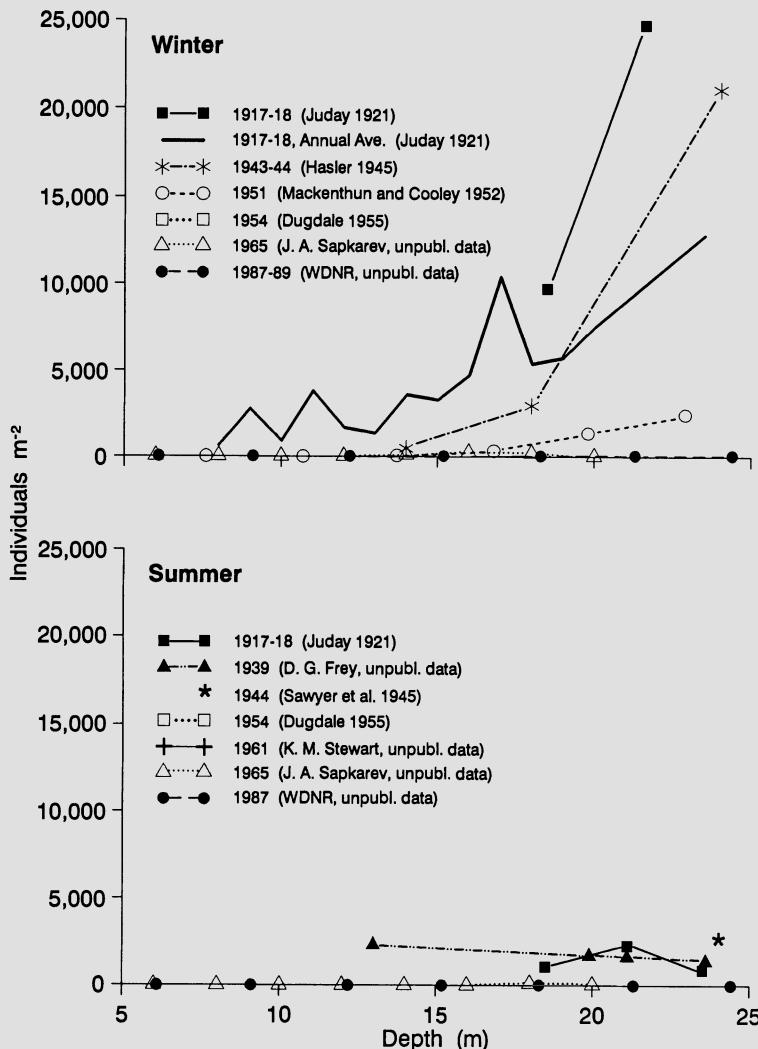
Many animal groups recorded in the littoral zone were found only occasionally or in small abundances in the sublittoral zone in Sapkarev's 1964–65 survey. Oligochaetes and chironomids were the most abundant

**Table 10-3.** Average monthly macroinvertebrate densities ( $N m^{-2}$ ) in the littoral zone of Lake Mendota during 1964–65 (from J.A. Sapkarev, unpubl. data). (Densities are averages from water depths of 0, 1, 2, 3, and 4 m.)

Animal group	1964			1965						Monthly avg.			
	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	
Hydrida	2,381	2,238	1,092	1,787	133	314	22	966	999	1,143	1,232	1,432	1,145
Turbellaria	728	524	400	249	44	18	0	417	648	440	871	755	424
Gastropoda	222	364	471	204	172	127	80	373	391	133	799	324	305
Sphaeriidae	9	0	9	0	0	0	0	18	0	9	9	9	6
Oligochaeta	3,614	657	391	466	605	1,114	377	977	968	11,162	7,637	1,812	2,482
Hirudinea	322	211	211	89	100	78	200	211	200	142	1,907	635	359
Ostracoda	115	622	98	44	211	144	33	551	107	44	9	22	167
Amphipoda	2,122	1,501	1,199	244	189	111	233	1,332	959	897	1,607	959	946
Hydracarina	1,048	1,119	1,581	366	744	566	511	453	20,202	13,258	4,582	2,220	3,888
Chironomidae	4,664	1,341	1,031	3,509	2,247	799	1,279	3,428	2,193	1,812	1,642	1,518	2,122
Other Diptera	9	0	18	80	62	0	0	0	0	0	0	0	14
Coleoptera	80	98	44	36	18	9	9	27	18	18	18	18	33
Ephemeroptera	133	151	133	80	35	107	35	71	80	53	80	107	89
Trichoptera	18	0	18	0	18	0	89	391	9	0	0	160	59

**Table 10-4.** Average monthly macroinvertebrate densities ( $N \cdot m^{-2}$ ) in the sublittoral and profundal zones in Lake Mendota during 1964–65 (from J.A. Sapkarev, unpubl. data). (Sublittoral densities are averages from water depths of 6, 8, and 10 m; profundal densities are averages from depths of 12, 14, 16, 18, 20, 22, and 24 m.)

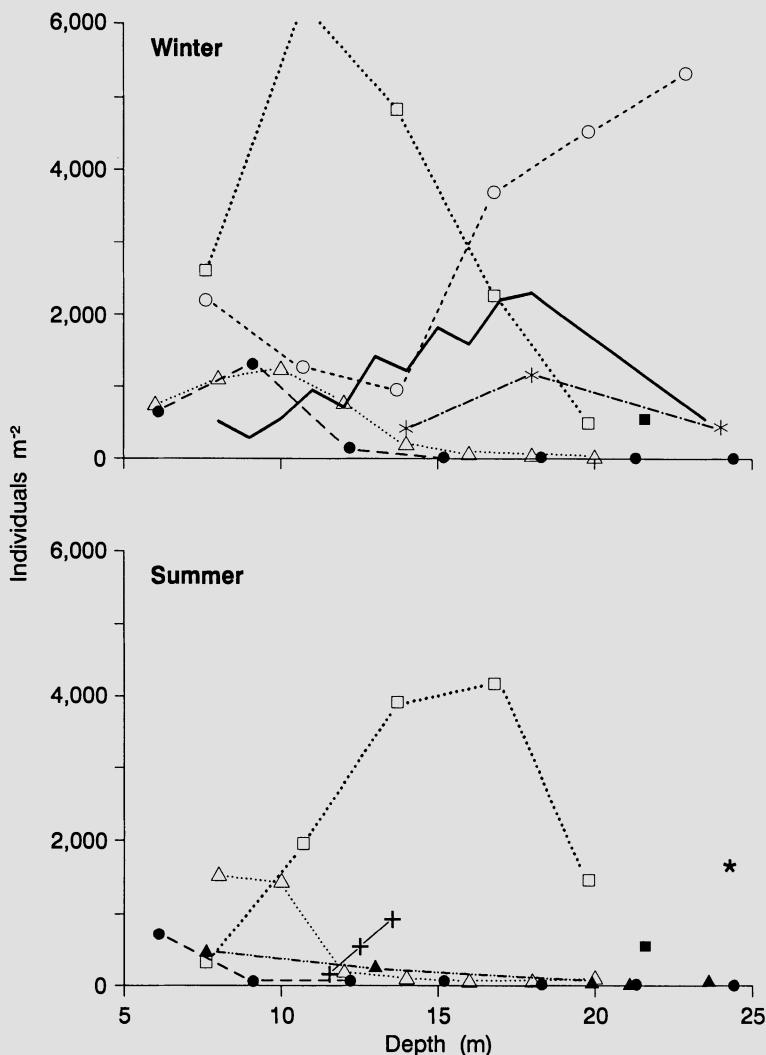
Animal group	1964			1965			1966			Monthly avg.	
	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	
Sphaeriidae											
Sublittoral	15	30	15	30	15	30	30	15	15	15	21
Profundal	11	11	0	0	11	0	11	9	9	6	6
Oligochaeta											
Sublittoral	1,051	252	799	1,806	1,880	1,252	1,880	2,028	696	518	651
Profundal	277	696	1,561	2,442	3,186	2,057	1,920	3,525	2,371	2,886	2,531
Ostracoda											
Sublittoral	133	89	1,214	232	696	503	207	178	115	59	30
Profundal	122	98	178	366	400	144	89	115	27	18	9
Hydracarina											
Sublittoral	74	74	651	104	355	30	681	207	133	192	326
Profundal	33	27	44	22	56	44	44	53	18	18	62
Chaoborinae											
Profundal	166	355	417	231	122	122	111	124	284	284	53
Chironomidae											
Sublittoral	1,258	281	1,776	696	1,983	2,013	1,332	4,233	2,420	622	782
Profundal	63	44	203	247	254	291	311	488	311	184	216



**Figure 10-1.** *Chaoborus punctipennis* densities ( $N\ m^{-2}$ ) in the sediments  $>5\ m$  water depths during winter and summer months in Lake Mendota. (Legends summarize sampling dates and data sources used for Figures 10.1–5)

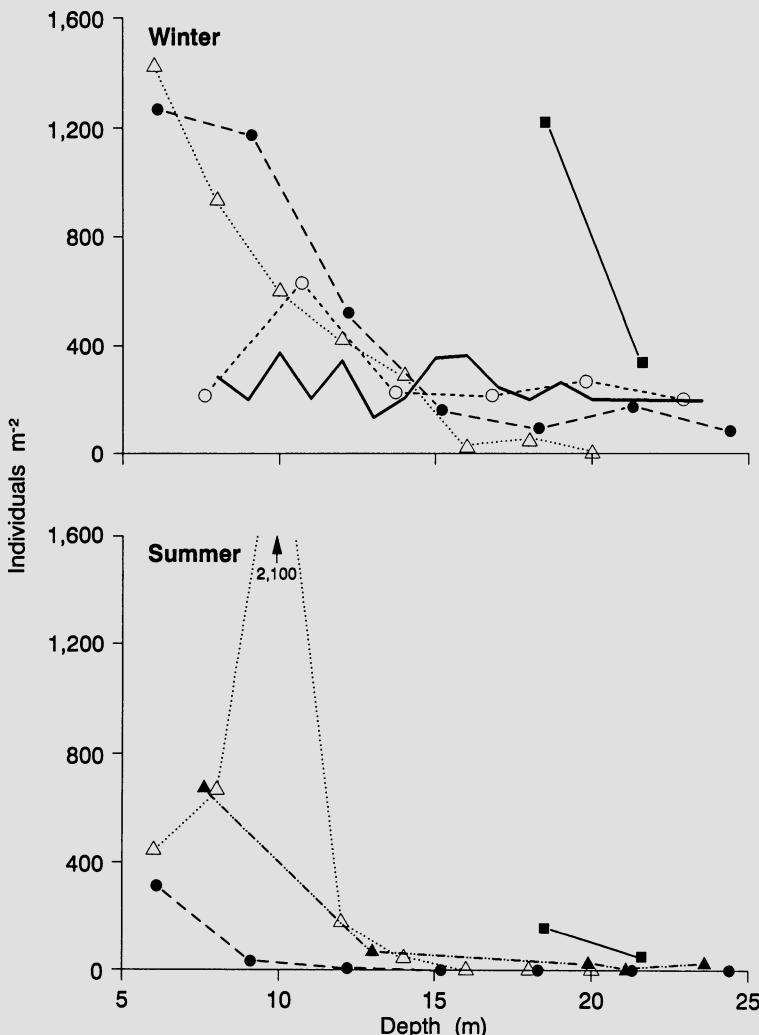
sublittoral benthos (Table 10.4). Ostracods and water mites were also important. Similar findings were found by Muttkowski's (1918) survey in 0- to 7-m depths and Juday's (1921) survey in 8 to 24 m.

Long-term benthos density data for winter and summer months indicated that sublittoral and profundal sediments were inhabited by similar organism groups, but densities differed during the 1900s. In the winters of 1917–18, phantom midge larvae *Chaoborus punctipennis* occurred in



**Figure 10-2.** *Chironomus* spp. densities ( $\text{Nm}^{-2}$ ) in the sediments  $>5\text{ m}$  water depths during winter and summer months in Lake Mendota. (Sampling dates and data sources same as in Figure 10.1.)

moderate densities in water depths of 8–9 m, although their densities were much higher in deeper waters (Figure 10.1). They were not found in more recent surveys in sublittoral sediments. Both *Chironomus* spp. and *Procladius* spp. were important sublittoral species (Figures 10.2 and 10.3). In 1965 and 1987–89, *Procladius* was much more abundant in sublittoral sediments than in profundal sediments. Conversely, oligochaetes generally were more abundant in profundal sediments than in sublittoral sediments in most of the past surveys (Figure 10.4). The fingernail clam *Pisidium* sp. also was abundant in sublittoral sediments in 1917–18 and

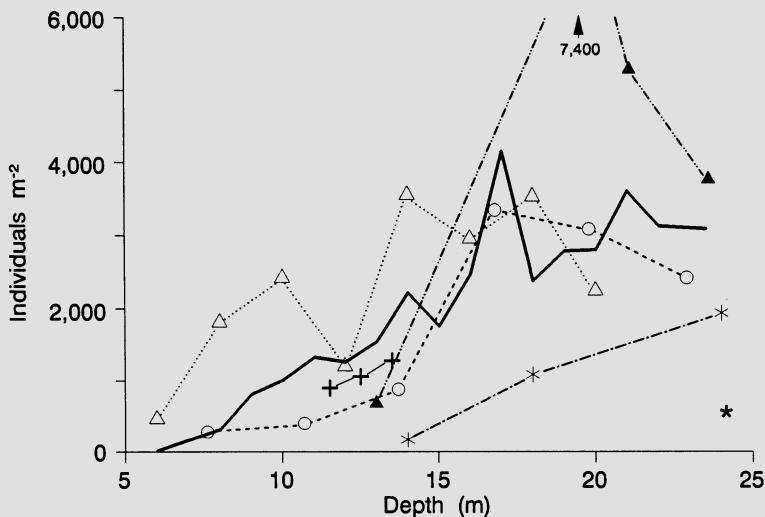


**Figure 10-3.** *Procladius* spp. densities ( $N m^{-2}$ ) in the sediments  $>5$  m water depths during winter and summer months in Lake Mendota. (Sampling dates and data sources same as in Figure 10.1.)

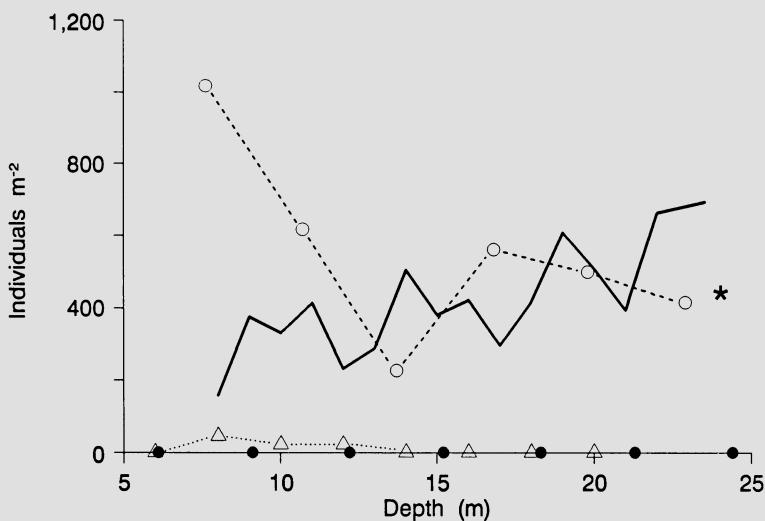
1951 (Figure 10.5). Densities had declined dramatically by 1965; the clam was not found in 1987–89.

### Profundal Zone

Dramatic benthos density changes occurred in Lake Mendota's profundal sediments during the 1900s. *C. punctipennis*, the organism with the highest recorded densities, decreased from  $20,000\text{--}25,000 m^{-2}$  in the Deep Hole region ( $>20$  m) in the winters of 1917–18 and 1943–44 to



**Figure 10-4.** Oligochaeta densities ( $N\ m^{-2}$ ) in the sediments  $>5$  m water depths in Lake Mendota. (Sampling dates and data sources same as in Figure 10.1; data combined for both winter and summer months.)



**Figure 10-5.** *Pisidium* sp. densities ( $N\ m^{-2}$ ) in the sediments  $>5$  m water depths in Lake Mendota. (Sampling dates and data sources same as in Figure 10.1; data combined for both winter and summer months.)

about  $2,400\text{ m}^{-2}$  in 1951 (Figure 10.1). Although winter densities were historically less in water depths of 10–20 m, similar declines in this region also occurred in 1951. In 1965 and 1987–89, winter *Chaoborus* densities throughout the profundal zone were  $<60\text{ m}^{-2}$ . Because of emergence and predation losses, summer *Chaoborus* densities through the mid-1940s were about 10% of winter densities (Judy 1921), providing further evidence that populations were very abundant in those early years. *Chaoborus* were rare during the summer of 1965 and were not found during the summer of 1987.

From the early 1900s through the mid-1950s, *Chironomus* spp. were also an important component of the profundal benthos (Figure 10.2). Average annual densities in 1917–18 increased from approximately  $600\text{ m}^{-2}$  at 10 m to  $2,300\text{ m}^{-2}$  at 18 m and declined to  $600\text{--}900\text{ m}^{-2}$  in the Deep Hole region. Winter densities recorded in 1943–44 also indicated that *Chironomus* were moderately abundant. Densities in August 1939 were relatively low throughout the profundal zone, but this may have been after emergence. In July 1944, densities in the Deep Hole region were much higher ( $1,900\text{ m}^{-2}$ ), but they probably reflected total chironomids including *Procladius*. However, in winter of 1951 and in both winter and summer of 1954, *Chironomus* densities (exceeding  $4,000\text{ m}^{-2}$  at many depths) were more abundant in Lake Mendota's profundal sediments than at any other period. Densities had declined by summer of 1961. During the winter months, no *Chironomus* were found in the Deep Hole region in 1965 and only  $2\text{ m}^{-2}$  were found in 1987–89. Average profundal zone densities were 210 and  $130\text{ m}^{-2}$  in the two surveys, respectively. Summer densities were also very low.

*Procladius* spp. generally did not exhibit major density changes throughout the 1900s, although relatively high winter densities at 18.5 m in University Bay were reported in 1916–18 (Figure 10.3). Densities were higher in 10- to 15-m depths than in deeper water in the winters of 1951, 1965, and 1987–89. In depths  $>15$  m, densities averaged 230, 22, and  $130\text{ m}^{-2}$  in the three surveys, respectively.

Oligochaetes did not exhibit any major density changes in the surveys conducted through 1965. Densities were generally  $2,000\text{--}4,000\text{ m}^{-2}$  in sediments  $>15$  m water depths, except in the summer of 1939, when even higher densities were recorded in 19- to 21-m depths (Figure 10.4). Densities were less in 10- to 15-m depths but still significant. Howmiller (1974) reported densities of oligochaetes at  $489\text{ m}^{-2}$  in the Deep Hole region of Lake Mendota during one summer around 1970. In May 1991, oligochaete densities in two unsieved dredge samples collected at 22 m were  $4,700\text{ m}^{-2}$  (R. Lathrop, unpubl. data). Further study is needed to confirm current densities.

In surveys conducted through 1951, the fingernail clam *Pisidium* sp. exhibited relatively stable average densities of  $400\text{--}600\text{ m}^{-2}$  for the entire profundal zone (Figure 10.5). In 1965, no organisms were recorded in the

Deep Hole region and  $15\text{ m}^{-2}$  were recorded in 10- to 15-m depths. In 1987–89, *Pisidium* were not found in the profundal zone of Lake Mendota.

## Discussion

The benthic macroinvertebrate community in the littoral zone has been extensive in both number of species and total abundances. However, there is evidence that densities may have increased following the invasion of Eurasian water milfoil in the 1960s. Total densities were less in both the 1914–15 and 1939–41 surveys than in the 1964–65 survey, although differences in sampling methods make comparisons difficult. Prior to the 1960s, the littoral macrophyte community was dominated by wild celery and broad-leaved pondweeds, all plants with relatively undissected leaves. These plants had significantly lower numbers of macroinvertebrates per unit plant weight than plants with highly dissected leaf structures such as milfoil and coontail (Andrews and Hasler 1943; Andrews 1946). Undissected leaves probably supported less food for plant-dwelling macroinvertebrates and provided less cover for invertebrates from fish predation. Whether these higher densities of macroinvertebrates on highly dissected plants are found in the current macrophyte community (dominated by milfoil and coontail) will be confirmed by research in the recently initiated littoral zone project. Comparisons between past and current total numbers of littoral benthic macroinvertebrates also must consider that the current littoral area is smaller than it was in earlier years.

Sublittoral zone benthos were represented by fewer species than the littoral zone, which has a more diverse habitat. Sublittoral species also were found in the profundal zone, although in different densities. Oligochaetes, *Chironomus* spp., and *Procladius* spp. were the most important sublittoral benthos. Their densities remained relatively stable throughout the 1900s. However, fingernail clams (*Pisidium* sp.), which were abundant in sublittoral sediments through the early 1950s, declined dramatically by the mid-1960s. In recent years, this organism was absent.

Lake Mendota's profundal zone ( $>10\text{ m}$ , representing 63% of the lake area) has historically had large densities of benthos (Lathrop 1991). *Chaoborus punctipennis*, which in its later instars is benthic during daylight hours and planktonic during the night when it feeds (Juday 1921), was the most abundant species. Winter deep-hole ( $>20\text{ m}$ ) densities exceeded  $20,000\text{ m}^{-2}$  in the early 1900s through the mid-1940s. *Chironomus* spp. (including *C. plumosus*), oligochaetes, *Procladius* spp., and *Pisidium* sp. were also dense in the profundal sediments in these early years. The chironomid and *Chaoborus* midge larvae were an important food source for yellow perch, one of the most important and abundant fish species in Lake Mendota (Lathrop et al. 1992; Magnuson and Lathrop, Ch. 11).

These midges comprised 25–60% of the perch diet by volume during the open-water period (Pearse and Achtenberg 1920).

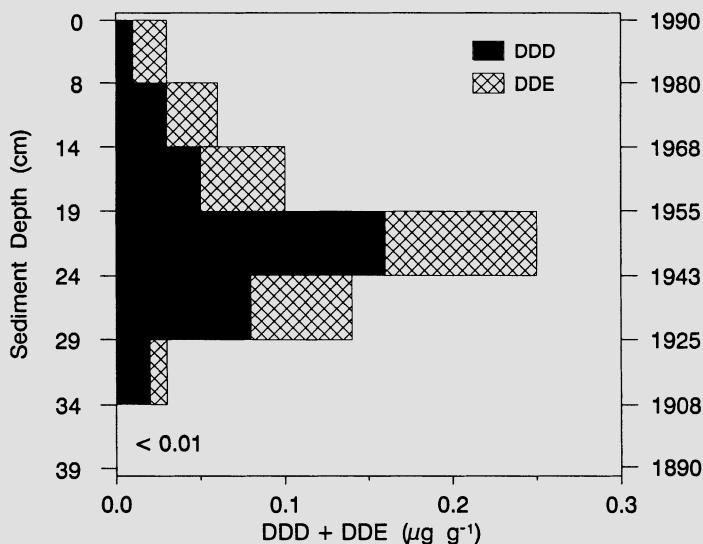
Between the mid-1940s and the early 1950s, profundal benthos began to change (Lathrop 1991). Densities of *Chaoborus* had declined to about 10% of earlier densities, while *Chironomus* had increased by as much as 700%. These higher densities of *Chironomus* that occurred during the early to mid-1950s coincided with a period of excellent perch fishing in Lake Mendota (Lathrop et al. 1992). By the mid-1960s, *Chaoborus* and the fingernail clam *Pisidium* were almost absent from the entire profundal zone, and *Chironomus* populations were greatly diminished in all but its shallowest depths. *Procladius* was similarly restricted to the shallower profundal depths. Oligochaete densities did not decline through 1965. By the late 1980s, *Pisidium* was extirpated, *Chaoborus* and *Chironomus* populations remained low, but *Procladius* had increased to densities similar to those in the early 1950s. Further testing is needed to determine current oligochaete densities, but preliminary results for May 1991 indicate that they remain high.

Four possible reasons for the decline in Lake Mendota's profundal benthos can be suggested: (1) decline in food availability, (2) increase in fish predation, (3) use of toxic insecticides in the drainage basin, and (4) changes in the profundal sediment environment. Each of these factors is discussed separately.

Based on available data, the hypothesis that food availability caused the decline seems unlikely. Crustacean zooplankton, which are heavily utilized by *Chaoborus* larvae, have not changed significantly during the 1900s (Brock 1985; Lathrop and Carpenter, Ch. 8). Phytoplankton, including diatom populations, exhibited similar species composition and presence of blooms throughout the 1900s (Lathrop and Carpenter, Ch. 7). These algae, after sinking to the lake sediments, would have been a major food source for *Chironomus*, *Pisidium*, and oligochaetes.

An increase in fish predation by bottom-feeding fish may have occurred in Lake Mendota, because carp and freshwater drum populations increased during the mid-1900s (Lathrop et al. 1992; Magnuson and Lathrop, Ch. 11). However, fish predation should not have caused the massive density declines of all the different profundal benthos species while leaving *Procladius* and sublittoral populations of chironomids unaffected. Kajak (1988) reviewed case studies in which benthivorous fish predation reduced benthos densities, and he found that larger organisms and the more mobile invertebrate predators such as *Procladius* were preferentially selected as prey over smaller nonpredatory organisms. Thus if the benthos declines in Lake Mendota had been caused by a possible shift in fish predation, *Procladius* should have also declined, which it did not.

Toxic insecticides that may have entered Lake Mendota from runoff were considered a possible cause of the benthos decline. Aldrin,



**Figure 10-6.** Sediment profile of p,p'-DDD + DDE concentrations from a Deep Hole core collected in May 1990. (Sediment core dating estimated by J.P. Hurley from  $^{137}\text{Cs}$  and sediment compaction data for a similar core summarized in Hurley et al., Ch. 5)

dieldrin, and heptachlor for agricultural crops (mostly corn) and DDT for mosquito and elm disease control had their heaviest use during the 1950s and 1960s (W. Gojmerac, UW-Extension, pers. comm.). However, insecticide concentrations determined by the Wisconsin State Laboratory of Hygiene on sediments that I sectioned from a deep-hole core taken in May 1990 revealed that aldrin, dieldrin, and heptachlor and its epoxide were all  $< 0.01 \mu\text{g g}^{-1}$  dry weight for all sediments deposited during the 1900s. While the long-term breakdown rates of these chemicals are variable, at least dieldrin is quite stable and probably would have been detected had it entered the lake in large quantities (D.E. Armstrong, Water Chemistry Program, UW-Madison, pers. comm.). The p,p'-DDD + DDE derivatives of DDT (DDT was not found) had the highest concentration of  $0.25 \mu\text{g g}^{-1}$  in sediments deposited around the early 1940s and early 1950s (Fig. 10.6). Concentrations declined in sediments deposited in more recent years, particularly since the late 1960s after DDT was banned. DDE is known to be relatively stable in anoxic lake sediments (D.E. Armstrong, pers. comm.). DDD + DDE concentrations were detectable in both early and recent sediments, possibly due to bioturbation, chemical migration, or slight differences in sedimentation rates between this core and the core dated by J.P. Hurley (WDNR, pers. comm.). He estimated these dates from cesium-137 dating and sediment

compaction data given in Hurley et al. (Ch. 5) for a core taken in the same location.

However, based on literature data, these concentrations of DDD + DDE, particularly in more recent sediments, do not appear to be toxic to most of the benthos species. Low-level concentrations of DDD + DDE found in lake sediments bioaccumulate in chironomids and oligochaetes and are not acutely toxic to these organisms (Johnson et al. 1971; Oliver 1984). Large doses of DDD that were used to kill *Chaoborus* larvae in Clear Lake, California in 1949, 1954, and 1957 did not prevent their return in large densities in ensuing years (Rudd and Herman 1972; Brown 1978). Bottom mud residues of DDD + DDE built up in Clear Lake to  $0.8 \mu\text{g g}^{-1}$ , which was much higher than concentrations found in Lake Mendota's sediments. It would seem unlikely that similar massive doses of organochlorine insecticide could have entered Lake Mendota during isolated runoff events because its large lake size and volume would have diluted any insecticide inputs. Finally, sublittoral benthos densities in Lake Mendota were not affected, except for *Pisidium*.

One factor that may have contributed to the decline in profundal zone benthos densities is a change in the sediment environment. Many authors have stressed that as the duration of anoxia in the hypolimnion increases, only the most tolerant benthos species such as the oligochaetes and *Procladius* can survive (Carr and Hiltunen 1965; Brinkhurst 1974; Wiederhom 1980; Bazzanti and Seminara 1987). Jónasson (1984), in his 20-year study of Lake Esrom, which experienced an increasing summer period of hypolimnetic anoxia, reported a 400% increase in oligochaete densities to about  $20,000 \text{ m}^{-2}$  and an 85% decrease in *Pisidium* densities to about  $690 \text{ m}^{-2}$ . This density of *Pisidium* was similar to that found in Lake Mendota in early years before 1965. While hypolimnetic depletion rates and the extent and duration of anoxia have not changed in Lake Mendota during the 1900s (Stewart 1976; Brock 1985), other signs of eutrophication have occurred that may have adversely affected the profundal sediment environment for benthos survival. Lake Mendota probably became more eutrophic after the mid-1940s because of higher nutrient loadings (Lathrop, Ch. 6). As a result of these higher loadings, hypolimnetic ammonium concentrations tripled between the 1920s–1930s and the 1970s–1980s. Free ammonia concentrations, which are toxic, would have increased as a result. Data on hypolimnetic hydrogen sulfide concentrations are not extensive, but concentrations appear to have also increased (Lathrop, Ch. 3). Average sulfate concentrations in Lake Mendota's surface waters have doubled since the late 1940s (Lathrop, Ch. 6). This suggests that higher sulfide levels may have been produced during anoxia in the hypolimnion because higher substrate concentrations were available for sulfide production.

It is not known if these hypolimnetic ammonia and hydrogen sulfide increases that most likely occurred around the 1950s could have been

responsible for the decline of *Chaoborus* and *Chironomus* and the loss of *Pisidium*. However, even though dissolved oxygen conditions have not changed, the chemical environment of the profundal sediments probably has been more severe than in earlier years when benthos densities were much higher. The additional combined role of fish predation and toxic insecticides cannot be discounted to also have contributed to the decline. Further research on this decline is needed.

Because of the lack of profundal benthos in Lake Mendota, a major food source is missing for yellow perch, one of the central pelagic fish in the lake. If the reason for the benthos decline was past inputs of toxic insecticides that are no longer present in large concentrations in recent sediment deposits, then excessive predation by perch and other fishes may be preventing the reestablishment of these benthic species. In their absence, macroinvertebrates such as amphipods and chironomids found only in the littoral and sublittoral zones are a major food item for perch, as well as limnetic items such as *Leptodora* and smaller zooplankton (Rudstam et al., Ch. 12).

*Acknowledgments.* I thank P.J. Garrison, J.P. Hurley, and C. Luecke for critical reviews of this chapter and S.H. Nehls for editorial assistance. Data collection was supported by the WDNR. Benthos enumerations for 1987–89 were made by J.V. Adams, E.R. Deppe, and L.C. Theis. G.D. Wegner and G.I. Quinn conducted the field sampling and R.P. Narf gave advice on enumeration procedures. Special thanks are also given to D.G. Frey and K.W. Stewart for providing the raw benthos data summarized in their Ph.D. theses and particularly to J.A. Sapkarev for providing data on his unpublished benthos survey.

## References

- American Public Health Association, American Water Works Association, and Water Pollution Control Federation (1971) Standard methods for the examination of water and wastewater. 13th edn. Am. Public Health Assn., Am. Water Works Assn., and Water Pollut. Control Fed., Washington, D.C.
- Andrews JD (1946) The macroscopic invertebrate populations of the larger aquatic plants in Lake Mendota. Ph.D. Thesis, University of Wisconsin, Madison
- Andrews JD, Hasler A (1943) Fluctuations in the animal populations in the littoral zone of Lake Mendota. Trans. Wis. Acad. Sci. Arts Lett. 35:175–186
- Bazzanti M, Seminara M (1987) Profundal macrobenthos structure as a measure of long-term environmental stress in a polluted lake. Water Air Soil Pollut. 33:435–442
- Berg K (1938) Studies on the bottom animals of Esrom Lake. Kgl. Danske Vidensk. Selsk. Skr. Nat. Math. Afd. 9 Rk 8
- Brinkhurst RO (1974) The benthos of lakes. St. Martin's Press, New York
- Brock TD (1985) A eutrophic lake: Lake Mendota, Wisconsin. Ecol. Stud. Vol. 55. Springer-Verlag, New York

- Brown AWA (1978) Ecology of pesticides. John Wiley & Sons, New York
- Carr JF, Hiltunen JK (1965) Changes in the bottom fauna of western Lake Erie from 1930 to 1961. Limnol. Oceanogr. 10:551–569
- Dugdale RC (1955) Studies in the ecology of the benthic Diptera of Lake Mendota. Ph.D. Thesis, University of Wisconsin, Madison
- Frey DG (1940) Growth and ecology of the carp *Cyprinus carpio* Linnaeus in four lakes of the Madison region, Wisconsin. Ph.D. Thesis, University of Wisconsin, Madison
- Hasler AD (1945) Observations on the winter perch population of Lake Mendota. Ecology 26:90–94
- Howmiller RP (1974) Studies on aquatic Oligochaeta in inland waters of Wisconsin. Trans. Wis. Acad. Sci. Arts Lett. 62:337–356
- Johnson BT, Saunders CR, Sanders HO, Campbell RS (1971) Biological magnification and degradation of DDT and aldrin by freshwater invertebrates. J. Fish. Res. Board Can. 28:705–709
- Jónasson PM (1955) The efficiency of sieving techniques for sampling freshwater bottom fauna. Oikos 6:183–207
- Jónasson PM (1984) Oxygen demand and long term changes of profundal zoobenthos. Hydrobiologia 115:121–126
- Juday C (1921) Quantitative studies of the bottom fauna in the deeper waters of Lake Mendota. Trans. Wis. Acad. Sci. Arts Lett. 20:461–493
- Kajak Z (1988) Considerations on benthos abundance in freshwaters, its factors and mechanisms. Int. Rev. Ges. Hydrobiol. 73:5–19
- Lathrop RC (1989) The abundance of aquatic macrophytes in the Yahara lakes. Res. Manage. Find. No. 22. Wisconsin Department of Natural Resources, Madison
- Lathrop RC (1991) Decline in zoobenthos densities in the profundal sediments of Lake Mendota (Wisconsin, USA). Hydrobiologia (in press)
- Mackenthun KM, Cooley HL (1952) The biological effect of copper sulfate treatment on lake ecology. Trans. Wis. Acad. Sci. Arts Lett. 41:177–187
- Muttkowski RA (1918) The fauna of Lake Mendota. Trans. Wis. Acad. Sci. Arts Lett. 19:374–482
- Oliver BG (1984) Uptake of chlorinated organics from anthropogenically contaminated sediments by oligochaete worms. Can. J. Fish. Aquat. Sci. 41:878–883
- Pearse AS, Achtenberg H (1920) Habits of yellow perch in Wisconsin lakes. Doc. No. 885. U.S. Bureau of Fisheries, Washington, D.C., pp 293–366
- Rudd RL, Herman SG (1972) Ecosystem transferral of pesticide residues in an aquatic environment. In Matsumura F, Boush GM, Misato T (eds) Environmental toxicology of pesticides, Academic Press, New York
- Sapkarev JA (1967–68) The taxonomy and ecology of leeches (Hirudinea) of Lake Mendota, Wisconsin. Trans. Wis. Acad. Sci. Arts Lett. 56:225–253
- Sawyer CN, Lackey JB, Lenz AT (1945) Investigations of the odor nuisance occurring in the Madison lakes particularly Lakes Monona, Waubesa, and Kegonsa from July 1943 to July 1944. Rep. to Gov. Comm., Madison
- Stewart KM (1965) Physical limnology of some Madison lakes. Ph.D. Thesis, University of Wisconsin, Madison
- Stewart KW (1976) Oxygen deficits, clarity, and eutrophication in some Madison lakes. Int. Rev. Ges. Hydrobiol. 61:563–579

- Welch PS (1948) Limnological methods. Blakiston, Philadelphia  
Wetzel RG (1983) Limnology. 2nd edn. CBS Coll. Publ., Philadelphia  
Wiederholm T (1980) Use of benthos in lake monitoring. J. Water Pollut. Control Fed. 52:537–547

# 11

## Historical Changes in the Fish Community

**John J. Magnuson and Richard C. Lathrop**

### Introduction

Historical records of the fish community indicate that species richness, species composition, and the abundances of individual taxa have changed dramatically in Lake Mendota from 1900 to 1989. Yet most of the species present in 1900 continued to be present or abundant in the 1980s. Extirpations (species losses), invasions, and introductions are common; populations of individual species such as the cisco and yellow perch have varied repeatedly from high to low numbers. The evidence on which these changes are based is scanty prior to the 1940s and becomes increasingly strong thereafter.

Coincident with the changes in the fish community are numerous human-caused changes to the Lake Mendota environment. Even before the turn of the century, the outlet had been dammed and the water level raised 1.2 to 1.5 m, the drainage basin had been invaded by European settlers who had cleared the land and altered sediment and nutrient loadings to the lake, and common carp and goldfish had been introduced. Human-caused disturbances and management manipulations have continued to the date of this writing. Some of these alterations include reductions in wetlands, conversion of grain and hay fields to corn, use of agricultural fertilizers, urbanization of the shoreline, sewage input and diversion, fish introductions, piscivore stocking, state and commercial "rough fish" removal (mostly common carp), commercial and recreational fishing, use of herbicides and cutters to reduce aquatic plant growth, invasion of Eurasian watermilfoil, and water level control. Some

of these modifications can be directly related to the dynamics of the fish community, but many of them interact or have been coincident, which often prevents reduction of fish community dynamics to clear individual causes.

Our purposes are to (1) describe the fish community as it existed in the 1980s with respect to species richness, composition, abundance, and body size, as well as thermal, feeding, and reproductive guilds; (2) analyze the changes in these same features of the community from 1900 to 1990; and (3) discuss these dynamics with respect to the other changes in the Lake Mendota environment.

## Materials and Methods

### Data Sources

The aggregation of the fish data was greatly facilitated by use of papers by McNaught (1963), Lyons (1989), and especially a draft report by Lathrop et al. (in press), which will be published in the 1992 Wisconsin Department of Natural Resources (WDNR) Technical Bulletin. These provided references to the original published papers and unpublished records which allowed the compilation of presence/absence and relative abundance data. Additional unpublished materials were provided by the University of Wisconsin-Madison Center for Limnology and the WDNR. Data sources from 1853 to 1989 are listed in Table 11.1. News clippings from 1980 to 1989 were provided by Ken Christensen from his column in The Capital Times. Mr. Paul Zoch of Madison also provided his personal catch records for cisco from 1976 to 1986. Changes to the Lake Mendota environment were taken almost exclusively from Lathrop et al. (in press) and are summarized in other chapters in this volume, including Ch. 3, 6, 9 and 10.

### Presence/Absence

All data sources (Table 11.1) were used to determine presence/absence. However, some species listed as present in several data sources have been discounted. In some cases later identifications by Lyons (1989) were made of specimens in the Zoological Museum at the University of Wisconsin-Madison. In other cases we found that differences in common names in the early records had led to errors in reports in the WDNR electronic file, e.g., yellow bass between 1900 and 1920 was actually smallmouth bass (Table 11.1), and in McNaught (1963) the earliest records of grass pickerel were actually northern pike. Common names used in our chapter are taken from the list of common and scientific names of fishes prepared

**Table 11-1.** Sources of data for determining fish relative abundance and presence/absence. Data summaries by gear and time period are on file with the North Temperate Lakes Long Term Ecological Research program, Center for Limnology, University of Wisconsin-Madison. Note that no quantitative data exist from 1921 to 1938. Sampling gears used for calculating relative abundance are grouped by gears that catch (a) medium to large littoral fishes, (b) small to medium littoral fishes, (c) sport fishes, (d) pelagic fishes, and (e) large "rough" fishes. The Fish Distribution Database (Fago) was a 1987 printout. The Magnuson LTER Database is found under Long Term Ecological Research Program, National Science Foundation, J.J. Magnuson, Center for Limnology, University of Wisconsin-Madison. Tibbles data found under Tibbles (1956).

Period	Years sampled	Number of fish in sample	Sampling gear	Source
Before 1900	1852–99 ca. 1843	— Unknown	Stocking records Unknown	Lathrop et al. (in press) Mollenhoff (1982, p. 41)
1900–20	1902–03	226	a. Hook and line, trammel net	Marshall and Gilbert (1905)
	1914	946	b & c. Seine, dipnet, hook and line	Pearse (1918)
	1917	1,557	c? Unknown	Jacobs (1956)
	1900, 1905–06, 1911, 1914–15	>671	Seines, gill net, sport fishing, miscellaneous	Fish Distribution Database, Fago (1982, 1988) includes Greene's collections
	1900–05, 1914–16	Unknown	Various	Lyons (1989)
	Various	Unknown	Various	McNaught (1963)
1939–57	1956–57	22,395	a. Spring fyke nets for white bass	Horrall and Voigtlander in Lathrop et al. (in press)
	1947	799	a. Summer fyke nets	Mackenthum (1947) in Lathrop et al. (in press)
	1952	5,222	c. Summer creel survey	Lathrop et al. (in press)
1954–55		7,812	d. Year-round vertical gill net	Tibbles (1956)
	1946, 1948	2	Unknown	Fish Distribution Database, Fago (1982, 1988)
1939–47	Unknown	Various		Lyons (1989)
Various	Unknown	Various		McNaught (1963)
1958–69	1958–69	89,172	a. Spring fyke nets for white bass	Horral and Voigtlander in Lathrop et al. (in press)
	1966	1,057	b. Summer small-mesh seine	Lathrop et al. (in press)
	1960–69	1,087,109	e. Rough fish catch	Lathrop et al. (in press)
	1963	1	Fyke net	McNaught (1963)
	1963–65	Unknown	Small-mesh seine, fyke net	Fish Distribution Database, Fago (1982, 1988)
	1958–65	Unknown	Various	Lyons (1989)
1970–74	1970, 1972	459	a. Fall electroshocker	Lathrop et al. (in press)
	1970–73	11,111	a. Spring and fall fyke net	Lathrop et al. (in press)

**Table 11-1.** *Continued*

Period	Years sampled	Number of fish in sample	Sampling gear	Source
	1971	2,385	a. Spring fyke nets for white bass	Horrall and Voigtlander in Lathrop et al. (in press)
	1973–74	59,959	c. Year-round creel survey	Lathrop et al. (in press)
	1972–78	Unknown	Various	Lyons (1989)
1975–79	1977–79	1,604	a. Fall electroshocker	Lathrop et al. (in press)
	1977–78	26,300	a. Spring fyke net	Lathrop et al. (in press)
	1977–79	1,274	b. Summer small-mesh seine—day	Lathrop et al. (in press)
	1976–79	273,800	e. Rough fish catch	Lathrop et al. (in press)
	1972–78	Unknown	Various	Lyons (1989)
	1975, 1977, 1978–79	1,835	Various	Fish Distribution Database, Fago (1982, 1988)
1980–84	1980–83	2,508	a. Summer electroshocker	Lathrop et al. (in press)
	1981	106	a. Summer electroshocker	Magnuson LTER Database
	1981–82	429	a. Summer fyke net	Magnuson LTER Database
	1981–82	118	a. Summer trammel net	Magnuson LTER Database
	1980	890	b. Summer small-mesh seine—day	Lathrop et al. (in press)
	1981	1,514	b. Summer small-mesh seine—day	Magnuson LTER Database
	1981–84	8,594	b. Summer small-mesh seine—night	Magnuson LTER Database
	1984	3,608	b. Summer survey seine	Lathrop et al. (in press)
	1981–82	342,598	c. Year-round creel survey	Lathrop et al. (in press)
	1981–84	1,295	d. Summer vertical gill net	Magnuson LTER Database
	1980–84	60,503	e. Rough fish catch	Lathrop et al. (in press)
	1980	9	Electroshocker	Fish Distribution Database, Fago (1982, 1988)
	1981–87	Unknown	Various	Lyons (1989)
1985–89	1985	315	a. Fall electroshocker	Lathrop et al. (in press)
	1987–88	11,099	a. Spring fyke net	Johnson et al. (1991)
	1985	78	a. Spring fyke net	Lathrop et al. (in press)
	1988–89	10,245	b. Summer mini-fyke net	Johnson et al. (1991)
	1987, 1989	1,054	b. Summer small-mesh seine—day	Johnson et al. (1991)
	1985–89	196	b. Summer small-mesh seine—night	Magnuson LTER Database
	1987–89	1,240,088	c. Summer creel survey	Lathrop et al. (in press)
	1987–89	354,114	c. Winter creel survey	Lathrop et al. (in press)
	1985–89	1,105	d. Summer vertical gill net	Magnuson LTER Database

by Robins et al. (1980). We concluded that northern pike, walleye, and muskellunge were native to Lake Mendota because newspaper accounts (Mollenhoff 1982, p. 41) from the mid-1800s list both pickerel and pike as abundant in the Madison lakes as well as "muscalung."

### Rank Abundance

A rank of relative abundance for each taxon (see the Appendix) was estimated for each of the seven periods by which the data sources are grouped in Table 11.1. No estimates could be made prior to 1900 nor from 1921 to 1938 owing to the paucity of quantitative data. The total catch of each taxon was listed by individual gear types or, from 1900 to 1920, by data source. Gear types include dipnets, day shoreline seines, night shoreline seines, electrofishing, large fyke nets, mini-fyke nets, vertical gill nets, horizontal gill nets, minnow traps, trammel nets, recreational creel survey in summer and winter, commercial fishing records, and "rough fish" removal projects. When there was more than one year of collection for a gear type in a period, the numbers caught in each year were summed across years within the period. The number of each taxon collected or recorded by each gear type in a period was then relativized to 100% of the total number of fish caught by that gear type. The number of columns of relative abundance data, one for each gear type in Table 11.1, ranged from three for 1900–20 and 1958–69 to 11 for 1980–84. Gear was grouped into five types in Table 11.1 by those which caught primarily (a) medium to large littoral fishes, (b) small to medium littoral fishes, (c) sport fishes, (d) pelagic fishes, and (e) large "rough fishes." Gear types "a," "b," and "c" were used to estimate the relative abundance of most fishes because these gears were used in most periods. Source type "a" was available from all periods, and "b" and "c" from five of the seven periods, while "d" and "e" were each only available in three of the seven periods. The percentages for each taxon were averaged across gear for each gear type ("a," "b," or "c") for each period and the relative abundance of each taxon was estimated, i.e.,  $(a + b + c)/3$ , giving each gear type equal weight.

From the percent estimates of relative abundance, the taxa were ranked into seven levels of abundance: 0% = absent, <0.1% = rare, 0.1–0.9% = uncommon, 1.0–4.9% = common, 5.0–9.9% = abundant, 10–19% = more abundant, and  $\geq 20\%$  = very abundant. Species listed by Lyons (1989) as uncommon, common, or abundant were assigned those categories and added to the dataset after the numerical rankings for a period were completed. Our assumption of a correspondence between the two ranking systems is not entirely satisfactory, because Lyons' rankings are based on relative abundances in the museum collections, while ours are based on relative abundances in survey catches. If both numer-

ical data and Lyons' abundance assignments were available, we usually used the numerical data from surveys to set the rank abundance for the species. Species recorded as present but without numerical data or abundance assignments by Lyons were ranked as rare. The relative abundances of cisco, common carp, and bigmouth buffalo were determined from other data sources supplemented with the above estimates. Cisco rank abundances were judged from the pelagic fish data, i.e., gear type "c," and records and comments in Neuenschwander (1947), John (1954), Telford (1954), and other miscellaneous sources. Common carp and bigmouth buffalo rank abundances were judged from the "rough fish" and commercial fish catches, i.e., gear type "d", tabled in Lathrop et al. (in press) and the initial stocking date of common carp.

### **Classification by Body Size; Feeding, Reproductive, and Thermal Guilds; and Abundance Trends**

Body size classification for each species was taken as the median adult size recorded in Becker (1983) except for goldfish, which was taken from Ken Christensen's newspaper column. Fishes were divided into four categories on the basis of total length: 0.0–9.9 cm = small, 10.0–19.9 cm = medium, 20.0–31.9 cm = large, and >32.0 cm = very large.

Fish species were assigned to three thermal guilds (Hokanson 1977; Magnuson et al. 1979) based on their preferred temperatures, as tabulated in Coutant (1977), Magnuson et al. (1979), or Becker (1983): 10–17°C = cold water, 18–26°C = cool water, and ≥27°C = warm water.

Based on spawning habitat identified in Balon (1975) or Becker (1983), fish species were classified into eight reproductive guilds as defined by Balon (1975). Terminology for Balon's guilds used in the text and tables is based on spawning substrate and the following derivations: litho- for rock, rubble, and gravel; pelago- for open water; phyto- for plants, living or dead; psammo- for sand or plant roots on sand; speleo- for holes or crevices; poly- for various substrates; and -phils for lovers. Thus, a phytophil likes to release its eggs over or on plants. These reproductive guilds were grouped into three broader classes for analyses of changes in the guild structure of the community: substrate spawners = Balon's lithopelagophils, psammophils, lithophils, and speleophils; pelagic spawners = Balon's pelagophils; and vegetation spawners = Balon's polyphils, phytolithophils, and phytophils.

Three feeding guilds—benthivores, zooplanktivores, and piscivores—were used for analyses of changes in the guild structure of the community based on the food habits described in Becker (1983). Our zooplanktivores included Becker's planktivores, zooplanktivores, neustonivores, and zooplanktibenthivores.

Species were classified by general trends in their rank abundance from 1900 to 1989 by linear regression of rank abundance on the seven time periods. The method we used for detecting long-term trends over the century does not detect finer temporal changes, such as high or low abundance only in the middle of the record or at the very end of the record. The three classes were "increasing," "no trend," and "decreasing." If  $r^2 < 10\%$ , they were assigned to no trend; those with  $r^2 \geq 10\%$  were assigned to increasing or decreasing, depending on the sign of the slope. Species that were never more abundant than rare were not assigned a trend classification. Trends at the species level could not be examined for bullheads and crappies because species in each genus often were lumped in older data; thus we treated crappies as a group and bullheads as a group except in the 1980s.

A key for the above classifications and the classifications of each taxon are in the Appendix.

### **Historical Events Regarding Cisco and Yellow Perch**

Historical accounts of die-offs, spawning runs, or good fishing years, and the origin of large year classes for cisco and yellow perch are sufficient to view the occurrences of these species back to the 1870s. The records are more detailed after 1910. To allow direct comparisons with changes in Madison's summer weather, we plotted these events on a time series of annual air temperatures (mean from 1 June through 31 August).

### **Caveats**

Fish data as summarized here for presence/absence and relative abundance should be viewed with caution. Early sampling effort was sparse. As pointed out by Lyons (1989), the absence of a species in the early years may have resulted from low sampling effort relative to the later years. However, the loss of a species in recent years is probably accurately reflected in the data owing to the intensity of sampling in the 1980s.

The calculated relative abundance of a taxon also could be influenced by changes in the abundance of another species or changes in the kind and intensity of gear used in each period. For example, changes in the abundance of the more abundant and very abundant species of medium zooplanktivores such as yellow perch, bluegill, crappies, and white bass could alter the abundance rank of other species. However, the abundance of these taxa in the 1980s is similar to their abundance from 1900 to 1920, so as a group they should not have caused an artificial decline or increase in the relative abundance of other species. Changes in the real abundance of uncommon to common species should have little influence numerically

on the calculations for other taxa. For an example of possible bias related to gear type, quantitative data from gear that catch small fishes in the littoral zone were not available for two periods, 1939–57 and 1970–74. Thus, lower abundances of small species in these two periods could be a result of sample bias. To lessen this kind of bias, each type of gear, “a,” “b,” and “c,” was given equal weight in a time interval regardless of the intensity of the effort or the number of fish caught in any one type of gear. This kind of bias cannot be eliminated, however, because the same kinds of gear were not always used in a period. It is important that the increase in the apparent abundance of cisco in periods with pelagic sampling does not bias the abundance of other species in those time periods because pelagic gear was not used in the calculation of species other than cisco. The same is true for the abundance of common carp and bigmouth buffalo in periods when “rough fishing” and commercial fishing occurred. Finally, our rationale for the use of ranked abundance data was to reduce the apparent precision of the data and help prevent making conclusions from small apparent differences in abundance.

Regardless of the coarse nature of the historic fish data on Lake Mendota, a number of striking patterns emerge above the noise and biases in this interesting dataset which we developed from available records (see the Appendix). We point out some of the qualifications in the text that need to be made in drawing our conclusions.

### **1980s Fish Assemblage**

Forty-one species of fishes (and two hybrids) from 28 genera and 16 families were reported from Lake Mendota in the 1980s (Table 11.2). Of these, 2 species were very abundant, 2 were more abundant, 5 were abundant, 10 were common, 10 were uncommon, and 14 were rare.

Of the 18 species and 1 hybrid (Table 11.2) which were common to very abundant in the 1980s, 37% were large, 32% were medium, 21% were very large, and 10% were small. The dominant feeding guild was zooplanktibenthivores, which constituted 42% of these fishes, followed by benthivores (27%), piscivores (21%), a neustonivore (5%), and a zooplanktivore (5%). The food web with emphasis on the pelagic system is diagramed in Rudstam et al. (Ch. 12). The most frequent spawning guild among the common to very abundant species was phytophilis (32%), followed by lithophils (26%). About 50% used vegetation and, with some overlap, about 50% used the bottom substrate; only one species was a pelagic spawner.

Of the 24 species and 1 hybrid (Table 11.2) which were rare to uncommon, 37% were small, 29% were very large, 17% were large, and another 17% were medium. Very large and small species were represented here in greater numbers than among the common to very

**Table 11-2.** Species, size, guild, and taxonomic structure of the Lake Mendota fish community in the 1980s listed in decreasing order of abundance. See Methods for definitions.

Abundance	Size	Feeding guild	Reproductive habitat	Thermal guild	Species	Family
Very abundant	Medium	Zooplanktibenthivore	Phytolithophil	Cool	Yellow perch	Percidae
	Medium	Zooplanktibenthivore	Lithophil	Warm	Bluegill	Centrarchidae
More abundant	Very large	Piscivore	Lithophil	Cool	Walleye	Percidae
	Small	Neustonivore	Phytolithophil	Warm	Brook silverside	Atherinidae
Abundant	Very large	Benthivore	Phytophil	Warm	Common carp	Cyprinidae
	Large	Zooplanktibenthivore	Phytophil	Cool	Black crappie	Centrarchidae
	Large	Zooplanktivore	Litho-pelagophil	Cold	Cisco	Salmonidae
	Large	Benthivore	Pelagophil	Warm	Freshwater drum	Sciaenidae
	Large	Piscivore	Phytophil	Warm	Largemouth bass	Centrarchidae
Common	Very large	Zooplanktibenthivore	Phytophil	Warm	Bigmouth buffalo	Catostomidae
	Very large	Piscivore	Phytophil	Cool	Northern pike	Esocidae
	Large	Benthivore	Lithophil	Cool	White sucker	Catostomidae
	Large	Piscivore	Lithophil	Warm	Smallmouth bass	Centrarchidae
	Large	Zooplanktibenthivore	Phytolithophil	Warm	White bass	Serranidae
	Medium	Zooplanktibenthivore	Phytophil	Cool	White crappie	Centrarchidae
	Medium	Zooplanktibenthivore	Polyphil	Warm	Sunfish hybrid	Centrarchidae
	Medium	Benthivore	Lithophil	Cool	Rock bass	Centrarchidae
	Medium	Zooplanktibenthivore	Polyphil	Warm	Pumpkinseed	Centrarchidae
	Small	Benthivore	Speleophil	Warm	Bluntnose minnow	Cyprinidae

Table 11-2. *Continued*

Abundance	Size	Feeding guild	Reproductive habitat	Thermal guild	Species	Family
Uncommon	Very large	Piscivore	Phytolithophil	Warm	Longnose gar	Lepisosteidae
	Large	Benthivore	Speleophil	Warm	Brown bullhead	Ictaluridae
	Large	Benthivore	Speleophil	Warm	Yellow bullhead	Ictaluridae
	Medium	Zooplanktibenthivore	Lithophil	Warm	Black bullhead	Ictaluridae
	Medium	Zooplanktibenthivore	Lithophil	Warm	Yellow bass	Serranidae
	Medium	Zooplanktibenthivore	Lithophil	Warm	Green sunfish	Centrarchidae
	Small	Benthivore	Psammophil	Cool	Spottail shiner	Centrarchidae
	Small	Benthivore	Speleophil	Cool	Iowa darter	Percidae
	Small	Benthivore	Psammophil	Cool	Logperch	Percidae
	Small	Benthivore	Psammophil	Cold	Mottled sculpin	Cottidae
Rare	Very large	Piscivore	Phytophil	Warm	Bowfin	Amiidae
	Very large	Piscivore	Phytophil	Cool	Muskellunge	Esoxidae
	Very large	Piscivore	Phytophil	Cool	Tiger muskellunge	Esoxidae
	Very large	Benthivore	Speleophil	Cool	Channel catfish	Ictaluridae
	Very large	Benthivore	Litho-pelagophil	Cool	Lake sturgeon	Acipenseridae
	Very large	Benthivore	Phytophil	Warm	Goldfish	Cyprinidae
	Large	Benthivore	Lithophil	Cool	Shorthead redhorse	Catostomidae
	Large	Piscivore	Lithophil	Cold	Brown trout	Salmonidae
	Medium	Zooplanktibenthivore	Phytophil	Cool	Golden shiner	Cyprinidae
	Small	Benthivore	Phytophil	Cool	Central mudminnow	Umbridae
Small	Small	Benthivore	Speleophil	Warm	Fathead minnow	Cyprinidae
	Small	Benthivore	Speleophil	Cool	Johnny darter	Percidae
	Small	Zooplanktibenthivore	Phytolithophil	Warm	Spotfin shiner	Cyprinidae
	Small	Zooplanktibenthivore	Pelagophil	Cool	Emerald shiner	Cyprinidae

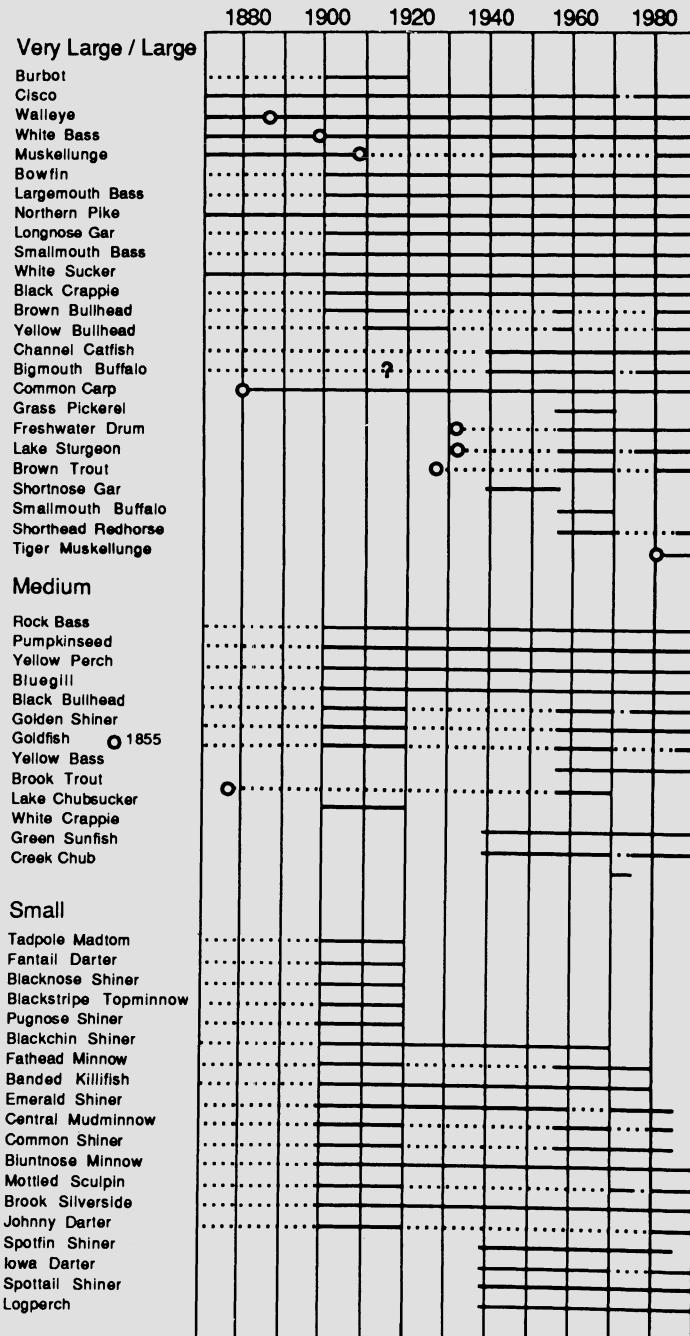
abundant species, which were dominated by medium and large fishes. The most common feeding guild was benthivores, which comprised about 58% of the species, followed by zooplanktibenthivores (21%) and piscivores (21%). Benthivores were about twice as frequent among the rare and uncommon species as they were among the common to very abundant species. The reproductive guilds, in order of frequency of occurrence, were phytophilis (25%), speleophils (25%), lithophils (20%), psammophils (12%), phytolithophils (8%), a litho-pelagophil (4%), and a pelagophil (4%). The rare to uncommon species included relatively more lithophils, speleophils, and psammophils, while the common to very abundant species included relatively more phytophilis and phytolithophils.

Counting species and hybrids, Lake Mendota in the 1980s harbored 21 warm-water fishes, 20 cool-water fishes, and 3 cold-water fishes. We should note that by our thermal guild classification, some species in families of largely warm-water fishes were placed into the cool-water guild; for example, the black and white crappies and the rock bass. Of the common to very abundant species, 58% were warm-water fishes compared with only 42% of the rare to uncommon species, where cool-water species predominated. One cold-water species, the cisco, was common in the 1980s, the mottled sculpin was uncommon, and the brown trout was probably only a seasonal resident from an upstream tributary. Of the more abundant to very abundant species, half were warm-water species (the bluegill and brook silverside) and half were cool-water species (yellow perch and walleye). All three thermal guilds were represented among the common to very abundant fishes.

## Changes from 1900 to 1989

### Species Richness

A total of 56 fish species has been recorded from Lake Mendota since the late 1800s, but in any one year, a maximum of 48 were recorded (Figure 11.1). In addition, 2 hybrids occurred, pumpkinseed  $\times$  bluegill (not shown in Figure 11.1) and northern pike  $\times$  muskellunge (tiger muskellunge). The compilations on richness below do not include the hybrids. Before human introductions, an estimated 37 species lived in the lake, but this is likely an underestimate owing to the sparse sampling prior to 1920. By 1900 to 1920, the numbers had increased by 4 species, 3 of which were known to be stocked (Lathrop et al. 1989) and the other of which was represented only by single specimens and never found at later dates. By 1970, numbers had grown to 48 species, even though 7 found from 1900 to 1920 had disappeared. These 7 losses had been replaced numerically by 12 new species, most of which arrived in the 1930s and early 1940s at the time when fish removed from drying backwaters of the



Mississippi River were being released into Lake Wingra and presumably other lakes in the Yahara River chain, i.e., fish rescue operations (Noland 1951; Bauman et al. 1974). By 1989 the species richness had declined to 38 species or only 2 more species than present prior to introductions of common carp and goldfish. Owing to the intensive sampling in the 1980s, the number present in 1989 probably represents an actual decline in richness of about 10 species or 21% of those present in the 1970s. The low richness of 35 species in 1930 may, in part, be a result of the paucity of fish sampling in the 1920s and 1930s.

Arrivals of new species and extirpations (losses) of species have been high (Figure 11.1). By 1989, 19 species once in the lake were absent; 14 of these were species present from 1900 to 1920. Of the original 36 species, i.e., known to be present in 1900–20 and not introduced, 11 (31%) appear to have been extirpated. Similarly, by 1989, 18 species occurred or had occurred that had been introduced by stocking or had not been present in the records from 1900 to 1920. Thus, 32% of the species reported apparently were introduced or had invaded since about 1920. At the time of maximum richness in 1970, the community was constituted as follows: 31 (64%) original species, 6 (13%) known stocked, and 11 (23%) from the fish rescue operations or from unknown sources or present but missed in early records. By late 1989, the percent composition was similar: 25 (67%) original species, 5 (14%) known stocked, and 7 (19%) introduced through the fish rescue program or other sources or missed in early records. There are no endemic species unique to Lake Mendota.

Species turnover rates from 1900 to 1989 have averaged about 2 species per decade: 1.8 new species and 2.4 species lost per decade. Losses were greatest from 1920 to 1940 (3.5 species per decade) and 1970 to 1989 (5.5 species per decade). Gains were greatest from 1920 to 1940 (5 species per decade).

The persistence of species differed among various groups (Figure 11.1). For example, of the original 36 species, 25 (68%) persisted until 1989, compared with 83% of the 6 known stocked species and only 6 (54%) of

---

**Figure 11-1.** Changes in the fish community of Lake Mendota from 1870 to 1989 as interpreted from presence/absence data. Solid lines represent dates when a species was known to be present, except from 1921 to 1938 where a solid line was used for species known to be present just before and just after this interval. Dashed lines represent other periods when the species was interpreted to be present between dates when records were available. A question mark represents a less certain extrapolation of the presence of a species into the 1800s based on our evaluation of the record. Circles represent dates of first known stocking. Lake trout, stocked as fry from 1900 to 1903, were never recorded in surveys. Pumpkinseed × bluegill hybrids are not listed but were recorded from the 1980s.

the 11 others not present in early records and not known to be stocked for certain. All 6 species that did not persist from the later group were known only from a single specimen and probably never were established in the lake; they may have come in with the fish rescue introductions from the Mississippi River.

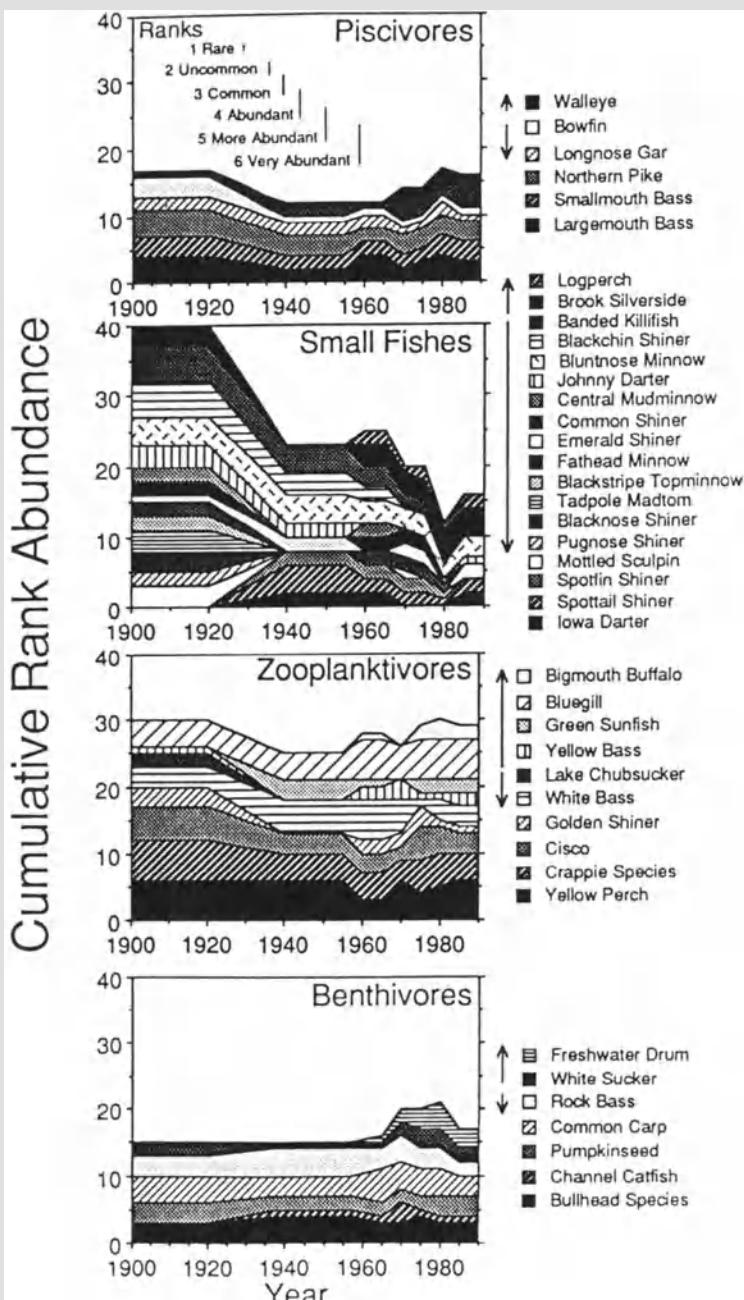
The group with the lowest persistence was the original small-bodied species, many of which were common or abundant in the early records (Lyons 1989). Of the 15 original small species recorded from 1900 to 1920, only 4 (27%) persisted to 1989 (Figure 11.1). This persistence is remarkably lower than for the medium to very large original species; 14 out of 15 (93%) large or very large species persisted, and 7 out of 7 (100%) medium-sized species persisted. Lyons discovered this high extirpation rate of small native fishes in Lake Mendota; our analyses indicate that the small fishes are the only size group in the lake with such a high rate of extirpation. The extirpations of small species were concentrated from 1920 to 1940 (6 species) and again from 1970 to 1989 (7 species). Overall, the small fishes account for 12 of the 19 (63%) species losses; among the original species, small fishes account for 12 of the 13 (92%) species losses.

Four of the 6 species known to be purposely introduced by stocking were large to very large in size (Figure 11.1). None of the 6 have been important contributors to the recreational fishery: lake sturgeon, common carp, goldfish, lake trout, brown trout, and brook trout. One, the common carp, is considered to be a pest species. Three were cold-water species. One, the lake trout, never appeared in any lake surveys. The others are rare.

### Changes in Relative Abundance

Only 4 taxa had a mean rank abundance of 4 or greater (abundant, more abundant, or very abundant), while 13 taxa had a mean rank abundance between 2 and 3.9 (uncommon or common), and 22 had a rank of 1 (rare) (the Appendix). The data feature species that have remained abundant, common, or rare consistently from 1900 to 1989 and other species that have increased or decreased markedly between absent and abundant. Overall from 1900 to 1989 (the Appendix), it appeared that 9 taxa (17%) increased in relative abundance, 17 taxa (31%) decreased, and 15 (28%) exhibited no obvious trend. Another 13 taxa (24%) were too rare to observe whether a trend occurred or not.

Changes in relative abundance are most apparent among the small fishes, but visible changes also occurred among medium to very large fishes: the piscivores, zooplanktivores, and benthivores (Figure 11.2). The greater temporal resolution after 1950 (Figure 11.2) serves as a reminder that there are few data prior to 1950 and that each of these



**Figure 11-2.** Changes from 1900 to 1989 in the rank relative abundances among piscivores, small fishes, medium to very large zooplanktivores, and medium to very large benthivores.

groups of fishes contains species characterized by short-term variation resulting from strong and weak year classes and other factors. Our evaluation of changes in this chapter is based on differences in relative abundance on a coarse temporal scale.

*Piscivores.* Dominant trends among the piscivores were the large increase in the relative abundance of walleye in the 1970s and 1980s relative to other piscivores, the reduced relative abundance of piscivores from ca. 1930 to 1970, and the decline of bowfin and longnose gar (Figure 11.2). Walleye were reported in the Madison lakes in newspaper accounts as early as 1843 (Mollenhoff 1982, p. 41) and recorded as present in Frank L. Pierstorff's catches from Lake Mendota in 1917 (Jacobs 1956). Walleye were apparently rare in the early years, as indicated by attempts to increase their populations. They were periodically stocked as fry between 1885 and 1945 and as fingerlings and fry in ensuing years. Piscivores appear to have been more abundant relative to other kinds of fishes early in the century and again after 1970. Prior to 1930, largemouth bass and northern pike were abundant and smallmouth bass and bowfin were common. After 1970, walleye were abundant to more abundant while smallmouth bass, largemouth bass, and northern pike were common. The low abundance of piscivores in the middle of the century appears to have been the result of declines in both black basses and in the bowfin. Regardless, there seems to have been a reduction in piscivory in the middle of the century from ca. 1930 to 1970. Both bowfin and longnose gar, the two piscivores not sought or managed for sport fishing, have declined from common (bowfin) and uncommon (longnose gar) to rare. Bowfin declined between the 1910s and the 1940s, the gar around 1970.

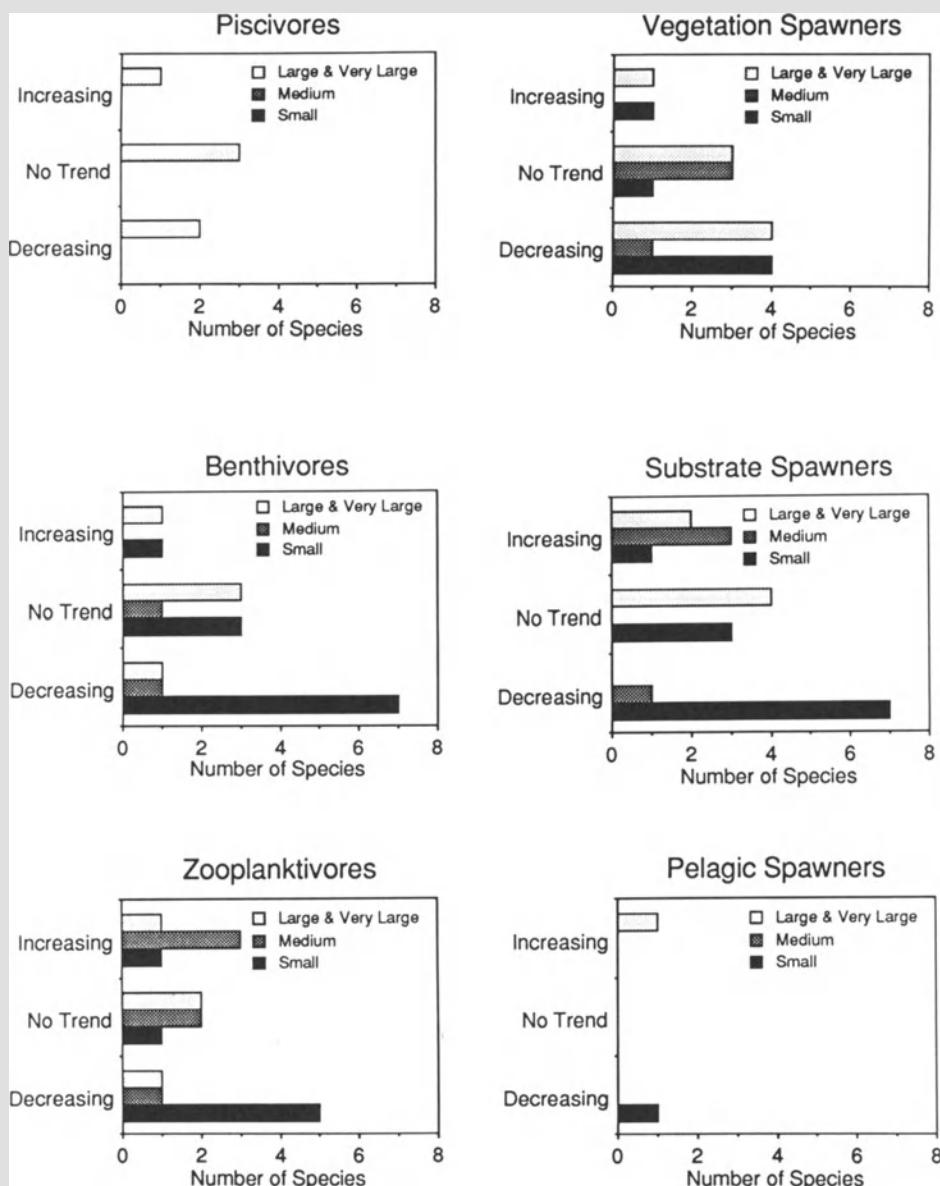
*Small Fishes.* The decline of small fishes in Lake Mendota has been clearly indicated from presence/absence data. The same pattern is apparent in changes in the relative abundance (Figure 11.2) abundant enough to demonstrate trends, i.e., those which were not always rare or absent. The cumulative rank abundance of all taxa declined from an index of 40 early in the century to about 14 in the 1980s. The greatest declines in abundance occurred between 1920 and 1940 and between 1970 and 1985. The most striking trends are the declines associated with the extirpations of fishes.

The most striking increases in relative abundance among small fishes occurred in the brook silversides and logperch populations since 1950 (Figure 11.2). The logperch had not been observed prior to the 1960s. Another striking pattern is apparent for spotfin shiner, spottail shiner, and Iowa darter. These species were not observed prior to 1940, were most abundant from 1940 to 1960, then declined during the 1960s. In the 1970s the only abundant small species was the brook silversides;

bluntnose minnow were common; logperch, mottled sculpin, spottail shiner, and Iowa darter were uncommon; and johnny darter were rare. This contrasts markedly with the status from 1900 to 1920 when banded killifish were ranked as more abundant; blackchin shiner and bluntnose minnow as abundant, brook silverside, mottled sculpin, johnny darter, tadpole madtom, and blacknose shiner as common; five other species as uncommon; and one other as rare (Figure 11.2).

*Medium to Large Zooplanktivores.* Over all taxa, medium to very large zooplanktivores have cumulative rank abundances in the 1980s similar to those observed from 1900 to 1920 (Figure 11.2). Slightly lower cumulative rank abundances were apparent in the 1940s and 1950s. None of the four species which increased—bigmouth buffalo, green sunfish, yellow bass, and, apparently, white crappie—were observed in early collections. Yellow bass were not reported in the Yahara River system by Greene (1935) and were first observed in Lake Mendota in 1957 (Wright 1968). They were thought to have been expanding their range into the Yahara lakes (Wright 1968). Their first appearance in Lake Wingra in the mid-1930s was thought to be from the fish rescue operations (Bauman et al. 1974). The white crappie also may have entered the Yahara River system from fish rescue operations, because Greene (1935) did not report this species as present in southern Wisconsin. Bluegill, the most abundant species in the lakes by our relative abundance index, was always at least abundant but increased to very abundant for most periods after 1960 (Figure 11.2; the Appendix). Of the two declining species (Figure 11.2), the lake chubsucker was uncommon from 1900 to 1920 and was extirpated by the 1940s, while the white bass varied from very abundant in the 1960s to rare in the late 1970s after a major die-off in 1976 (Lathrop et al., in press). Three of the four taxa that had no apparent long-term trend—cisco, crappie sp., and yellow perch—were common to very abundant over the years, while the other species, the golden shiner, varied from absent to common.

*Medium to Very Large Benthivores.* Except for the addition of the freshwater drum, medium to very large benthivores as a group have cumulative rank abundances in the 1980s similar to those observed from 1900 to 1920 (Figure 11.2; the Appendix). Of the two increasing species, the freshwater drum was first recorded in the 1950s and has increased to common or abundant levels, while the white sucker was observed as rare or uncommon until the late 1970s and 1980s, when it increased to uncommon or common. Mallots, or mullets, probably white suckers, also were noted as an abundant food fish in the Yahara lakes in the mid-1800s (Mollenhoff 1982, p. 41). The rock bass declined from abundant or common to common or uncommon. Common carp, pumpkinseed, channel catfish, and bullhead species had no apparent long-term trend. Common



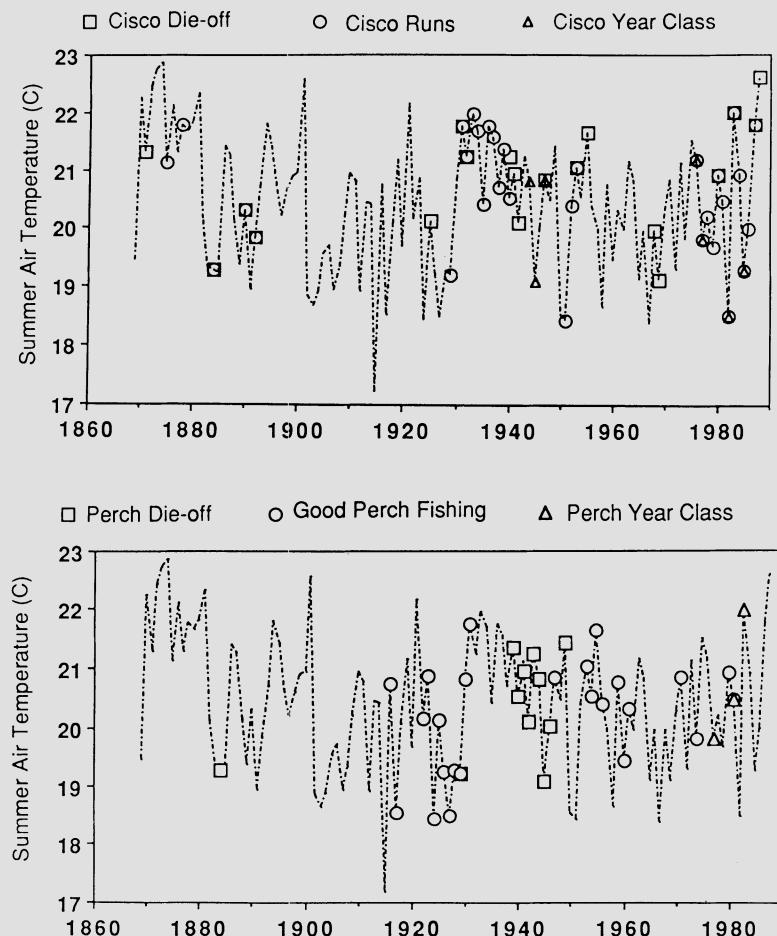
**Figure 11-3.** Differences in abundance trends from 1900 to 1989 for different size fishes in various reproductive guilds (substrate, pelagic, or vegetation spawners) and feeding guilds (benthivores, zooplanktivores, and piscivores).

carp appeared to be most abundant in the 1960s based on the largest "rough fish" catches from 1963 to 1966 (Lathrop et al., in press), averaging 120 metric tons per year. Another period of apparent abundance was in the 1930s, when an average of 65 metric tons was caught per year from 1935 to 1938. Declines in the 1940s and after the 1960s may have resulted from the state "rough fish" removal program. The estimates of carp abundance prior to and after "rough fish" and commercial catches are crude approximations based on their occurrence in sampling efforts. In Lake Wingra carp were judged to reach maximum abundances by the 1930s (Bauman et al. 1974). Individual species of bullheads were not always noted and had to be lumped for this index of relative abundance. As a group they ranged from common to abundant. Pumpkinseeds and channel catfish varied from rare to common.

*Guild versus Body Size.* Guilds with the most decreasing taxa (Figure 11.3; the Appendix) were the vegetation spawners, with 9 of 18 taxa, and the benthivores, with 9 of 18 taxa. The numbers of declining taxa in the other species-rich guilds were only slightly less: 8 of 21 taxa for substrate spawners and 7 of 17 taxa for zooplanktivores.

Trends in relative abundance for taxa in a given reproductive or feeding guild differed markedly among size groups, with the small species in each guild more frequently decreasing than increasing (Figure 11.3). This is apparent for all guilds with enough small species to detect a pattern, i.e., benthivores, zooplanktivores, substrate spawners, and vegetation spawners. Even the single small pelagic spawner declined, which was consistent with the general pattern of decline of small species. Medium-sized fish had no consistent pattern across guilds, but appeared to have more taxa increasing than decreasing for substrate spawners and for zooplanktivores. Large and very large taxa also had no consistent pattern across guilds, but appeared to have more taxa decreasing for vegetation spawners and increasing for substrate spawners. Small species tended to decrease in all guilds in which they were represented, while medium, large, and very large species had no consistent pattern independent of reproductive and feeding guilds. Thus, the decline of small species was not dependent on their reproductive or feeding guilds, but most likely was related to their adult body size.

The proportion of taxa with increasing trends in relative abundance was greater for warm-water than for cool-water guilds (see the Appendix). Among the 23 warm-water taxa, 6 (26%) had increasing trends compared with only 2 (8%) of the 26 cool-water fishes. Those with decreasing trends were similar: 39% of the warm-water taxa and 35% of the cool-water taxa. For the 4 cold-water species, one was increasing, one had no trend, and 2 were too rare to judge. Overall declines in relative abundance of certain taxa were unrelated to their thermal guild.



**Figure 11-4.** Reported occurrences of cisco and yellow perch die-offs, spawning runs or good fishing, and strong year classes from 1869 to 1988 plotted on a time series of summer air temperatures for Madison. Earlier cisco die-offs were reported for 1858 (Wisconsin State Journal, 16 August 1858) and prior to 1849 (Wisconsin Union, 15 December 1967), and successful spear fishing was reported for 1867 (John 1954; John and Hasler 1956). Some of the years of strong year classes for cisco are likely off by a year or so owing to errors in aging (Rudstam 1991, pers. comm.).

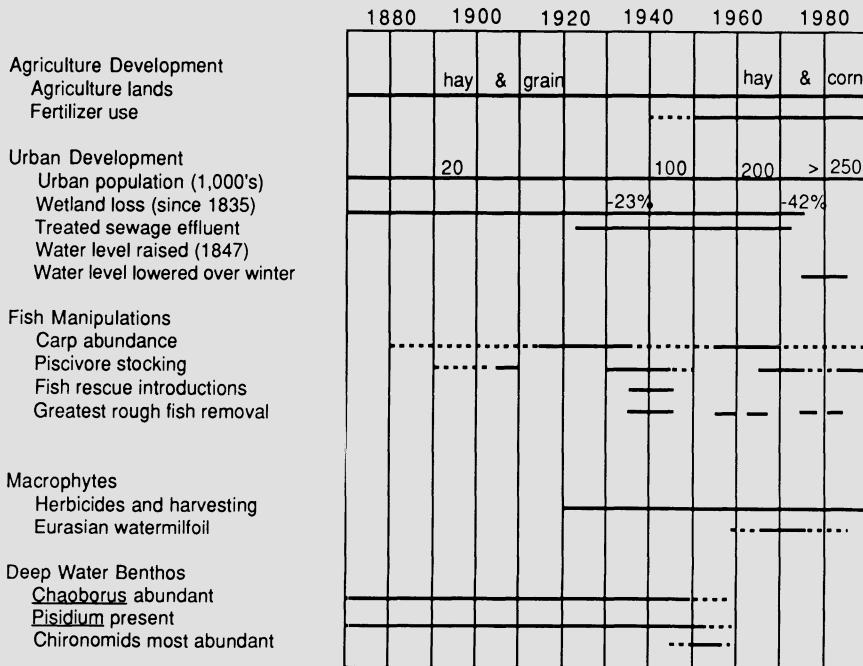
#### Changes in Selected Species

The cisco population has fluctuated greatly from 1870 to 1989 based on records of die-offs, large spawning runs, good fishing, and occasional formation of strong year classes (Figure 11.4). The absence or rarity of

such records from 1892 to 1924 and again from 1957 to 1975 makes the interpretation of long-term change difficult. After the die-offs in the early 1950s, ciscos were thought to have disappeared from Lake Mendota (Arthur D. Hasler, personal communication). However, our judgment is that cisco may have been abundant in the early part of the 1900s as populations built up to the numbers producing large die-offs in the 1930s. John and Hasler (1956) thought that the absence of useful catch data from 1892 and 1928 reflected the reluctance of fishers to report large catches. Fishing was done with gill nets during these years, but the legal 10-day season did not always correspond with the cisco run, and according to newspaper reports, violations of the fishing season were common. Summer temperatures from 1900 to 1930 also were usually cooler than in other periods (Figure 11.4), which could have contributed to reduced die-offs and conditions generally more suitable for the cold-water cisco. When die-offs, strong runs, and strong year classes occur together, such as from 1871 to 1892, 1924 to 1956, and 1976 to 1988, it is clear that cisco are abundant. For the first two of these periods, gill-net catch-per-effort data suggested that the abundance of cisco was greater in 1890, with maximum catches of 200–260 cisco per 100 feet of gill net, than in 1931, with maximum catches of 80 cisco per 100 feet, or in 1949, with 16 per 100 feet (John 1954; John and Hasler 1956). The same difference between the abundance in the late 1800s and mid 1900s is indicated by dipnetting (John 1954; McNaught 1963). Cisco die-offs are an indication that cisco have been, and often still are, abundant. Frequently, good runs occurred in the same year as a cisco die-off. In 1947, a die-off even occurred in the same year as the origin of a strong year class. Large fluctuations in the abundance of cisco are indicated by die-offs prior to 1849 (Figure 11.4) and abundances low enough to stimulate stocking fingerling and adult cisco from Lake Michigan from 1852 to 1855 and fry in the 1880s (Lathrop et al., in press). A die-off reported for 1858 (Figure 11.4) could have included some of these stocked fish.

Changes in the abundance of cisco markedly influenced the zooplankton populations and the water clarity. The major die-off in 1987 resulted in increased abundance of daphnids, altered phytoplankton populations, and increased water clarity in the following years (Lathrop and Carpenter, Ch. 8; Rudstam et al., Ch. 12; Vanni et al. 1990). Also, the changes in the long-term abundance of daphnids in the observed record (Lathrop and Carpenter, Ch. 8) and in the paleolimnological record (Kitchell and Sanford, Ch. 4) mirror, in general, the changes in abundance of cisco indicated by our historical records (Figure 11.4).

Yellow perch also fluctuated greatly in abundance based on reports of die-offs, good fishing, and strong year class formation (Figure 11.4). Perch, unlike cisco, were never so rare as to be thought extirpated. As indicated in these general historical records, perch were abundant in the



**Figure 11-5.** Anthropogenic and other changes in the Lake Mendota environment from 1870 to 1989 summarized from Lathrop et al. (in press).

early 1880s, 1916, 1917, 1922–31, 1940–61, and 1971–83. Conversely, they were not as abundant in 1894–1915, 1918–21, 1932–39, 1962–70, and 1984–88. There was no obvious relation, positive or negative, between perch and cisco abundance from these records. The low abundance of perch noted here for the 1960s does correspond with their low relative abundance in the same years from more numerical data in Figure 11.2; thus confidence for the decline of perch in the 1960s is increased somewhat. Patterns apparent in Figure 11.4 do not correspond with Bardach's (1951) analysis of catch per effort, body size, and creel surveys. He argued that the perch were low in abundance in the 1940s because of the die-offs.

### Possible Explanations for Changes in the Fish Community

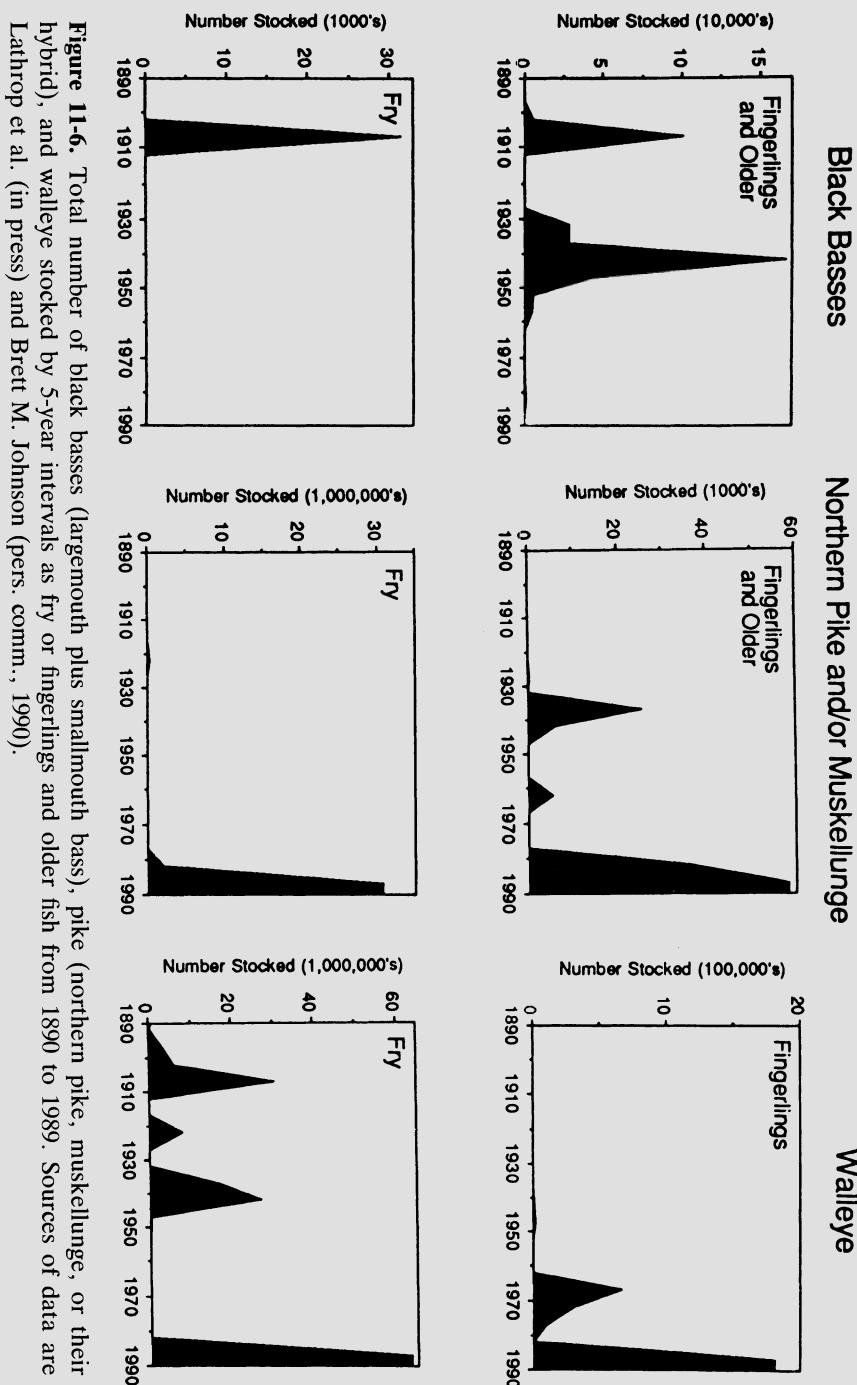
Untangling the complex interactions between the historic changes in the fish community (Figures 11.1–4), other changes in the Lake Mendota environment (Figures 11.5 and 11.6), and species interactions in the fish

community itself generates an interesting range of hypotheses and speculations. Major changes in the fish community appear to have resulted from agricultural and urban development of the drainage basin, water level control, aquatic macrophyte invasions and control programs, and fishery manipulations including introductions of exotic fishes, "rough fish" removal, and intense stocking of piscivores. These changes to the Lake Mendota environment are briefly described below and then discussed with respect to fish community dynamics.

### Changes to the Lake Mendota Environment

Anthropogenic changes to the Lake Mendota environment began before any of the historic records on the fish community presented here (Lathrop et al., in press). Notable events prior to 1900 associated with the invasion of Europeans were the raising of the water level 1.2 to 1.5 m with the construction of the locks at the outlet in 1847 and the introduction of intensive agriculture in the basin in the mid-1800s. By 1880, the drainage basin had been largely developed for agricultural use, with 300,000 ha converted to use for hay and wheat production. By 1900, wheat had been replaced by oats, other small grains, and corn. The urban population had exceeded 20,000 by 1900. The exotics—common carp, goldfish, and lake trout—had been introduced, and populations of native fishes had been supplemented by stocking of white bass, walleye fry, brook trout, and cisco. Cisco had been stocked as early as 1852–55 and again in the 1880s. Among the early introduced exotics (carp, goldfish, and lake trout), only carp was to become an important member of the fish community. The early stocking of cisco, walleye, and white bass probably reflects attempts to supplement the populations of these high-valued species during periods of low abundance.

By 1940 (Figure 11.5), the total area of agricultural lands had not changed appreciably from 300,000 ha nor had the type of crops, but the use of fertilizers had begun and 23% of the wetlands around the lake had been drained. The urban population had reached ca. 75,000. Beginning in the 1920s, treated sewage effluents from DeForest (1923) and Waunakee (1928) were discharged into streams flowing into the lake, and herbicides and weed cutters were used to reduce macrophyte growth. Muskellunge populations had been supplemented in 1906, brown trout introduced in 1927, and perhaps as many as 9 other species (Figure 11.1) were introduced during the Mississippi River fish rescue program beginning in the late 1930s. Populations of black basses, walleye, and northern pike were supplemented by stocking (Figure 11.6). Intense "rough fish" removals, focusing on carp, were in progress by 1936; in half of the years between 1935 and 1942, catches, primarily of carp, exceeded 2,200 metric tons.



**Figure 11-6.** Total number of black basses ( largemouth plus smallmouth bass ), pike ( northern pike, muskellunge, or their hybrid ), and walleye stocked by 5-year intervals as fry or fingerlings and older fish from 1890 to 1989. Sources of data are Lathrop et al. (in press) and Brett M. Johnson (pers. comm., 1990).

In the 1950s or shortly thereafter, large changes occurred in the animal benthos in deep water (Lathrop, Ch. 10 and in press). The fingernail clam, *Pisidium* sp., disappeared; the phantom midge, *Chaoborus* sp., declined in abundance; and for a short period chironomid midges became very abundant compared with earlier or later years (Figure 11.5). These changes in the deep-water benthos took place when carp were very abundant and at a time approximately 30 years after treated sewage began entering the lake, 30 years after herbicides and weed cutters were first used, and approximately 70 years after maximum agricultural acreage had been developed. As Lathrop suggests, the cause was most likely a change in the sediment environment. A slow change in the sediment chemistry owing to eutrophication seems likely. The heavy use of insecticides in the 1950s and 1960s is also a possibility (Lathrop, Ch. 10).

By 1960 (Figure 11.5), most of these stressors on the lake had intensified, but no major new changes were apparent. The urban population reached ca. 150,000 corn slowly continued to replace oats and small grains as a major crop, and agricultural fertilizer use increased after the 1940s. The town of Windsor added its treated sewage to a Lake Mendota tributary beginning in 1962. The fish rescue program had ended in the mid-1940s and no new species had been intentionally introduced since then. Stocking of piscivores was intense in the early 1940s, but was not from 1945 to 1964 (Figure 11.6). Removals of "rough fish" were large in the late 1950s.

By 1980 (Figure 11.5), some stressors were reduced while others continued to intensify. In addition, several new changes took place. Total acreage farmed had decreased slowly since 1880 to ca. 250,000 ha. Hay and corn remained the principal crops, with corn almost completely replacing oats and other small grains. Sewage effluents from DeForest, Waunakee, and Windsor were diverted around Lake Mendota in 1971 through the Madison Metropolitan Sewage District. The urban population exceeded 210,000. Forty-two percent of the wetlands had been lost compared with the 23% lost by 1940. Winter drawdown of water levels began in 1974 to prevent high water in spring. "Rough fish" removals were especially large, i.e., >100,000 lb per year, in the mid-1960s and again in 1977. Piscivore stocking increased in the 1960s and declined somewhat in the 1970s (Figure 11.6). A very visible change was the development of dense, almost monospecific growths of the exotic macrophyte, Eurasian watermilfoil, in the littoral zone from ca. 1964 to 1975 (Nichols et al., Ch. 9). Interestingly, these growths developed after about 10 years of intensive carp removal in the late 1950s and mid-1960s, and the declines were coincident with the initiation of winter drawdowns of water level. It is tempting to hypothesize causal relations between carp removal and the timing of the watermilfoil expansion, and between winter water level controls and the timing of milfoil declines. Control of winter water

level can probably be discounted because similar declines in watermilfoil occurred in the lower lakes, where water level controls were not as great.

During the 1980s (Figure 11.5), several notable changes occurred. The last large catch of carp in the commercial "rough fish" removal program occurred in 1977. Poor market prices for the carp substantially reduced the commercial fishing effort for carp on all Yahara lakes (Lathrop et al., in press). Piscivore stocking increased greatly in the late 1980s as part of the Lake Mendota biomanipulation project (Figure 11.6). Winter drawdown of water level continued through the 1980s, but beginning in 1988 higher spring water levels were maintained on the recommendation of the WDNR to maintain northern pike spawning sites. Macrophyte control with herbicides and weed cutters continued. The urban population passed 250,000.

### Causal Relations

The principal changes in the fish community from 1900 to 1989 have been (1) the development of populations of carp and other exotics; (2) the 1920s and 1930s decline of small-bodied littoral fishes; (3) the 1970s and 1980s decline of small-bodied littoral fishes; (3) the changes in dominance and relative abundance of piscivorous species; and (4) the large variations in the abundance of some of the medium to large zooplanktivores.

The principal causes for these changes include (1) modification and loss of the inshore habitat owing to eutrophication and sedimentation, water level controls, loss of wetlands, invasions of carp and Eurasian watermilfoil, and macrophyte manipulations with herbicides and weed cutters; (2) modification of deep-water benthic habitat from eutrophication and sedimentation and declines of fingernail clams and insect larvae; and (3) changes in piscivory from stocking or not stocking black basses, walleye, northern pike, muskellunge, and northern pike × muskellunge hybrids. Because many of these changes were occurring simultaneously and have interacting, delayed, or chronic effects, and because the specifics important to the ecology of fishes usually were documented poorly, the cause of most changes can only be ascribed in very general terms.

*Development of Exotic Populations of Fish.* Of the 13 species of fish present in Lake Mendota in the 1980s that either were introduced or not recorded as present before 1920, the carp, freshwater drum, and spottail shiner became at least abundant in some years. Only the carp and brown trout are not native to North America. Freshwater drum, white crappie, yellow bass, and spottail shiner, if present earlier, should have been found in reliable numbers during the sampling from 1900 to 1930; they probably are exotics to Lake Mendota. The anthropogenic explanation for the apparent expansion of these species appears to be simply that they

were intentionally introduced (common carp) or came in with the fishes released from the fish rescue program (freshwater drum, white crappie, yellow bass, and possibly spottail shiner). Only the carp reached nuisance levels; this stimulated an extensive “rough fish” removal program which persisted from 1936 to 1966 by the Wisconsin Conservation Department and later in 1974 by commercial fishers. The carp apparently were reduced by “rough fish” removal in the 1930s and 1960s from more abundant levels to common. Years of maximum abundance were judged to be in the late 1920s and 1930s and in the 1960s. Freshwater drum has become common to abundant and may reach nuisance levels in the future, as it has in lakes such as Lake Winnebago, Wisconsin. The spottail shiner appears to be declining and was rare to uncommon in the 1980s.

*Decline of Small-Bodied Fishes.* The declines and extirpations of many of the small-bodied littoral fishes appeared to occur in two pulses: the first between the 1920s and 1940s and the second in the 1970s and 1980s. Because the small species have a short life span, they are not buffered from a few consecutive years of poor conditions and thus may be more susceptible to extirpation than longer-lived species. The anthropogenic explanations for the two periods of decline appear to differ, but they include degradation of the inshore habitat and increased piscivory from stocked piscivores. Habitat degradation may have been more important for the first period and piscivory more important for the second.

The loss of species in the 1920s and 1930s was coincident with a wide variety of anthropogenic changes in the littoral zone that would negatively affect the small littoral species (Figure 11.5). Many of these species depended on the benthic environment for food and spawning substrate; others depended on the vegetation for reproduction and the zooplankton for food. Increased primary production and nocturnal anoxia associated with eutrophication from the sewage effluents that began in the 1920s may be an important mechanism interfering with benthic spawners. Loss of wetlands and physical disturbance by common carp of the bottom and rooted macrophytes may have reduced those species that use vegetation or the bottom. Competition with young carp, which must have increased in abundance in the littoral zone during the 1920s and 1930s, also seems likely. Black bass fingerlings, walleye fry, and northern pike were stocked intensively in the 1930s and 1940s (Figure 11.6), which should have increased piscivory on small-bodied littoral species; interestingly, the species that were extirpated tended to be smaller than those that persisted. Macrophyte cover may have been reduced by the disturbance from large carp, which would further expose these small species to predatory fishes. The relative importance of these various factors cannot be separated with available information.

A wide variety of human-caused changes also were coincident with the declines in small-bodied fishes in the 1970s and 1980s and could have contributed to the declines. These changes included the expansion of watermilfoil, intensive stocking of walleye fingerlings in the late 1960s and the 1970s (Figure 11.6), winter drawdown of water level, macrophyte control programs, and a continued loss of wetland habitat. Of these, we favor increased piscivory as the primary explanation for the declines of small fishes, because most small fishes, not just those that use a particular spawning substrate or food type, have been declining. In small lakes, piscivores are known to exclude small, soft-rayed species but not medium-sized, spiny-rayed species (Magnuson et al. 1989; Tonn et al. 1990; He and Kitchell 1990). The declines in the 1970s and 1980s begin soon after the most intense stocking of piscivores in the history of the lake (Figures 11.1, 11.3, 11.5, and 11.6). Three times more fingerling walleye were stocked from 1965 to 1979 than fingerlings of all species from 1900 to 1960. The species losses continued in the late 1980s with four more species, and we expect the extirpations to continue. The total number of piscivores stocked in the five years between 1985 and 1989, 96 million, exceeds the number stocked in the 100 years from 1885 to 1984, 81 million. Thus, the greatest influence of piscivore stocking should occur in the 1990s when, as outlined by Johnson et al. (Ch. 16), maximum piscivory will result from the fishery management program.

The fish community as it existed in the late 1980s provides further evidence for the importance of piscivory as a principal factor important to the decline of small species. The 7 species remaining in 1985–89 (Figure 11.1) were the brook silverside, bluntnose minnow, mottled sculpin, logperch, Iowa darter, johnny darter, and spottail shiner. All but one of these are benthivores, so some small benthivores have persisted, at least in low numbers. Three are psammophils, 3 are speleophils, and 1 is a phytolithophil, so all can and do use bottom substrates to spawn. Psammophils and speleophils are overrepresented in this group of survivors. These 7 species also tend to be larger than those small fishes that are rare or extirpated: 5 out of 7 (71%) have a maximum length greater than 60 mm, compared with only 5 out of 12 (42%) of the extirpated species. The bias towards loss of the smaller of the small species again implicates piscivory as a factor in the declines.

Lyons (1989) speculated that the growth of the exotic Eurasian watermilfoil was an important habitat change for these species in the littoral zone and noted that the declines of blackchin shiner and banded killifish were coincident with the milfoil expansion. Both the blackchin shiner and the banded killifish spawn on vegetation, so the loss of their particular spawning substrate could have been important. During the milfoil expansion, the blackchin shiner was extirpated and the banded killifish declined greatly, but the killifish was not extirpated until after the subsidence of

the milfoil (Figures 11.1, 11.3, and 11.5). Both species disappeared from Lakes Monona and Wingra, which also had experienced milfoil invasions, but both were common in Lake Opinicon, Ontario, before and after Eurasian watermilfoil invaded (Lyons 1989). Also, the banded killifish persisted in Fish Lake, Dane County, Wisconsin, despite dense growth of milfoil (Brett Johnson, pers. comm., 1990). The role of Eurasian watermilfoil in the extirpation of blackchin shiner and banded killifish is equivocal. Milfoil expansion was unimportant for species losses in the 1920s and 1930s, which occurred several decades before milfoil was abundant; also, the declines of blackchin shiner and spottail shiner began a decade before milfoil was abundant.

The persistence of the brook silverside deserves comment. It is a small, slender species without protective spines and it is the only small species that has been abundant to more abundant in the 1980s. How could it persist in the presence of intense piscivory when other small, soft-rayed species have declined so markedly? Several features of its behavior would appear to provide protection, especially from walleye predation. First, both the young and the adults live and feed usually within 10 to 12 cm of the surface and never deeper than 1 m (Cahn 1927); as a consequence, they would not be near the bottom where walleye live. Second, from 1 to 6 months after hatching they are offshore at the surface over deep water (Cahn 1927), again well away from piscivores except for longnose gars and white bass. Third, older fish migrate offshore at the surface during the day and spend the night at the surface in the shallows (Cahn 1927). This would continue to protect them from diurnal littoral predators like the black basses and northern pike or muskellunge. Finally, they are a schooling fish with a semitransparent silvery coloration. The coloration provides effective camouflage for the open-water environment and schooling serves as an antipredator adaptation (Godin 1986).

None of the species losses in Lake Mendota represents a global extinction, because none of the species were endemic. Although these species were extirpated from the lake, some would be expected to reinvade if the predator populations decrease after year 2000. Some of the small extirpated species have occurred in the streams of the region (Fago 1982), e.g., banded killifish, blacknose shiner, blackchin shiner, blackstripe topminnow, emerald shiner, fantail darter, pugnose shiner, and tadpole madtom. An updated survey for these species in surrounding streams is warranted.

*Changes in Piscivores.* The increase in walleye abundance in the 1970s and 1980s has resulted from intensive fingerling stocking. They were stocked first as fry in the 1880s and first as fingerlings in the 1940s (Figure 11.6). Except for the 1910s, they were stocked as fry or fingerlings in every decade from the 1880s to the 1980s. In spite of the large numbers of

fry stocked, walleye were uncommon before the 1970s. The totals of 1.1 million fingerling walleye stocked from 1965 to 1979 and 1.8 million from 1985 to 1989 provide the best explanation for the recent increase in the relative abundance of walleye. This increased abundance of walleye has had a large influence on the sport fishery (Johnson and Staggs, Ch. 17).

The two piscivores that declined from 1900 to 1989, the bowfin and the longnose gar, have not been stocked, nor were they the object of a sport fishery. Bowfin was common from 1900 to 1920 and has been rare ever since. It is a phytophil and may have been influenced by changes in the littoral macrophytes as carp became abundant. In addition, bowfin may have been reduced by the "rough fish" removal program of which they were a part (200 were removed in 1963) or by competition with the stocked piscivores. The longnose gar was uncommon prior to 1970 and usually was rare from 1970 to 1989. It is a phytolithophil and could have been influenced by the general degradation of the littoral zone. Longnose gar adults often occur in the offshore regions at the surface (Haase 1969) and brook silverside can be important in their diet. In the 1960s the "rough fish" program removed 400 gar, and in the late 1960s a study of the ecology of gar sacrificed an unknown number of adults for stomach, gonad, or growth analyses and 600 young of year were collected and preserved (Haase 1969). Longnose gar declined from uncommon to rare at the end of the 1960s.

*Cisco and Yellow Perch Die-Offs.* We provided some of the historical evidence for the high variability in cisco and yellow perch populations in Lake Mendota. The same features of high variability also characterize black crappie, bluegill, brook silverside, and other species. The variability is initially generated by large year-to-year variation in the reproductive success and recruitment to the juvenile and adult populations. The causes of such variability are the topics of entire treatises on fisheries and fish ecology (Pitcher and Hart 1982; Rothschild 1986; Magnuson et al. 1989). Our explanations will be more parochial and focus on the die-offs.

Like obnoxious algal blooms, cisco die-offs catch the attention of the Madison papers and populace. In Lake Mendota cisco grow large enough that they are not vulnerable to piscivory; likewise, neither the commercial nor the recreational fisheries appear to have reduced their abundances significantly. Thus, large numbers of older and sometimes middle-aged cisco die in midsummer and float to the shore where they are easily noticed by the people around the lake. The fish are usually robust and may not appear to be diseased. The popular and scientific belief has been that this occurs in unusually warm summers when the cold-water cisco are forced out of the cold but anoxic hypolimnion into the too-warm epilimnion. However, Lake Mendota cisco not only spend most of the

summer in the epilimnion at depths similar to those of yellow perch, even in summers without die-offs (Rudstam and Magnuson 1985), but they also experience die-offs in both warm- and cool summers (Figure 11.4). In addition, there are many warm summers without cisco die-offs. Our interpretation is that die-offs of cisco occur when the population of older animals is very abundant and becoming senescent. If warmer and cooler summers alternate, such as in the 1980s, the die-offs are more likely in warmer summers; but if a warmer summer does not come along to catalyze the die-off, it occurs anyway, such as in 1890, 1892, 1968, and 1969. Not all cisco are lost in years of a die-off. Large spawning runs often occur in the years immediately following a die-off, for example after the 1932, 1933, and 1980 die-offs. Another point to be noted is that the years in which strong year classes are formed are not always those with cool summers. A mechanistic explanation for cisco die-offs and year class variation remains to be developed.

Yellow perch die-offs occasionally made the newspapers, but were reported less frequently than for cisco (Figure 11.4). The 1884 die-off coincided with the cisco die-off, as did some of the die-offs in the 1940s. Perch die-offs did not appear to be related to either warm or cool summers. Die-offs between 1939 and 1949 coincided with reports of diseased animals (Bardach 1951); outbreaks of a myxosporidian, *Myxobolus* sp., were most intense in 1939 and 1946. Ten tons of perch were removed from a 10-block stretch in 1 week in 1939, and 19 tons were removed in 1946. No perch die-offs have occurred since 1950.

## Summary

1. The 1980s fish community of Lake Mendota contained 41 species and 2 hybrids. The feeding guild with the most species was the benthivores. Reproductive guilds were represented by a broad array of vegetation and substrate spawners. Warm- and cool-water thermal guilds were equally represented, and 3 coldwater species were present. Most species were medium to large in body size; small and very large species were underrepresented.

2. Species richness prior to the anthropogenic effects of European settlers was about 36 species. The maximum number was 48 in 1970, which declined to 38 by the late 1980s. The species composition from 1970 to 1989 was about 66% original species, 14% known stocked, and 20% introduced by the fish rescue program or other sources or missed in early records. Species turnover rates have averaged about 2 species per decade. The group of species with the lowest persistence was the original small-bodied species, of which only 27% were still present in 1985–89.

3. Among the piscivores, walleye have increased markedly in recent years and bowfin and longnose gar have decreased. As a group, piscivores appeared less common in the middle of the century. Stocking of fingerlings accounted for the increase in walleye in the 1970s and 1980s.

4. The decline of small species occurred in two periods, between the 1920s and 1940s and in the 1970s and 1980s. The first decline resulted from habitat degradation in the littoral zone, the second from the stocking of piscivores. The only small species remaining abundant in the 1980s was the brook silverside, which has a number of effective antipredator adaptations. The Eurasian watermilfoil did not appear to contribute significantly to the decline of small species.

5. The medium to very large zooplanktivores were about as abundant in the 1980s as early in the century. This group, while characterized by high year-to-year variation in abundance, constituted the most consistently abundant fishes in the lake over the long term and included a warm-water (bluegill), a cool-water (yellow perch), and a cold-water (cisco) species. The yellow bass invaded in the 1950s and has been rare to common.

6. The medium to very large benthivores as a group changed little in abundance. Common carp reached nuisance levels of abundance and were the object of a major "rough fish" removal project which appeared to lower their abundance in the 1940s and again after the 1960s. The freshwater drum invaded and has increased in the 1970s and 1980s.

7. Smaller species declined more than medium or larger species, regardless of their reproductive or feeding guild. Of the warm-water taxa, 26% increased, compared with only 8% of the cool-water taxa.

8. Cisco was characterized by major die-offs and periods of high and low abundance, which were noted even before 1849 and have continued into the 1980s. Die-offs of older and middle-aged fish occurred in large numbers and were easily noted. Surprisingly, die-offs of this cold-water species in a lake with an anaerobic hypolimnion seemed unrelated to summer temperatures.

The many anthropogenic changes to Lake Mendota, its drainage basin, and its fish community have contributed to the continuously changing assemblage and abundances of fishes in the lake. Some cause–effect evidence can be noted, but many of the changes were coincident with multiple cause and defy reduction. Important factors contributing to changes in the fishes resulted from agricultural development, urban development, invasions and control of macrophytes, and fishery management practices.

*Acknowledgments.* We thank Jennifer A. Drury, Judith Hoffman, and Jennifer L. Morgan for extracting the information from the literature and assistance with preparation of the text, figures, and tables. We appreciate the useful reviews by Brett M. Johnson, John Lyons, and Lars G.

Rudstam during the preparation of the manuscript. This research was supported by the Federal Aid in Sport Fish Restoration Act Project No. F-95-P, the WDNR, and the National Science Foundation's Long Term Ecological Research Program (Grant No. BSR-9011660).

## References

- Balon ED (1975) Reproductive guilds of fishes: A proposal and definition. *J. Fish. Res. Board Can.* 32:821–864
- Bardach JE (1951) Changes in the yellow perch population of Lake Mendota, Wisconsin, between 1916 and 1948. *Ecology* 32:719–728
- Bauman PC, Kitchell JF, Magnuson JJ, Kayes TB (1974) Lake Wingra, 1837–1973: A case history of human impact. *Trans. Wis. Acad. Sci. Arts Lett.* 62:57–94
- Becker GC (1983) *Fishes of Wisconsin*. University of Wisconsin Press, Madison
- Cahn AR (1927) An ecological study of southern Wisconsin fishes the brook silversides (*Labidesthes sicculus*) and the cisco (*Leucichthys artedi*) in their relations to the regions. *Ill. Biol. Monogr.* 11(1):1–151.
- Coutant CC (1977) Compilation of temperature preference data. *J. Fish. Res. Board Can.* 34:739–745
- Fago D (1982) Distribution and relative abundance of fishes in Wisconsin. I. Greater Rock River Basin. Wisconsin Department of Natural Resources Technical Bulletin 136, Madison WI
- Fago D (1988) Retrieval and analysis system used in Wisconsin's state wide distribution survey. Wisconsin Department of Natural Resources Research Report 148, December, 1988, 2nd edn.
- Godin JGJ (1986) Antipredator function of schoaling in teleost fishes; a selective review. *Nat. Can.* 113:241–250
- Greene CW (1935) The distribution of Wisconsin fishes. State Conservation Commission of Wisconsin, Madison
- Haase BL (1969) An ecological life history of the longnose gar, *Lepisosteus osseus* L., in Lake Mendota and in several other lakes of southern Wisconsin. Ph.D. Thesis, University of Wisconsin, Madison
- He X, Kitchell JF (1990) Direct and indirect effects of predation on a fish community: A whole-lake experiment. *Trans. Am. Fish. Soc.* 119:825–835
- Hokanson KEF (1977) Temperature requirements of some percids and adaptations to the seasonal temperature cycle. *J. Fish. Res. Board Can.* 34:1524–1550
- Jacobs H (1956) *The Middletown Centennial Book, 1856–1956*. Middletown Centennial, Inc., Middletown, Wisconsin
- John KR (1954) An ecological study of the cisco, *Leucichthys artedi*, in Lake Mendota, Wisconsin. Ph.D. Thesis, University of Wisconsin, Madison
- John KR, Hasler AD (1956) Observations on some factors affecting the hatching of eggs and the survival of young shallow-water cisco, *Leucichthys artedi* LeSueur, in Lake Mendota, Wisconsin. *Limnol. Oceanogr.* 1:176–194
- Johnson BM, Stewart RS, Gilbert SJ (1992) Ecology of fishes in the Madison Lakes. Fish Management Report No. 148. Technical Bulletin, Wisconsin Department of Natural Resources, Madison (in press)

- Lathrop RC (1991) Decline in zoobenthos densities in the profundal sediments of Lake Mendota (Wisconsin, USA). *Hydrobiologia* (in press)
- Lathrop RC, Nehls SH, Brynildson CL, Plass KR (1992) The fishery of the Yahara lakes. Wisconsin Department of Natural Resources Technical Bulletin (in press)
- Lyons J (1989) Changes in the abundance of small littoral-zone fishes in Lake Mendota, Wisconsin. *Can. J. Zool.* 67:2910–2916
- Magnuson JJ, Crowder LB, Medvick PA (1979) Temperature as an ecological resource. *Am. Zool.* 19:331–343
- Magnuson JJ, Paszkowski CA, Rahel FJ, Tonn WM (1989) Fish ecology in severe environments of small isolated lakes in northern Wisconsin. In Sharitz RR, Gibbons JW (eds) *Freshwater wetlands and wildlife*, CONF-8603101, DOE Symposium Series No. 61, USDOE Office of Scientific and Technical Information, Oak Ridge, Tennessee
- Marshall WS, Gilbert NC (1905) Notes on the food and parasites of some fresh-water fishes from the lakes at Madison, Wisconsin. In Appendix to the Report of the Commissioner of Fisheries to the Secretary of Commerce and Labor for the year ending June 30, 1904, U.S. Department of the Interior, Washington, DC, pp 513–522
- McNaught DC (1963) The fishes of Lake Mendota. *Trans. Wis. Acad. Sci. Arts Lett.* 52:37–55
- Mollenhoff DV (1982) *Madison: A history of the formative years*. Kendall/Hunt Publishing Company, Dubuque, Iowa
- Neuenschwander HE (1947) The history of the ciscoes (*Leucichthys artedi mendotoe*) in Lake Mendota, Wisconsin. Unpublished manuscript, Department of Zoology University of Wisconsin-Madison, supervised by AD Hasler, professor
- Noland WE (1951) The hydrography, fish, and turtle population of Lake Wingra. *Trans. Wis. Acad. Sci.* 40:5–58
- Pearse AS (1918) Food of the shore fishes of certain Wisconsin lakes. *Bull. U.S. Bur. Fish.* 35:245–292
- Pitcher TJ, Hart PJB (1982) *Fisheries ecology*. AVI Publishing Company, Westport, Connecticut
- Robins CR, Bailey RM, Bond CE, Brooker JR, Lachner EA, Lea RN, Scott WB (1980) A list of common and scientific names of fishes from the United States and Canada. 4th edn. *Am. Fish. Soc. Special Publication No. 12*
- Rothschild BJ (1986) *Dynamics of marine fish populations*. Harvard University Press, Cambridge, Massachusetts
- Rudstam LG, Magnuson JJ (1985) Predicting the vertical distribution of fish populations: Analysis of cisco, *Coregonus artedii*, and yellow perch, *Perca flavescens*. *Can. J. Fish. Aquat. Sci.* 42:1178–1188
- Telford J (1954) The life history of the cisco, *Leucichthys artedi* (LeSueur), with special reference to the Lake Mendota population. Class paper, Zoology 125, supervised by AD Hasler, professor
- Tibbles JG (1956) A study of the movements and depth distribution of the pelagic fishes in Lake Mendota. Ph.D. Thesis, University of Wisconsin, Madison
- Tonn WM, Magnuson JJ, Rask M, Toivonen J (1990) Intercontinental comparison of small-lake fish assemblages: The balance between local and regional processes. *Am. Nat.* 136:345–375

- Vanni MJ, Luecke C, Kitchell JF, Allen Y, Temte J, Magnuson JJ (1990) Effects on lower trophic levels of massive fish mortalities. *Nature* 334:333–335
- Wright TD (1968) Changes in the abundance of yellow bass (*Morone mississippiensis*) and white bass (*M. chrysops*) in Madison, Wisconsin, lakes. *Copeia* 1968:183–185

**Appendix.** Tabulation and code designations for adult body size; reproductive, feeding, and thermal guilds; index of rank relative abundances and trends in abundance for Lake Mendota fish taxa from 1900 to 1989.

	Abundance 1900–89	Trend in Mean rank abundance	Adult size mm	Reproductive guild			Feeding guild			Thermal guild			Rank abundance								
				General		Habitat	Specific		General	1900–20		1939–57		1958–69		1970–74		1975–79		1980–84	
				Code	Carc					1900	1939	1958	1969	1970	1974	1975	1979	1980	1984	1985	1989
Bluegill	5.3	1	152	2	4	7	4	1	3	4	4	4	4	4	6	5	6	6	6	6	6
Yellow perch	5.1	2	178	2	1	4	4	1	2	6	6	6	6	6	4	4	5	5	5	5	6
Crappie species	4.4	2	216	3	4	3	4	1	2	6	4	4	4	3	5	5	5	5	5	4	4
Common carp	3.8	2	431	4	1	3	5	2	3	4	3	5	4	4	4	4	4	4	4	4	3
White bass	3.7	3	228	3	1	4	4	1	3	3	5	6	5	6	5	1	3	3	3	3	3
Cisco	3.6	2	267	3	1	5	2	1	1	5	3	3	3	2	5	5	4	4	4	4	3
Bullhead species	3.3	2	200	3	4	7, 8, 8	5	2	3	3	4	3	3	4	3	4	4	4	4	4	3
Walleye	3.1	1	390	4	1	7	6	3	2	1	2	1	2	1	5	5	4	4	4	4	5
Largemouth bass	3.1	2	267	3	4	3	6	3	3	4	2	4	2	2	3	4	4	4	4	4	3
Rock bass	3.1	3	177	2	4	7	5	2	2	3	4	3	4	3	4	3	4	3	3	3	2
Bluntnose minnow	3.1	3	64	1	4	8	5	2	3	4	4	4	4	3	3	3	3	3	3	2	3
Brook silverside	3.0	1	63	1	1	4	3	1	3	3	0	3	3	3	3	3	3	3	3	5	4
Northern pike	3.0	2	508	4	1	3	6	3	2	4	3	3	3	3	3	3	3	3	3	3	3
Smallmouth bass	2.4	2	291	3	4	7	6	3	3	2	2	2	2	2	2	2	2	2	2	2	3
Pumpkinseed	2.4	2	158	2	4	2	5	2	3	3	2	2	2	2	2	2	2	2	2	2	3
Banded killifish	2.3	3	57	1	1	3	4	1	2	5	4	4	3	2	2	2	2	0	0	0	0
White sucker	2.0	1	241	3	1	7	5	2	2	2	1	1	1	2	3	3	3	3	3	2	2
Freshwater drum	1.9	1	305	3	1	1	5	2	3	0	0	0	1	1	2	3	4	4	4	3	3
Spottail shiner	1.9	2	63	1	1	6	5	2	0	4	2	2	2	2	2	2	2	1	1	2	2
Golden shiner	1.7	2	102	2	1	3	4	1	2	3	0	2	2	2	2	2	2	3	1	1	1
Longnose gar	1.6	3	500	4	1	4	6	3	3	2	2	2	1	1	2	2	1	1	2	1	1
Yellow bass	1.4	1	177	2	1	7	4	1	3	0	0	0	2	3	1	1	1	1	2	1	1
Green sunfish	1.4	1	114	2	4	7	4	1	3	0	3	1	0	2	2	2	2	2	2	2	2
Blackchin shiner	1.4	3	56	1	1	3	5	2	0	5	3	2	0	0	0	0	0	0	0	0	0
Spotfin shiner	1.3	2	64	1	1	4	4	1	3	0	2	2	2	2	2	2	2	1	1	0	0
Bowfin	1.3	3	500	4	4	3	6	3	3	3	1	1	1	1	1	1	1	1	1	1	1
Fathead minnow	1.3	3	51	1	4	8	5	2	3	0	2	2	0	2	2	2	2	1	1	0	0
Bigmouth buffalo	1.1	1	394	4	1													0	1	0	0

## **Appendix.** *Continued*

**Codes to the Appendix.**

	Category	Code	Measurement
Abundance Rank	Very abundant	6	$\geq 20$
	More abundant	5	$\geq 10$
	Abundant	4	5.0–9.9
	Common	3	1.0–4.9
	Uncommon	2	0.1–0.9
	Rare	1	<0.1
	Absent	0	
Trend	Increasing	1	Trend in rank relative abundance 1900–89 (see Methods)
	No trend	2	
	Decreasing	3	
	Never more abundant than rare	–	
Adult size	Small	1	0–99 mm
	Medium	2	100–200 mm
	Large	3	200–319 mm
	Very large	4	>320 mm
Reproductive guilds	Open substratum		Median adult size in Becker (1983)
Parental care	Spawners	1	Categories from Balon (1975)
	Substratum choosers	2	
	Brood hiders	3	
	Nest spawners	4	

			Categories from Balon (1975)
Habitat	Pelagophils	1	
	Polyphils	2	
	Phytophilis	3	
	Phytolithophils	4	
	Liatho-pelagophils	5	
	Psammophils	6	
	Lithophils	7	
	Speleophils	8	
Feeding guilds			
Specific	Planktivore	1	
	Zooplanktivore	2	
	Neustonivore	3	
	Zoobenthivore	4	
	Benthivore	5	
	Piscivore	6	
General	Zooplanktivores Benthivores	(corresponds to 1–4 specific)	
	Piscivores	1	
		2	
		3	
Thermal guilds	Cold	1	10.0–17.0 (°C)
	Cool	2	18.0–26.0 (°C)
	Warm	3	>27.0 (°C)



**Plate 3.** Ciscoes on a Lake Mendota beach as a result of the massive mortality that occurred during the late summer of 1987.

# 12

## Food Web Structure of Lake Mendota

**Lars G. Rudstam, Yvonne Allen, Brett M. Johnson,  
Chris Luecke, John R. Post, and Michael J. Vanni**

### Introduction

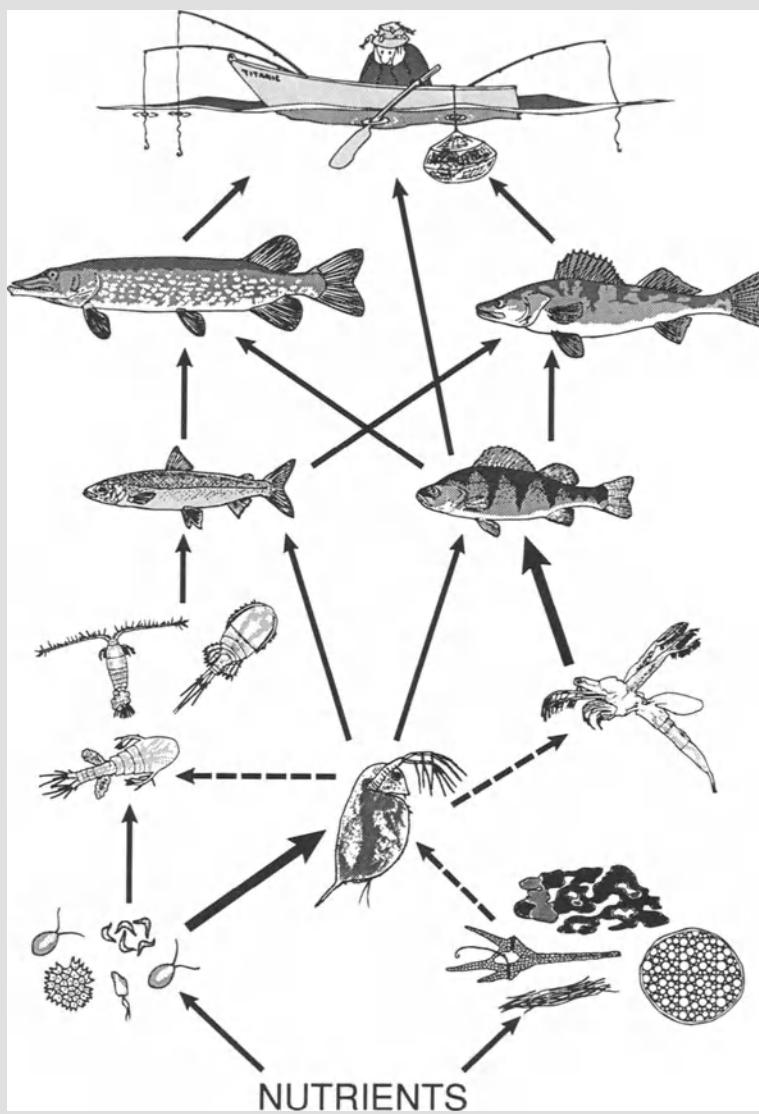
Although some classic studies (Hrbacek et al. 1961; Brooks and Dodson 1965) have shown strong effects of planktivorous fish on lower trophic levels, it is only in the last decade that effects of interactions among trophic levels on lake ecosystems have come to the forefront of limnological research (Andersson 1984; Carpenter et al. 1985; McQueen et al. 1986; Northcote 1988; Gulati et al. 1990). A present challenge is to understand the interplay between food web effects and nutrient loading (Benndorf 1988; Persson et al. 1988; Vadas 1989), a challenge that will require comparing experimental manipulations in lakes with varying nutrient loadings (Carpenter and Kitchell 1988; Carpenter et al. 1991). The objective of the food web manipulation in eutrophic Lake Mendota is to establish a large population of piscivorous fish (walleye and northern pike) and, through a cascade of trophic interactions, reduce the planktivorous fish, increase the herbivorous zooplankton, decrease algae, and increase water transparency (Kitchell, Ch. 1). In this chapter we describe the structure of the open-water food web in Lake Mendota and the dramatic changes in the planktivorous fish community that occurred during the summer of 1987. The following chapters in this section describe and interpret the behavior of different trophic levels during the first 3 years of the food web manipulation (1987–89).

## Food Web Structure

Lake Mendota has a rich assemblage of fish species. Magnuson and Lathrop (Ch. 11) list 43 species of fish present in the 1980s, but few of these fish were important components of the open-water food web. The primary open-water planktivores are perch (*Perca flavescens*) and cisco (*Coregonus artedii*). Other common planktivores are white bass (*Roccus chrysops*), freshwater drum (*Aplodinotus grunniens*), black crappie (*Pomoxis nigromaculatus*), and bluegill (*Lepomis macrochirus*). In addition, the larvae of some of the other more littoral or benthic species are planktivores in the open water (Post et al., Ch. 15). Major piscivores include walleye (*Stizostedion vitreum*), northern pike (*Esox lucius*), small-mouth bass (*Micropterus dolomieu*), largemouth bass (*M. salmoides*), and possibly longnose gar (*Lepisosteus osseus*) (Johnson et al., Ch. 16). There have been dramatic changes in the abundance of both piscivores and planktivores throughout the last century (Magnuson and Lathrop, Ch. 11). The invertebrate planktivores are primarily adult cyclopoid copepods and the cladoceran *Leptodora kindtii*. The latter is most common in summer and fall. Predatory insect larvae (e.g., *Chaoborus* sp.) have been rare in the lake for some time (Lathrop, Ch. 10).

Large *Daphnia* (*D. galeata* and *D. pulicaria*) are abundant and often dominate the zooplankton biomass (Lathrop and Carpenter, Ch. 8). Calanoid copepods, primarily *Leptodiaptomus siciloides*, are also common in the summer. One cyclopoid copepod (*Diacyclops bicuspidatus thomasi*) reached high densities in the early spring of 1987. Different cyclopoids occur in the summer (*Mesocyclops edax*, *Acanthocyclops vernalis*). Rotifers are rare, possibly due to the high abundances of *Daphnia* (Gilbert 1988). The same major zooplankton groups have been in the lake throughout this century (Lathrop and Carpenter, Ch. 8). Daphnidids are the most efficient and least selective grazers on phytoplankton of these zooplankton species (Richman and Dodson 1983) and do to some extent ingest blue-green algae (Lampert 1987; Davidowicz et al. 1988). This group is therefore of special interest in relation to food web manipulations (McQueen et al. 1986; Carpenter et al. 1991).

The phytoplankton consists of species typical of eutrophic lakes. We have recorded 85 species from 1987 through 1989, and the most common taxa are listed by Lathrop and Carpenter (Ch. 7). There is often, but not always, a spring bloom of diatoms, flagellates, and/or chrysophytes. The spring bloom is usually followed by a clear-water phase and a summer assemblage dominated by blue-green algae (*Aphanizomenon*, *Anabaena*, *Microcystis*, *Gloeotrichia*). The blue-greens can cause scum-forming blooms on the water surface. Gelatinous green algae and the dinoflagellate *Ceratium hirundinella* can be common in the summer. The biomass of bacterioplankton can be similar to that of the algae (Pedros-Alio and Brock 1982) and may be an important part of zooplankton diets (Pedros-



**Figure 12-1.** Key species and species groups in the open-water food web of Lake Mendota. Arrow size indicates interaction strength. The species are, from the top: human angler; northern pike and walleye; cisco and yellow perch; copepods, *Daphnia*, and *Leptodora*; edible algae and inedible algae (*blue-greens*, *Ceratium*).

Alio and Brock 1983). The study of bacterioplankton was unfortunately outside the scope of the present project. Brock (1985) provides for detailed information on Lake Mendota bacterioplankton.

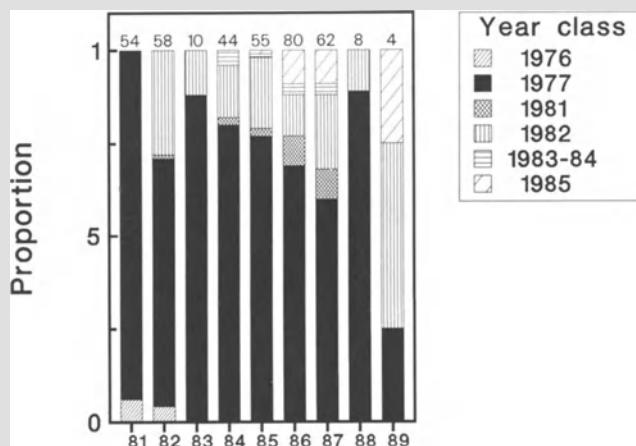
We have identified the key species and species groups in the open-water food web of Lake Mendota in Figure 12.1. The following chapters by Vanni et al. (Ch. 13) and Luecke et al. (Ch. 14) explore the interactions among planktivores, zooplankton, algae, and nutrients. The next two chapters emphasize the fish populations in Lake Mendota (fish larvae, Post et al., Ch. 15; piscivores and prey fishes, Johnson et al., Ch. 16). The larval and juvenile stages form a crucial link between piscivores and planktivores because piscivores will prey primarily on young fish. Cisco, for example, outgrow their predators by the end of their first year of life: young-of-year (YOY) cisco reached 17 cm and 45 g by October 1989. Finally, the analysis of the Lake Mendota food web is not complete without considering the anglers, the top predators in the lake (Johnson and Staggs, Ch. 17). Humans have extremely rapid information flow systems (magazines and telephones), and the result is a strong numerical response by anglers to a real or perceived increase in game fish.

### A “Natural” Food Web Manipulation

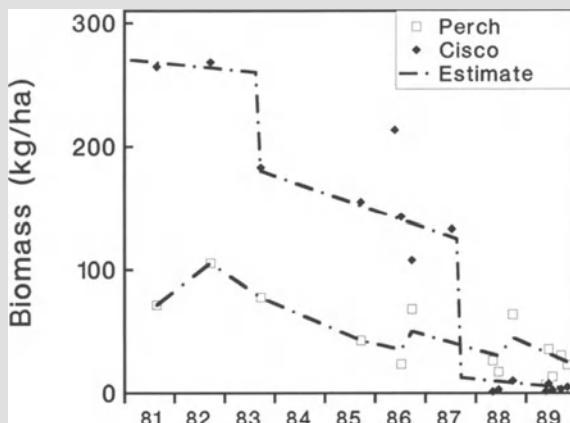
Our original projections indicated that the strongest effect of the stocked walleyes on planktivorous fish would occur in 1990–92. Given the continuously increasing harvest rates of walleyes by recreational anglers and declining survival of stocked fingerlings from 1987 through 1989, it appeared unlikely that the stocked walleyes could significantly reduce a strong planktivore year class (Johnson et al. 1992 and Ch. 16; Post and Rudstam, Ch. 19). However, the planktivorous fish population was reduced unexpectedly by other events during the summer of 1987.

The development of the cisco population between 1977 and 1989 has been dramatic. Cisco had been declining since the 1940s (John and Hasler 1956). The first reports on cisco in the lake in over 15 years came from gill nets set by the University of Wisconsin (UW) Limnology class in 1977. The conditions for a strong year class in 1977 must have been remarkable, as both cisco and perch produced very strong year classes that year. Two possible reasons are the almost complete disappearance of a major predator of larval fish in the lake, the white bass, in the fall of 1976 (Woolsey 1986) and a decrease in dense weed beds in 1975 and 1976 (Nichols et al., Ch. 9). The cisco year class of 1977 dominated the cisco population in the lake throughout the 1980s (Figure 12.2). Smaller recruitment events occurred in 1982 and 1985. Cisco was the major planktivore in the lake from 1981 until August 1987 (Figure 12.3).

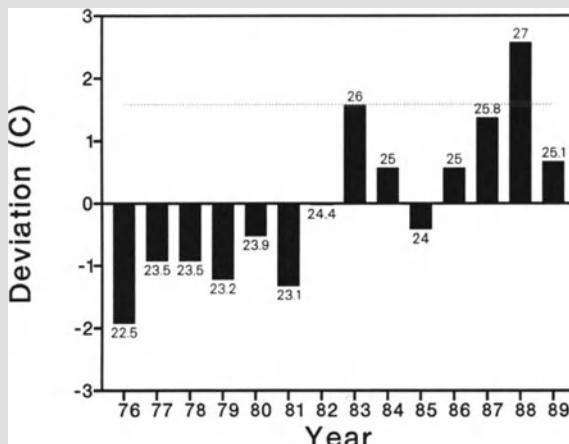
Cisco is a salmonid that prefers cold water (Rudstam and Magnuson 1985). The combination of an aging population and a warm summer



**Figure 12-2.** Cisco age class structure from 1981 through 1989. Age was determined from scales; up to 10 fish in each 1-cm size class were aged. Fish were caught in late summer in 1981 to 1985 (fall surveys of the NTL-LTER Project) and throughout the year in 1986 to 1989 (Biomanipulation Project). Note that the 1977 year class dominated the population throughout the decade. Four fish caught through the ice in 1979 were also from the 1977 year class. Five YOY fish were also caught in 1989. The number of fish aged is indicated on top of the bar.



**Figure 12-3.** Biomass of cisco and perch from 1981 through 1989. The acoustic biomass is based on the abundances of cisco and perch obtained with acoustics (NTL-LTER and Biomanipulation Projects, see Rudstam and Johnson, Ch. 26) and the average weight of cisco and perch caught in gill nets (Table 12.1). The lines indicate our estimates of the development of cisco and perch biomass in the lake. Cisco kills occurred in August of 1983, 1987, and 1988.



**Figure 12-4.** Deviation of maximum epilimnetic temperature at 6 m depth recorded between 12 July and 22 August from the 1976–89 average (from Robertson 1989 and Lathrop, unpubl.). The number by the bar is the actual temperature. The line represents 26°C, the upper lethal temperature for YOY cisco (Edsall and Colby 1970). Cisco kills occurred during the warm summers of 1983, 1987, and 1988. Cisco were also reported dead in 1980, a summer without unusually warm temperatures. See also Magnuson and Lathrop (Ch. 11).

probably caused the severe die-off of cisco in 1987 (Plate 3; Figure 12.4; Magnuson and Lathrop, Ch. 11). Cisco summer kills have been reported previously from Lake Mendota (Magnuson and Lathrop, Ch. 11) and from other lakes (Frey 1955; Colby and Brook 1969). We estimate that over 90% of the cisco population died in 1987 (Figure 12.3; Vanni et al. 1990a). The population has declined further since 1987, as some dead cisco were observed in the summer of 1988. The current (1989) cisco population consists of less than 25,000 large individuals primarily from the 1977 and 1982 year class (Figures 12.2 and 12.3), a decrease from approximately 2 million in 1981 (Figure 12.3; Rudstam et al. 1987). These fish were 8 or 13 years old in 1989 and weighed close to 1 kg (Table 12.1). The fishery for spawning cisco at the end of November, relished by a select group of hardy anglers who enjoyed cold nights, smoked cisco, and cisco caviar, has completely disappeared. No spawning fish were observed in 1988 or in 1989, although some recruitment did occur. Cisco larvae were caught in neuston nets in both years, and five YOY cisco were caught in gill nets during 1989.

At the same time there has been a decline in the perch population, as there has not been a strong year class since 1985. (Post et al., Ch. 15). This is also reflected in an increase in the average size of perch caught in gill nets from 1987 to 1989 (Table 12.1). The combination of poor recruitment, a harvest rate by anglers of 30–40% per year (Johnson and Staggs,

**Table 12-1.** Catch per unit effort (CPUE; a unit effort is eight vertical gill nets fished for 24 h as detailed in Rudstam and Magnuson 1985) and the mean weight (excluding YOY) of cisco and perch for fish caught in the fall [Northern Temperate Lakes Long-Term Ecological Research Project (NTL-LTER), August 1981, September 1982–89]. The most common other species were white bass, freshwater drum, and black crappie. The nets were set for 48 h in at least 18-m-deep water (except in 1983) and serviced every 6 h in 1981 and every 24 h in 1982–89.

Year	Cisco		Perch		Other species CPUE (#/24 h)
	CPUE	Mean weight (g)	CPUE	Mean weight (g)	
1981 <sup>a</sup>	72	432	124	145	10
1982	44	505	426	81	20
1983 <sup>b</sup>	11	428	82	87	6
1984	50	486	40	65	4
1985	80	542	8	112	16
1986	63	544	14	103	1
1987	3	623 <sup>c</sup>	129	107	5
1988	1	862 <sup>d</sup>	12	151	29
1989	1	814 <sup>d</sup>	15	168	0

<sup>a</sup> Only seven nets were used in 1981. The mesh size added in 1982 (25-mm stretch mesh) did not catch many fish in lake Mendota.

<sup>b</sup> Nets set in 12- to 15-m-deep water contributing to low cisco catches.

<sup>c</sup> Weight based on I+ and older cisco caught in September through December 1987 (32 fish).

<sup>d</sup> Weight based on all I+ and older cisco caught during the year (nine fish in 1988, four in 1989).

Ch. 17), and increased predation by stocked walleye and pike (Johnson et al., Ch. 16) has resulted in lower perch biomass in 1989 than observed in the lake since 1981 (Figure 12.3).

The cisco summer kill in 1987 and the lack of a compensatory response in the perch population provided us with a "natural" food web manipulation and a contrast between relatively high planktivory rates in 1987 and low planktivory rates in 1988 and 1989. During 1987 and 1988 the nutrient loading through spring runoff was relatively low (inferred from runoff measurements at the nearby Black Earth Creek; Lathrop, Ch. 7). In 1989 the spring runoff was higher than the 1976–89 average. The result is an interesting combination of nutrient loadings and food web configurations: 1987, high planktivory and low nutrient loading; 1988, low planktivory and low nutrient loading; 1989, low planktivory and high nutrient loading. The effects of the cisco die-off on the zooplankton community include an almost complete shift from the smaller *D. galeata* in 1987 to the larger *D. pulicaria* in 1988 and 1989 (Vanni et al. 1990a; Luecke et al., Ch. 14). An opposite shift from *D. pulicaria* to *D. galeata* occurred as the cisco population increased in 1977 (Vanni et al. 1990b; Lathrop and

Carpenter, Ch. 8), providing strong evidence of the effect of cisco on *Daphnia* species composition. Chapter 13 by Vanni et al. (emphasizing phytoplankton dynamics) and Ch. 14 by Luecke et al. (emphasizing zooplankton dynamics) represent our attempts to sort out the effects of changes in food web configuration and nutrient loading using field observations, models, and results from experiments on key interactions.

**Acknowledgments.** We thank Steve Carpenter, John Magnuson, Jim Kitchell, and Richard Lathrop for comments on this manuscript and acknowledge support from the Federal Aid in Sport Fish Restoration Act under Project F-95-P, the WDNR, the National Science Foundation (Northern Temperate Lakes Long Term Ecological Research Program), and the Swedish Forestry and Agriculture Research Council (to L.G.R.).

## References

- Andersson G (1984) The role of fish in lake ecosystems—and in limnology. In Bosheim S, Nicholls M (eds) Interactions between trophic levels in fresh water, Norsk Limnologforening, Oslo, pp 189–197
- Benndorf J (1988) Objectives and unsolved problems in ecotechnology and biomaniupulation: A preface. *Limnologica* 19:5–8
- Brock TD (1985) A eutrophic lake: Lake Mendota, Wisconsin. Springer-Verlag, New York
- Brooks JL, Dodson SI (1965) Predation, body size, and composition of zooplankton. *Science* 150:28–35
- Carpenter SR, Frost TM, Kitchell JF, Kratz TK, Schindler DW, Shearer J, Sprules WG, Vanni MJ, Zimmerman AP (1991) Patterns of primary production and herbivory in 25 North American lake ecosystems. In Cole J, Lovett G, Findlay S (eds) Comparative analysis of ecosystems: Patterns, mechanisms, and theories. Springer-Verlag, New York, pp 67–96
- Carpenter SR, Kitchell JF (1988) Consumer control of lake productivity. *Bioscience* 38:764–769
- Carpenter SR, Kitchell JF, Hodgson JR (1985) Cascading trophic interactions and lake productivity. *Bioscience* 35:634–639
- Colby PJ, Brook T (1969) Cisco (*Coregonus artedii*) mortalities in a southern Michigan lake, July 1968. *Limnol. Oceanogr.* 14:958–960
- Davidowicz P, Gliwicz M, Gulati RD (1988) Can *Daphnia* prevent blue-green algal bloom in hypertrophic lakes? A laboratory test. *Limnologica* 19:21–26
- Edsall TA, Colby PJ (1970) Temperature tolerance of young-of-year cisco, *Coregonus artedii*. *Trans. Am. Fish. Soc.* 99:526–531
- Frey DG (1955) Distributional ecology of the cisco, *Coregonus artedii*, in Indiana. *Invest. Indiana Lakes Streams* 4:177–228
- Gilbert JJ (1988) Suppression of rotifer populations by *Daphnia*: A review of the evidence, the mechanism, and the effects on zooplankton community structure. *Limnol. Oceanogr.* 33:1286–1303
- Gulati RD, Lammens EHRR, Meijer ML, vanDonk E (1990) Biomanipulation—tool for water management. Kluwer Academic Publishers, Dordrecht

- Hrbacek J, Dvorakova M, Korinak V, Prochazkova L (1961) Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the plankton association. Verh. Internat. Verein. Limnol. 14:192–195
- John KR, Hasler AD (1956) Observations on some factors affecting the hatching of eggs and survival of young shallow-water cisco, *Leucichthys artedi* LeSueur, in Lake Mendota, Wisconsin. Limnol. Oceanogr. 1:176–194
- Johnson BM, Luecke C, Stewart RS, Staggs MD, Gilbert SJ, Kitchell JF (1992) Forecasting effects of harvest regulations and stocking on prey fish communities in a eutrophic lake. No. Am. J. Fish. Manage. (in press)
- Lampert W (1987) Laboratory studies on zooplankton–cyanobacteria interactions. N. Zeal. J. Mar. Freshwat. Res. 21:483–490
- McQueen DJ, Post JR, Mills EL (1986) Trophic relationships in freshwater pelagic ecosystems. Can. J. Fish. Aquat. Sci. 43:1571–1581
- Northcote TG (1988) Fish in the structure and function of freshwater ecosystems: A “top-down” view. Can. J. Fish. Aquat. Sci. 45:361–379
- Pedros-Alio C, Brock TD (1982) Assessing biomass and production of bacteria in eutrophic Lake Mendota, Wisconsin. Appl. Env. Microbiol. 44:203–218
- Pedros-Alio C, Brock TD (1983) The impact of zooplankton feeding on the epilimnetic bacteria of a eutrophic lake. Freshwat. Biol. 13:227–239
- Persson L, Andersson G, Hamrin SF, Johansson L (1988) Predator regulation and primary production along the productivity gradient of temperate lake ecosystems. In Carpenter SR (ed) Complex interactions in lake communities. Springer-Verlag, New York, pp 45–68
- Richman S, Dodson SI (1983) The effect of food quality on feeding and respiration by *Daphnia* and *Diaptomus*. Limnol. Oceanogr. 28:948–956
- Robertson DM (1989) The use of lake water temperature and ice cover as climatic indicators. Ph.D. Thesis, University of Wisconsin, Madison
- Rudstam LG, Clay CS, Magnuson JJ (1987) Density and size estimates of cisco, *Coregonus artedi*: using analysis of echo peak PDF from a single transducer sonar. Can. J. Fish. Aquat. Sci. 44:811–821
- Rudstam LG, Magnuson JJ (1985) Predicting the vertical distribution of fish populations: An analysis applied to cisco (*Coregonus artedi*) and yellow perch (*Perca flavescens*). Can. J. Fish. Aquat. Sci. 42:1178–1188
- Vadas RL, Jr (1989) Food web patterns in ecosystems: A reply to Fretwell and Oksanen. Oikos 56:339–343
- Vanni MJ, Luecke C, Kitchell JF, Allen Y, Temte J, Magnuson JJ (1990a) Effects on lower trophic levels of massive fish mortality. Nature 344:333–335
- Vanni MJ, Luecke C, Kitchell JF, Magnuson JJ (1990b) Effects of planktivorous fish mass mortality on the plankton community of Lake Mendota, Wisconsin: Implications for biomanipulation. Hydrobiologia 200/201:329–336
- Woolsey EA (1986) Lake Mendota: Some trophic level interactions and their effect on community structure. Ph.D. Thesis, University of Wisconsin, Madison



**Plate 4.** *Daphnia galeata mendotae* (left) and *Daphnia pulicaria* are two of the most abundant zooplankton species in Lake Mendota.

# 13

## **Herbivory, Nutrients, and Phytoplankton Dynamics in Lake Mendota, 1987–89**

**Michael J. Vanni, Jo Temte, Yvonne Allen,  
Richard Dodds, Patricia J. Howard,  
Peter R. Leavitt, and Chris Luecke**

### **Introduction**

It is becoming increasingly clear that lake plankton communities are regulated by both predation and resources. Top predators, through effects on herbivores, can regulate phytoplankton community structure, biomass, and primary productivity (Carpenter et al. 1985; Carpenter and Kitchell 1988; Vanni and Findlay 1990). Increases in potential limiting nutrients, such as nitrogen and phosphorus, can stimulate phytoplankton production and biomass, and the ratio of limiting nutrients can influence community structure (Schindler 1977; Smith 1983). Recently, lake ecologists have realized that when attempting to explain phytoplankton dynamics, both nutrients and herbivory must be considered. Often the two interactions simultaneously influence phytoplankton, although their relative strengths may vary seasonally (e.g., Sommer et al. 1986; Vanni and Temte 1990). Furthermore, resource effects and herbivore effects may interact in complex ways to influence phytoplankton (Leibold 1989; Sterner 1990; Carpenter et al. 1991)—a case of the interactions themselves interacting (Roughgarden and Diamond 1986).

Lake Mendota has experienced substantial variation in nutrient loading and food web structure (and thus herbivore populations) in recent years. In this chapter, we detail the dynamics of phytoplankton in Lake Mendota from 1987 through 1989 and relate these to the dynamics of nutrients and zooplankton herbivory. The seasonal dynamics of the phytoplankton community are typical of eutrophic lakes (Brock 1985; Vanni and Temte 1990; Lathrop and Carpenter, Ch. 7) and are charac-

terized by a pronounced seasonal succession from small taxa capable of rapid growth to large taxa with much slower growth rates.

Superimposed on the general pattern of phytoplankton succession, however, is a significant amount of year-to-year variability in the timing of succession, community structure, and biomass of spring and summer phytoplankton (Lathrop and Carpenter, Ch. 7). Nutrient concentrations and herbivorous zooplankton populations vary considerably as well (Lathrop and Carpenter, Ch. 7 and 8). Furthermore, the 3 years analyzed here (1987–89) represent nearly the range of variation observed in the “historical record” since 1976. In particular, a “natural experiment” occurred in late summer 1987, in which a dominant planktivorous fish species, cisco (*Coregonus artedii*), was subject to mass mortality in which its biomass was reduced to ~5–10% of its previous level (Vanni et al. 1990a; Rudstam et al., Ch. 12; Luecke et al., Ch 14). Thus the three years represent one year when cisco was abundant (1987) and 2 years when this major planktivore was rare (1988 and 1989). Nutrient loading rates were also variable among these years (Lathrop, Ch. 6). Thus, the years 1987–89 provide an opportunity to observe the response of phytoplankton to a variable range of nutrients and zooplankton grazing.

## Methods of Sampling Lake Plankton and Nutrients

### Nutrients

Nutrients were sampled from the epilimnion in two ways. Researchers from the Center for Limnology (CFL) at the University of Wisconsin employed a tube sampler (inner diameter 2.5 cm) that collected an integrated water column from 0 to 10 m, the approximate depth of the epilimnion. Samples collected by the Wisconsin Department of Natural Resources (WDNR) were taken with a Van Dorn bottle at 0 and 4 m. Differences in nutrient concentrations between the two WDNR depths and between the CFL and WDNR methods were negligible because both methods sampled the mixed layer and analytical techniques were identical (see below). Therefore both sets of data were used, and when nutrients were sampled with the Van Dorn, a simple arithmetic mean of the two samples was used as the epilimnetic concentration. Samples were analyzed for total phosphorus (TP), soluble reactive phosphorus (SRP), total (Kjeldahl) nitrogen (TKN), ammonia nitrogen ( $\text{NH}_4\text{-N}$ ), and nitrite- and nitrate-N ( $\text{NO}_2/\text{NO}_3\text{-N}$ ), by the Environmental Sciences Section of the Wisconsin State Laboratory of Hygiene, using standard United States Environmental Protection Agency (1979) methods. TP (after persulfate digestion) and SRP were assayed using the ammonium molybdate method, and TKN with the micro-Kjeldahl method.  $\text{NH}_4\text{-N}$  and  $\text{NO}_2/\text{NO}_3\text{-N}$  were assayed with the phenol-hypochlorite and the cadmium reduction methods, respectively.

### Phytoplankton

Phytoplankton were sampled with the tube sampler described above for sampling nutrients. One integrated sample was collected per sampling date and preserved in Lugol's solution. The sample was later settled for 1–2 d and its contents quantified with inverted microscopy. Linear dimensions of up to 10 cells of each taxon were measured in each sample and cell volumes estimated using geometric formulae. Mean cell volume ( $\mu\text{m}^3 \cdot \text{cell}^{-1}$ ) was multiplied by population density ( $\text{cells} \cdot \text{mL}^{-1}$ ) to obtain biovolume ( $\mu\text{m}^3 \cdot \text{mL}^{-1}$ ).

### Zooplankton Herbivory

Zooplankton sampling and quantification methods are described in Luecke et al. (Ch. 14). Zooplankton were sampled with a Charke-Bumpus sampler. On each sample date, zooplankton were measured with a dissecting microscope, and mean length was used to generate mean individual mass of each species, using published length–mass regressions (see Luecke et al., Ch. 14). From mean individual zooplankton dry mass ( $\mu\text{g dry mass} \cdot \text{individual}^{-1}$ ), we estimated mean per individual herbivory rate for each species (here expressed as clearance rate, or the volume of water cleared of algal cells per unit time) using regressions developed by Peters and Downing (1984). For cladocerans, we used the cladoceran equation of Peters and Downing (their equation 4):

$$\log V = 0.173 + 0.750 \log W - 0.434 \log S - 0.0003C + 0.014C_a$$

where  $V$  = individual clearance rate ( $\text{ml} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$ ),  $W$  = animal mass ( $\mu\text{g dry mass} \cdot \text{individual}^{-1}$ ), and  $S$  = phytoplankton density ( $10^6 \mu\text{m}^3 \cdot \text{mL}^{-1}$ ).  $C$ , volume of experimental vessel, and  $C_a$ , volume of experimental vessel per animal, were derived by Peters and Downing from short-term laboratory feeding experiments and are not estimable from lake data. Therefore we used mean values from these derivations (their Table 3).

For calanoid copepods, we used the “all zooplankton” equation of Peters and Downing (their equation 2):

$$\begin{aligned} \log V = & 0.110 + 0.546 \log W - 0.260 \log S + 0.121 \log R \\ & + 0.0001C - 0.0002M \end{aligned}$$

where  $R$  = mean food particle volume ( $\mu\text{m}^3$ ).  $M$ , duration of experiment, was derived from lab experiments; we used mean values (from Table 3 of Peters and Downing 1984).

Cyclopoid copepods are the dominant zooplankter in Lake Mendota in early spring. These organisms feed on zooplankton as well as phytoplankton, and thus their grazing rates on phytoplankton may not be adequately described by the regressions above. Adrian (1988) has shown

experimentally that clearance rates of *Cyclops kolensis* and *C. vicinus* on phytoplankton are approximately 12.5% those of *Daphnia* of a similar size. Therefore, we estimated cyclopoid clearance rate by using the cladoceran equation above and multiplying the resultant rate by 0.125.

For each zooplankton species, a population clearance rate ( $d^{-1}$ ) was derived by multiplying individual clearance rate ( $L \cdot \text{individual}^{-1} \cdot d^{-1}$ ) by population density ( $\text{individuals} \cdot L^{-1}$ ). Community clearance, an estimate of total herbivory, was obtained by summing population clearance rates. Sterner (1989) points out that clearance rates obtained in this manner approximate potential per capita instantaneous mortality rates ( $d^{-1}$ ) for edible phytoplankton species. Therefore, we present the results in terms of potential instantaneous mortality rates of phytoplankton resulting from herbivory. Most clearance rate measurements used by Peters and Downing (1984) to derive the above equations are derived from experiments in which highly edible phytoplankton were used as the food source. Thus, clearance rates presented here may more correctly reflect mortality of small edible phytoplankton species than that of large, less edible species, and these rates should thus be viewed as maximum potential mortality attributable to herbivory.

## Experimental Investigations of Nutrient–Plankton Interactions

In addition to detailed observational study of the Lake Mendota plankton community, a number of field experiments were also conducted from 1986 to 1989 in the hopes of providing a mechanistic understanding of how nutrients and zooplankton herbivory affect phytoplankton (Table 13.1). These results are, or will be, published elsewhere and therefore will not be covered in detail here. Rather, we will attempt to summarize the findings of these experiments and relate them to the events occurring in the lake during 1987–89.

### Grazing and Nutrient Limitation of Phytoplankton

In 1986 and 1987, Vanni and Temte (1990) conducted short-term (3–5 d) experiments to assess the potential effects of grazing and nutrient limitation on phytoplankton. These experiments were conducted several times during the ice-free season to quantify seasonal variation in the relative strengths of grazing and nutrient limitation of phytoplankton. Experiments followed the approach of Lehman and Sandgren (1985). Gradients of zooplankton density were created in 19-L translucent containers suspended at the approximate depth of 50% surface light intensity for 3–5 days. Experiments were conducted using the ambient zooplankton assemblage, and with only large *Daphnia*. The latter gradients were assumed to impose maximal herbivory rates on phytoplankton, as large

**Table 13-1.** Summary of experiments conducted in Lake Mendota from 1986 to 1989 to investigate interactions among nutrients, phytoplankton, and zooplankton.

Experimental manipulation	Experimental vessel	Year(s)	Response variables	Reference
Zooplankton biomass; nutrients (N and P)	19-L containers	1986 and 1987	Phytoplankton biomass and taxa-specific growth rates; nutrient excretion rates	1,2,3
Zooplankton biomass	19-L containers	1988	Nutrient limitation of phytoplankton	3
Zooplankton biomass; nitrogen	3,900-L enclosures	1988 and 1989	Phytoplankton biomass	4,5

<sup>1</sup>Vanni and Temte (1990); <sup>2</sup>Vanni et al. (1990a); <sup>3</sup>Moegenburg and Vanni (1991); <sup>4</sup>Howard, in prep.; <sup>5</sup>Leavitt, in prep.

*Daphnia* typically have a greater impact on phytoplankton than other zooplankton taxa (Leibold 1989). Nitrogen and phosphorus were added, singly and together, to some containers to assess whether phytoplankton were limited by these nutrients. Response variables included total phytoplankton biomass (chlorophyll *a*), species-specific population growth rates of phytoplankton taxa, and concentrations of dissolved nutrients [to assess excretion of nutrients by zooplankton (Moegenburg and Vanni 1991) and uptake of nutrients by phytoplankton (Vanni et al. 1990a)].

### Regeneration of Nutrients by Zooplankton and Its Effects on Phytoplankton

In the summer of 1988, additional short-term experiments were conducted to assess the indirect effects of herbivores on phytoplankton, specifically to test whether regeneration of nutrients by zooplankton can reduce nutrient deficiency (limitation) of phytoplankton (Moegenburg and Vanni 1991). Zooplankton excrete considerable quantities of N and P in a form highly available to phytoplankton (e.g., Lehman 1980), and regeneration of nutrients can be a major source of nutrients for phytoplankton. Furthermore, recent theoretical and experimental studies show that nutrients excreted by zooplankton can potentially “tip the balance” of whether phytoplankton are limited by N or P (Elser et al. 1988; Sterner 1990).

It was hypothesized that if zooplankton excrete nutrients at a low N:P ratio, this could conceivably shift the phytoplankton to N-limitation, potentially favoring nitrogen-fixing cyanobacteria, blooms of which constitute a severe water quality problem. In contrast, if zooplankton regenerate nutrients at a high N:P ratio, this may favor more edible phytoplankton, which may then further the ability of zooplankton to suppress phytoplankton. Thus, depending on the ratio at which nutrients are excreted, nutrient regeneration by zooplankton may either enhance or counteract herbivore control of phytoplankton. Quite recently, Hessen (1990) has shown that large cladocerans (e.g., *Daphnia*) exhibit a low N:P ratio in their body tissues and therefore excrete nutrients at a high N:P ratio, while copepods and the small cladoceran *Bosmina* show the opposite pattern—they have a high N:P ratio in their bodies and excrete at a low N:P ratio. Thus these relatively subtle, indirect effects could potentially contribute to the mechanisms by which large grazers such as *Daphnia* can suppress phytoplankton.

Experiments addressing these questions were conducted in the same 19-L containers as the earlier experiments on grazing/nutrient limitation of phytoplankton (Moegenburg and Vanni 1991). Zooplankton were placed in the containers at densities above, equal to, or below ambient and incubated with lake phytoplankton as in the grazing/nutrient limita-

tion experiments. Response variables included ammonium enhancement response, an indicator of N-limitation, and alkaline phosphatase activity, an indicator of P-limitation. In addition, chlorophyll *a* was measured.

### **Effects of Zooplankton Grazing on Maintenance and Duration of the Clear-Water Period**

Relatively large-scale enclosure experiments were conducted in 1988 (Howard, in prep.) and 1989 (Leavitt, in prep.) during the clear-water period to assess whether the clear-water period can be maintained and prolonged by maintaining high population density of *Daphnia*. Enclosures were 1 m in diameter and 5 m deep, and were placed in University Bay of Lake Mendota during the clear-water period. Treatments included controls (natural or above-natural densities) and exclusion of *Daphnia*. N was added to some enclosures also, to test the hypothesis that increasing N:P ratio would shift the phytoplankton community away from cyanobacteria and toward more edible phytoplankton taxa, and that this would enhance the ability of *Daphnia* to suppress phytoplankton biomass. Enclosures were maintained and sampled for several weeks. Response variables included chlorophyll *a*, nutrient concentrations, and phytoplankton community structure.

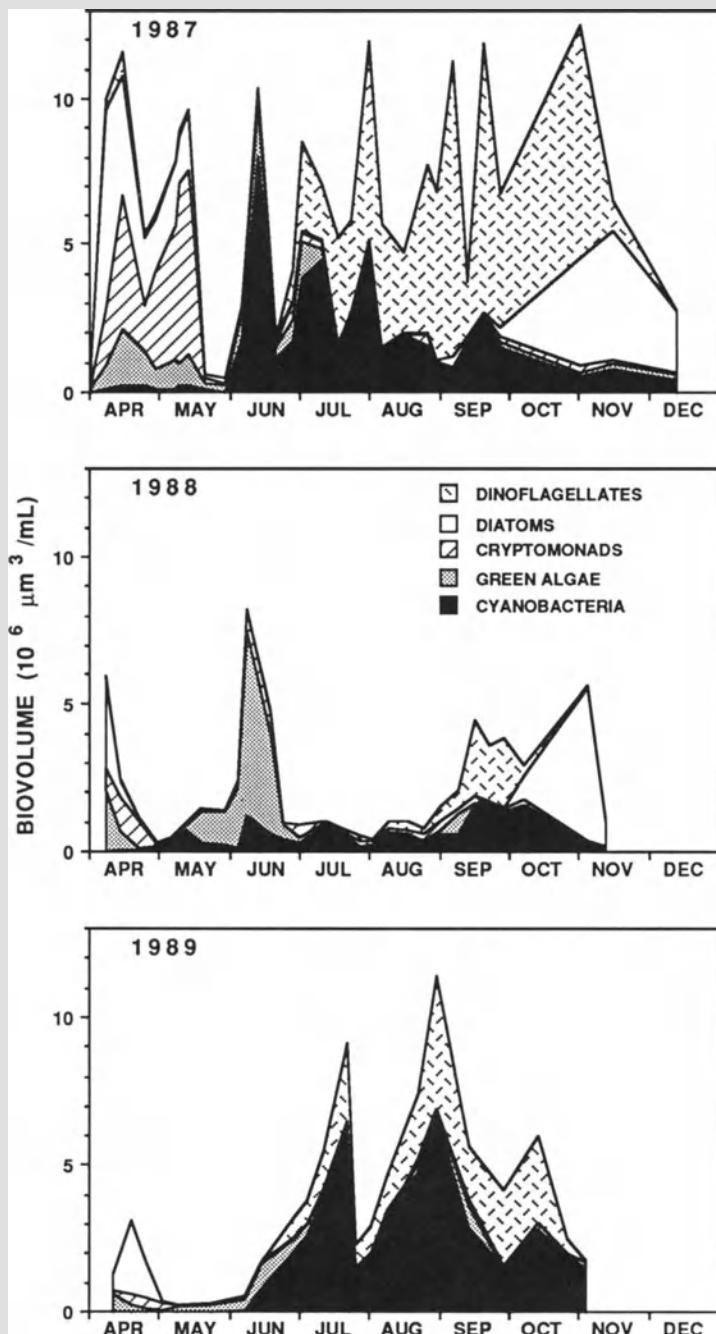
## **Results and Discussion**

### **Seasonal Succession of Phytoplankton**

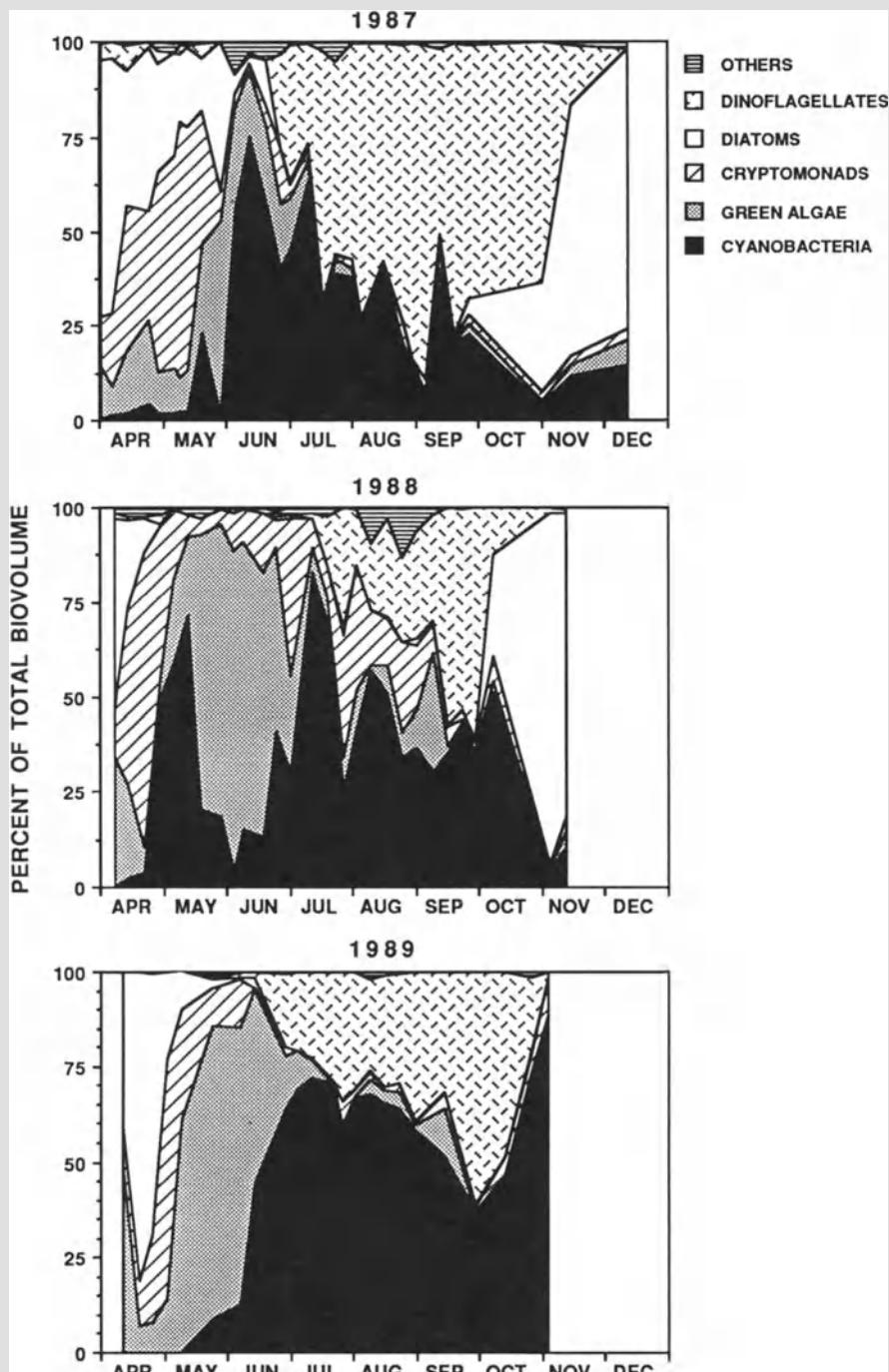
In all three years, the phytoplankton community underwent a seasonal succession fairly typical of temperate eutrophic lakes (Figures 13.1 and 13.2), as has occurred in the lake in most years at least since 1976 (Brock 1985; Lathrop and Carpenter, Ch. 7). However, superimposed upon this regularity was substantial year-to-year variability in the abundance and timing of certain phytoplankton groups and individual taxa.

In all three years, a spring “bloom” ( $\text{biovolume} > 2 \times 10^6 \mu\text{m}^3 \cdot \text{mL}^{-1}$ ) of phytoplankton developed following ice-out (Figure 13.1). In all years the bloom consisted mainly of cryptomonads and diatoms, as in previous years. The duration and magnitude of the spring bloom in 1987 was typical of most of the previous 11 years (Lathrop and Carpenter, Ch. 7). However, the duration and magnitude of the spring bloom were much reduced in 1988 and 1989 (Figure 13.1). In 1987 the spring bloom lasted  $> 6$  weeks and biovolume averaged  $> 7 \times 10^6 \mu\text{m}^3 \cdot \text{mL}^{-1}$ , while in 1988 and 1989 the “bloom” lasted only 1–2 weeks and biovolume was much lower.

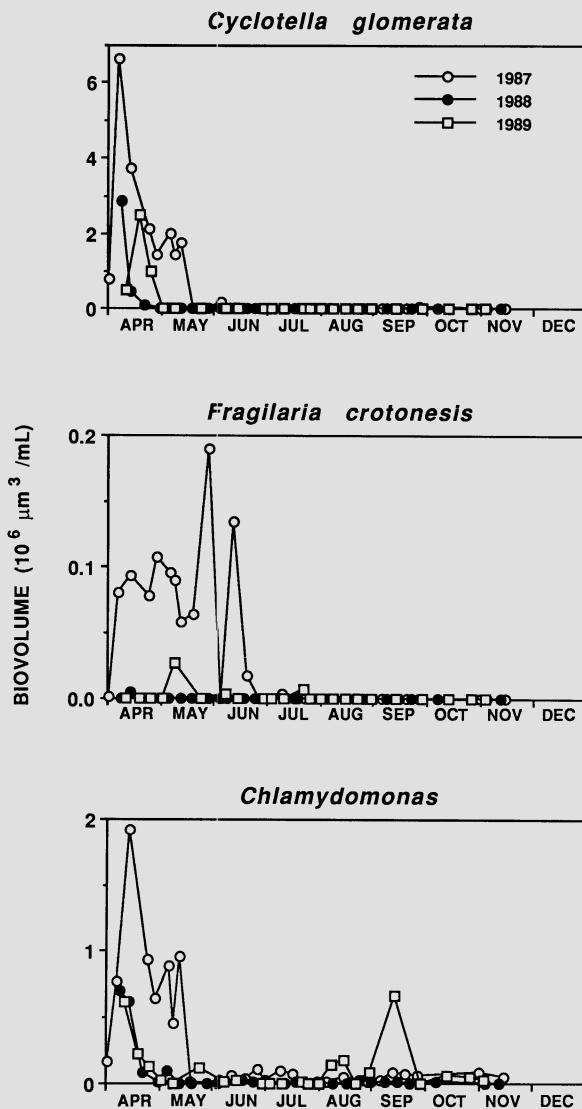
The relative abundances (percent of total biovolume) of the three major spring groups—cryptomonads, diatoms, and unicellular green



**Figure 13-1.** Seasonal patterns in biovolume of phytoplankton groups in Lake Mendota from 1987 to 1989.

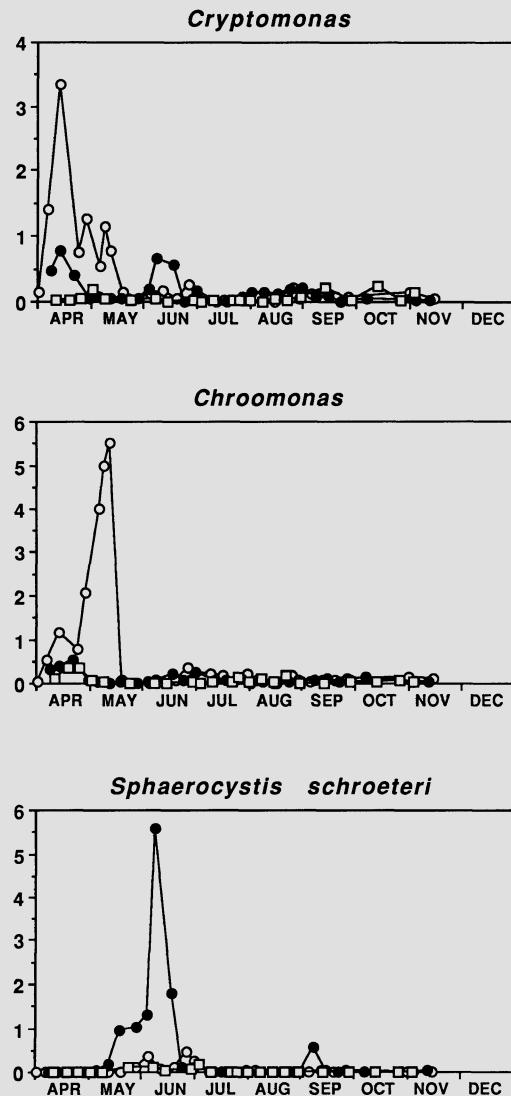


**Figure 13-2.** Seasonal patterns in the relative abundance of phytoplankton groups in Lake Mendota from 1987 to 1989. "Others" include euglenoids and chrysophytes.



**Figure 13-3.** Seasonal patterns of diatoms and green algae dominant in early spring in Lake Mendota, 1987 to 1989.

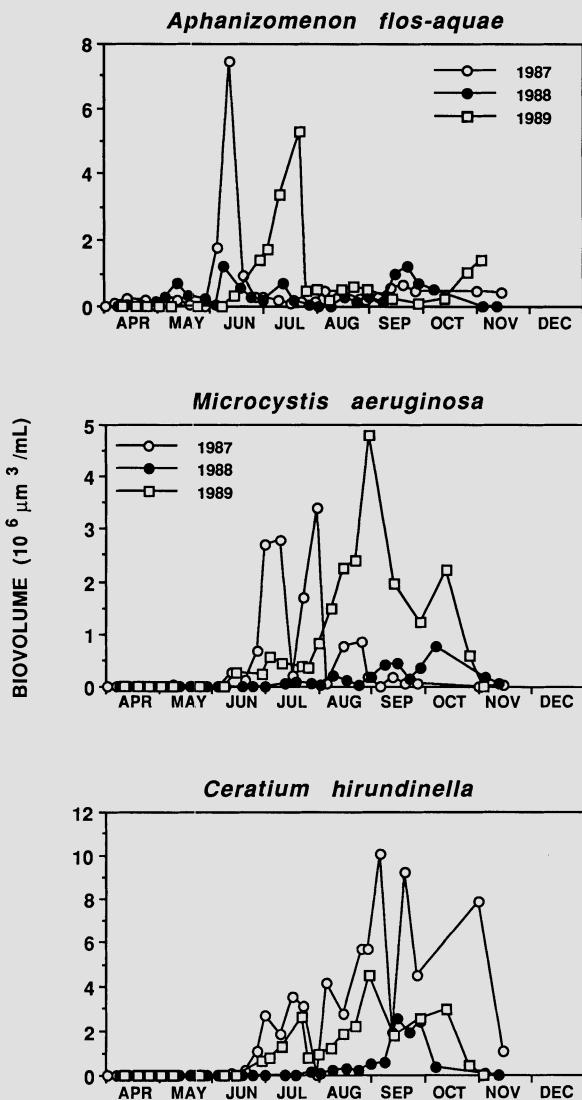
algae—were fairly similar in all three years (Figure 13.2). Furthermore, the same species dominated the spring assemblage in all three years. Among diatoms, *Cyclotella glomerata*, and to a much lesser extent *Fragilaria crotonensis*, were the dominant species (Figure 13.3). Green algae were dominated by *Chlamydomonas* (probably two or three species) (Figure 13.3), while cryptomonads were dominated by



**Figure 13-4.** Seasonal patterns of cryptomonads and green algae dominant in spring in Lake Mendota, 1987 to 1989.

*Cryptomonas* and *Chroomonas* (Figure 13.4). In 1987 *Chroomonas* succeeded *Cryptomonas*, while in other years the two taxa peaked at similar times.

In all years the spring bloom was followed by a clear-water period during which phytoplankton biomass was quite low and water transparency high (Figure 13.1). The duration of the spring clear-water period



**Figure 13-5.** Seasonal patterns of cyanobacteria and *Ceratium* in Lake Mendota, 1987 to 1989.

varied markedly among the three-years. In 1987 clear water lasted <2 weeks, typical of previous years (Lathrop and Carpenter, Ch. 7), while in 1988 and 1989 the clear-water period lasted much longer (Figure 13.1). Among previous years since 1976, only in 1976 and 1977 did the clear-water period last this long (Brock 1985; Lathrop and Carpenter, Ch. 7). In all three years between 1987 and 1989, green algae were a dominant

group during some or all of the clear-water period (Figure 13.2). The green algae assemblage was dominated by colonial taxa, including those with gelatinous sheaths or other coverings believed to offer protection against herbivores, such as *Sphaerocystis schroeteri* (Figure 13.4), and to a lesser extent *Oocystis*, *Coelastrum*, and *Schroederia*.

A characteristic summer phytoplankton assemblage succeeded the clear-water period. In all years cyanobacteria (blue-green algae) increased after the clear-water period, but the magnitude and timing of the increase was highly variable among years (Figure 13.1). In 1987 cyanobacteria increased rapidly to an annual maximum immediately after the clear-water period. Cyanobacteria increased at about the same time in 1988, but the increase was very much reduced compared to 1987. In 1989 yet another pattern emerged; in this year the cyanobacteria bloom commenced a month later than in the previous two years, but biovolume was similar to 1987. In all three years cyanobacteria comprised >50% of total biovolume during at least part of the summer (Figure 13.2), but cyanobacteria biovolume was much lower in 1988 than in the other two years (Figure 13.1).

Among cyanobacteria, in all three years *Aphanizomenon flos-aquae* was responsible for the initial summer increase and was succeeded by *Microcystis aeruginosa* in late summer (Figure 13.5). Other cyanobacteria taxa which in the past had formed blooms in Lake Mendota, such as *Anabaena*, *Gloeotrichia*, and *Lyngbya*, were present but relatively rare.

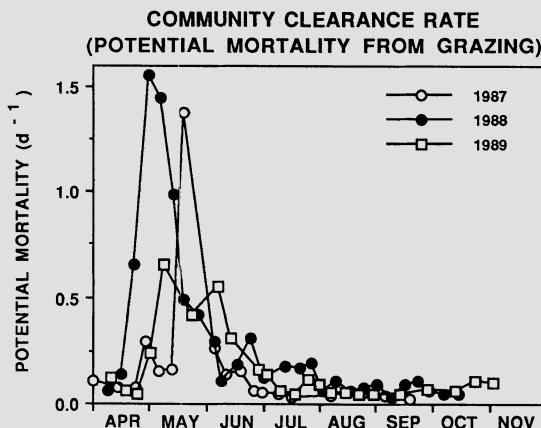
In all three years dinoflagellates became increasingly more abundant as summer progressed and by late summer were a dominant group in terms of relative abundance (Figures 13.1 and 13.2). In all years the summer dinoflagellate assemblage was composed exclusively of *Ceratium hirundinella* (Figure 13.5). As with the cyanobacteria, *Ceratium* displayed substantial among-year variability and was least abundant in 1987. Among-year variation in *Ceratium* abundance of this magnitude is also evident in the long-term database (1976–89; Lathrop and Carpenter, Ch. 7).

Because cyanobacteria and dinoflagellates were the dominant taxa during all summers, and because these groups were much less abundant in 1988 than in the other two years, summer total phytoplankton biovolume was also lowest in 1988 (Figure 13.1).

In 1987 and 1988, diatoms regained dominance in October (Figures 13.1 and 13.2). However, in 1989 diatoms had not yet increased when sampling ceased in early November.

### Seasonal Patterns of Herbivory

Details of zooplankton seasonal dynamics are presented in Luecke et al. (Ch. 14) and conform to the typical pattern for eutrophic, thermally stratified lakes (Sommer et al. 1986). Briefly, in all years the rich food

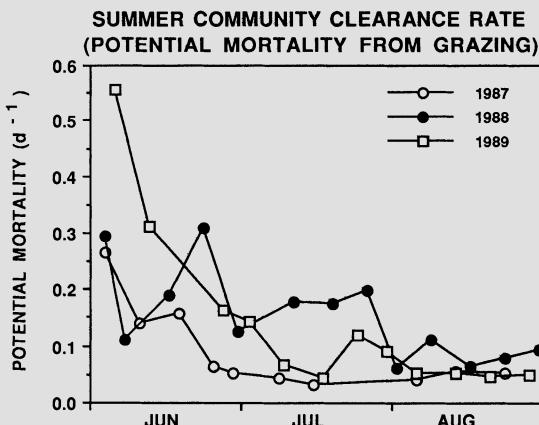


**Figure 13-6.** Community clearance rates in Lake Mendota, 1987–89.

source provided by the spring phytoplankton bloom led to increased zooplankton biomass in spring, followed by a decline as the clear-water period waned, and low biomass throughout summer. Maximal biomass occurred in spring each year (i.e., before 15 June). In all years total zooplankton biomass was much lower in summer than in spring.

In 1987 the relatively high spring zooplankton biomass was dominated by cyclopoid copepods in early spring and by *Daphnia galeata mendotae* in late spring. *Daphnia* was rare until early May, reached maximum biomass in late May, and rapidly declined during the later stages of the clear-water period. Copepods dominated the summer community. In late summer 1987, the biomass of cisco (*Coregonus artedii*), an important planktivorous fish, was reduced by 90–95% following massive mortality. This had a strong impact on zooplankton dynamics the following year (Vanni et al. 1990a; Luecke et al., Ch. 14). In 1988 the larger *Daphnia pulicaria* replaced *D. galeata mendotae* (Plate 4). Furthermore, *D. pulicaria* became abundant much earlier in the season compared to 1987 (shortly after ice-out) and dominated the community throughout spring. Copepods were much rarer in 1988 than 1987. *Daphnia* biomass declined in late spring 1988, as in previous years, but in 1988 *Daphnia* declined much more slowly compared to 1987, and comprised a relatively high percentage of summer zooplankton biomass compared to other years (Luecke et al., Ch. 14). Spring 1989 dynamics were similar to 1988; *Daphnia* was dominant from shortly after ice-out through late summer. However, peak *Daphnia* biomass and average early spring *Daphnia* biomass were both lower in 1989 than in 1988.

The among-year patterns of zooplankton biomass and community structure are reflected in community clearance rates, an estimate of maximum phytoplankton mortality arising from herbivory (Figure 13.6).

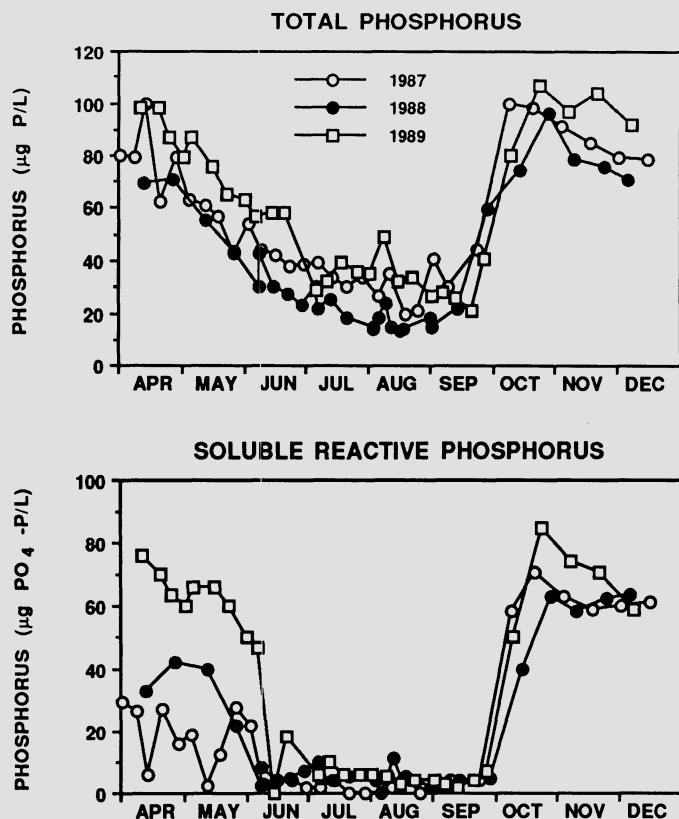


**Figure 13-7.** Community clearance rates in late spring–early summer in Lake Mendota, 1987–89. Note that the scale is different from that in Figure 13.6.

In each year, clearance rate rapidly increased to an annual maximum in spring and then declined in late spring–early summer, corresponding to the wax and wane of *Daphnia* biomass. In fact, *Daphnia* biomass explained most of the variation in clearance rates ( $r^2 = 0.84$ , linear regression of clearance rate on *Daphnia* biomass, using all sampling dates in all three years). Clearance rate remained relatively low during summer in all three years. Despite the similarities in clearance rates among years, substantial differences occurred, corresponding to the among-year variation in zooplankton community dynamics (Figure 13.6).

Maximal clearance rates were similar in 1987 and 1988, but the average spring rate was much higher in 1988 than 1987 because of the longer period of *Daphnia* dominance. In 1987 clearance rate exceeded  $0.4\text{ d}^{-1}$  on only one sampling date, while in 1988 it was  $>0.4$  from late April until early June (Figure 13.6). Maximal clearance rate was much lower in 1989 than in the other two years, but exceeded  $0.4$  on several dates (Figure 13.6).

The strong seasonal dynamics depicted in Figure 13.6 obscure differences among years in late spring and early summer clearance rates. Therefore June–August clearance rates are presented on a different scale in Figure 13.7. Late spring and early summer clearance rates also differed substantially among years. Summer rates were lowest in 1987 and highest in 1988. In 1989 late spring rates were higher than the other years, but by mid-July rates had declined to near 1987 levels. Thus, June clearance rates can be ranked as  $1989 > 1988 > 1987$ , while July rates can be ranked as  $1988 > 1989 > 1987$ . Clearance rates in August were similar in all years.



**Figure 13-8.** Epilimnetic concentrations of the various fractions of nitrogen and phosphorus in Lake Mendota, 1987–89.

The trends in clearance rates (which in turn reflect trends in *Daphnia* biomass) are reflected in the seasonal patterns of phytoplankton biomass (Figures 13.1, 13.6, and 13.7). Maximum clearance rates always occurred in late spring and coincided with the clear-water period. Low clearance rates in early spring and summer corresponded generally with high phytoplankton biomass.

#### Seasonal Dynamics of Nutrients

As with phytoplankton and herbivory, certain general patterns in epilimnetic nutrient concentrations were repeatable from year to year, yet considerable variation existed among years (Figure 13.8). Concentrations of all nutrients were highest in spring and fall in all years, with minima in summer, a pattern typical of stratified lakes. Total nitrogen (TN), however, declined less than other nutrients (Figure 13.8). Declines of nutrients in late spring–early summer probably reflect decreases in nutri-

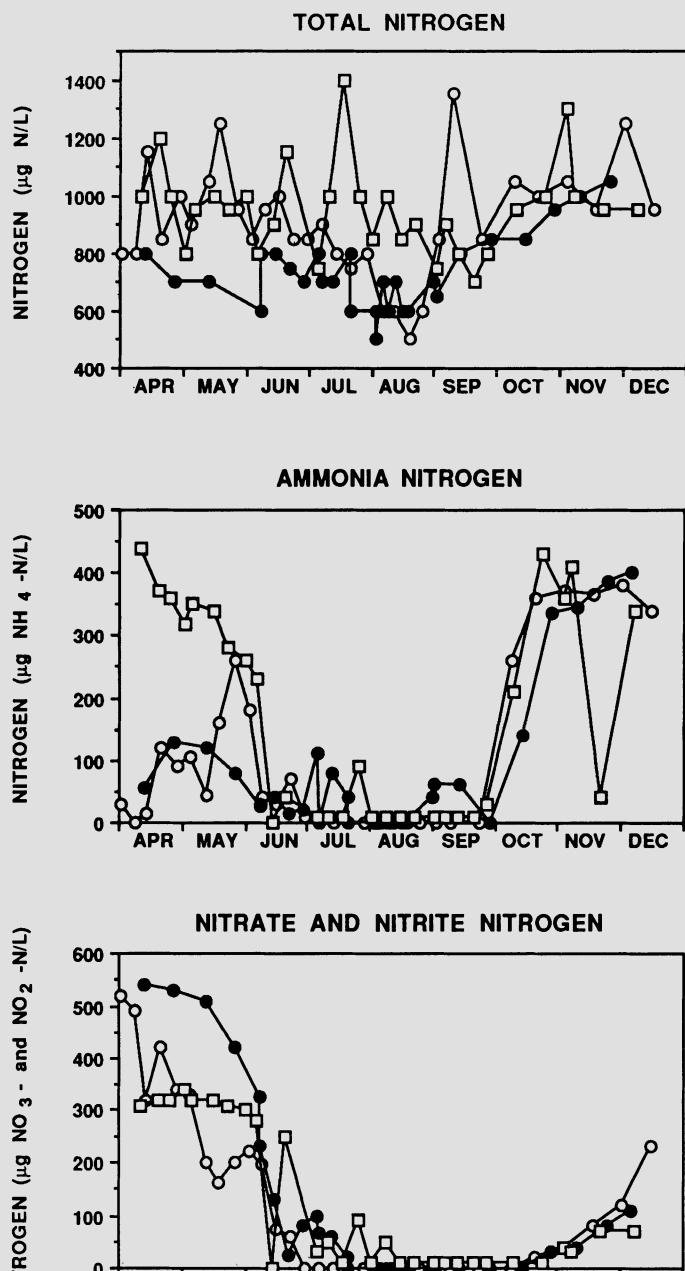
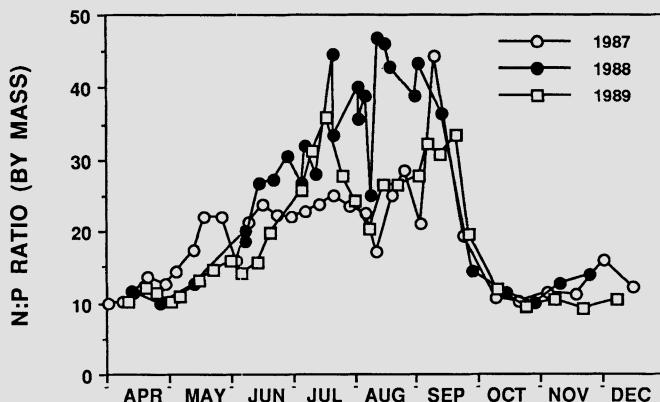


Figure 13-8. (continued)



**Figure 13-9.** Total nitrogen: total phosphorus, by mass, in the epilimnion of Lake Mendota, 1987–89.

ent loading rates (runoff) from the watershed, as well as increased sedimentation of nutrients to the hypolimnion (Brock 1985).

Spring TP was highest in 1989, while spring TP was similar in 1987 and 1988 (Figure 13.8). Summer TP was slightly lower in 1987 than in the other two years. The increase in autumn TP was similar in all three years. Spring TN was similar in 1987 and 1989, with 1988 lower (Figure 13.8). In summer, TN was higher in 1989 than in other years. As with TP, the autumn increase in TN was similar in all three years.

Concentrations of all three dissolved nutrient fractions declined more rapidly than total nutrients in all three years (Figure 13.8). SRP and NH<sub>4</sub>-N had relatively similar dynamics. Concentrations of both of these fractions were much higher in spring of 1989 than in other springs. SRP was generally higher in spring 1988 than spring 1987. NH<sub>4</sub>-N was higher in late spring 1988 than in late spring 1987. Concentration of NO<sub>2</sub>/NO<sub>3</sub>-N was higher in spring 1988 than in other springs (Figure 13.8). Early spring 1987 and 1989 concentrations were similar, but NO<sub>2</sub>/NO<sub>3</sub>-N declined more rapidly in late spring 1987 than in 1989.

Peaks in SRP and NH<sub>4</sub>-N in late spring 1987 and mid-spring 1988 corresponded to peaks in *Daphnia* biomass. At these times, *Daphnia* is apparently converting particulate nutrients (i.e., that in phytoplankton) to dissolved form through excretion. In addition, because phytoplankton biomass is low and phytoplankton taxa are not nutrient limited (see below), uptake of nutrients is low. Thus dissolved nutrients accumulate in the water column.

In all three years, concentrations of all dissolved fractions were below analytical detection limits on most summer dates, making among-year comparisons difficult. However, concentrations of SRP, NH<sub>4</sub>-N, and NO<sub>2</sub>/NO<sub>3</sub>-N were above analytical detection limits more often in 1988

and 1989 than in 1987, suggesting that nutrients were more available in summer in 1988 and 1989 than in 1987.

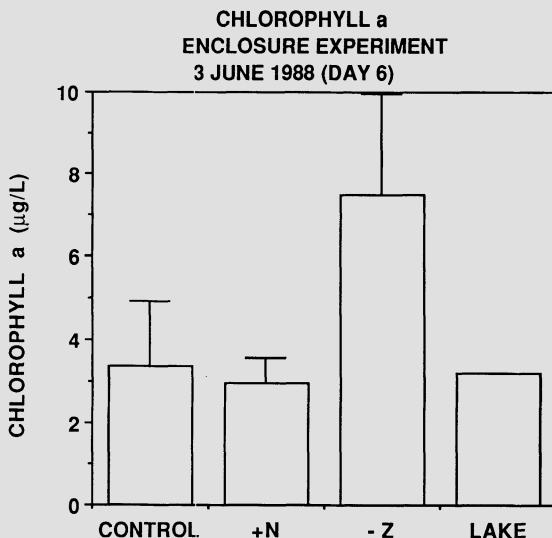
As a result of a more rapid decrease in P than N (Figure 13.8), the ratio of total N to total P (N:P ratio) increased steadily throughout spring and summer in all three years (Figure 13.9). However, the N:P ratio differed somewhat among years. The April and May N:P ratio was higher in 1987 than other years, but the July N:P was lower in 1987 than other years. The spring (April–June) N:P was similar in 1988 and 1989, but the two years diverged after this, with 1988 N:P higher than 1989 in summer. The summer N:P was considerably higher in 1988 than other years, especially in August and early September. In all years, the N:P ratio was above the Redfield ratio of 7:1 (by mass), suggesting that phytoplankton were more limited by P than N, particularly in summer when nutrients are most likely to be limiting.

### Results of Experimental Studies

The results of short-term experiments (3–5 d) are presented in Vanni and Temte (1990), Vanni et al. (1990a), and Moegenburg and Vanni (1991). In addition, results of the larger-scale experiments are expected to be published elsewhere in the future. Some results important in explaining the dynamics of phytoplankton are presented here.

Vanni and Temte (1990) found a strong seasonal pattern in the degree to which phytoplankton were limited by grazing and nutrients. Spring phytoplankton taxa were highly vulnerable to grazers, especially *Daphnia*. In experiments conducted during both the spring bloom and the clear-water period, *Daphnia* significantly reduced phytoplankton biomass (measured as chlorophyll *a*). Zooplankton assemblages dominated by copepods (as is typical in early spring) could depress phytoplankton typical of the spring bloom (especially diatoms) but not phytoplankton typical of the clear-water period (mostly colonial green algae). Grazing effects were much less evident in short-term experiments conducted in summer (August). In all summer experiments, neither ambient zooplankton nor *Daphnia* significantly depressed total phytoplankton biomass.

Nutrient limitation showed trends opposite that of grazing limitation. Very few phytoplankton taxa were limited by either N or P during the spring bloom or the clear-water period, while most taxa were limited by nutrients in summer. In most cases of nutrient limitation, taxa were co-limited by N and P; that is, biomass increased significantly when both N and P were added but not when either nutrient was added singly. Taken together, the results of Vanni and Temte (1990) suggest that grazing is an important control of phytoplankton in spring but not summer, and nutrient limitation is important in summer but not spring.



**Figure 13-10.** Response of phytoplankton biomass (chlorophyll *a*) in large enclosures, 6 days after the experiment began. Control: zooplankton added at densities approximating those in the lake; +N: zooplankton at lake densities plus addition of N as  $\text{NH}_4\text{Cl}$ ; -Z: zooplankton removed; Lake: chlorophyll *a* concentration in the epilimnion of Lake Mendota on this date (*Daphnia pulicaria* was abundant at the time). Error bars represent 1 SD.

Large-scale experiments conducted in 1988 and 1989 confirm the importance of *Daphnia* grazing in spring, and especially in causing and maintaining the clear-water period (Howard, in prep.). Within 6 days of excluding zooplankton (dominated by *D. pulicaria*), phytoplankton biomass doubled relative to enclosure with zooplankton (Figure 13.10). Enclosures with zooplankton and the lake had similar phytoplankton biomass (Figure 13.10). This shows that *Daphnia* grazing can maintain the clear-water period. Longer-term analysis of the impact of *Daphnia* grazing in these experiments was precluded because of methodological problems. *Daphnia* soon colonized enclosures intended to be free of zooplankton, perhaps by splashing in on surface waves. Upon colonizing enclosures, *Daphnia* became equally abundant in all treatments, as did phytoplankton biomass (Howard, in prep.).

Large-scale enclosure experiments were repeated during the clear-water period in 1989 and revealed dynamics similar to 1988 experiments (Leavitt, in prep.). Exclusion of *Daphnia* initially stimulated phytoplankton biomass, but soon *Daphnia* colonized, and became abundant in all enclosures. Furthermore, the dense *Daphnia* population in +*Daphnia* enclosures declined rapidly, and after this happened, phytoplankton increased markedly (Leavitt, in prep.).

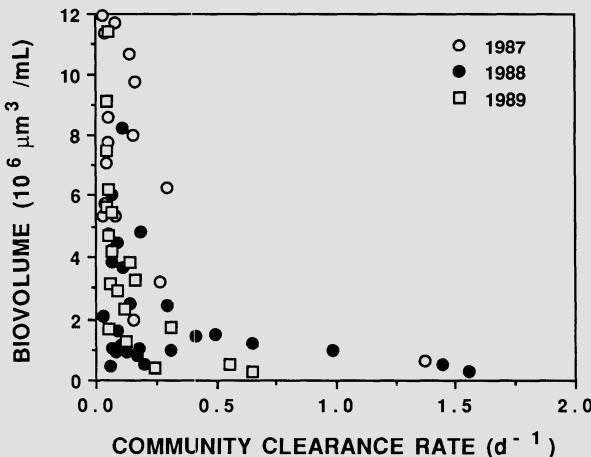
Thus, although the large-scale enclosures were fraught with methodological problems, the results of these experiments support the hypothesis that *Daphnia* grazing causes and maintains the clear-water period.

Moegenburg and Vanni (1991) attempted to ascertain some of the indirect effects of herbivores on phytoplankton, specifically whether nutrients excreted by zooplankton could reduce the degree to which phytoplankton were limited by nutrients. In all of these experiments, carried out in summer 1988, nutrients excreted by zooplankton reduced P limitation. N limitation was reduced by zooplankton excretion in only one experiment in September. Moegenburg and Vanni also present data on physiological indicators of N and P limitation of Lake Mendota phytoplankton (ammonium enhancement response for N and alkaline phosphatase activity for P). These indicators showed that in 1988 phytoplankton were more often limited by P than N; the phytoplankton community was, however, limited by N during the September experiment when zooplankton excretion reduced N limitation. Thus, there was a correspondence between the nutrient most limiting phytoplankton and the effect of zooplankton excretion on nutrient limitation: zooplankton excretion seemed to reduce the deficiency of whatever nutrient was most limiting at the time. Direct measurement of nutrients excreted by zooplankton showed that they release considerable amounts of N and P in a form highly available to phytoplankton.

Nutrient enrichment experiments were conducted *in situ* during three years (1986–88), by adding nutrients to phytoplankton in the 19-L containers described above and quantifying the response of phytoplankton biomass. In the summers of 1986 and 1987 (before the cisco mortality), addition of N and P together increased phytoplankton biomass (chlorophyll *a*) 3–5× over control enclosures (Vanni et al. 1990a). In 1988 (after the cisco mass mortality), additions of N and P did not increase phytoplankton biomass relative to controls (Vanni et al. 1990a). Thus, although phytoplankton were transiently limited by nutrients in 1988, as determined by physiological bioassays (Moegenburg and Vanni 1991), phytoplankton were less nutrient limited in 1988 than 1987, as determined by enrichment experiments in both years. Physiological bioassays were not conducted in 1987.

### Correlations Between *Daphnia* Biomass and Phytoplankton Biomass

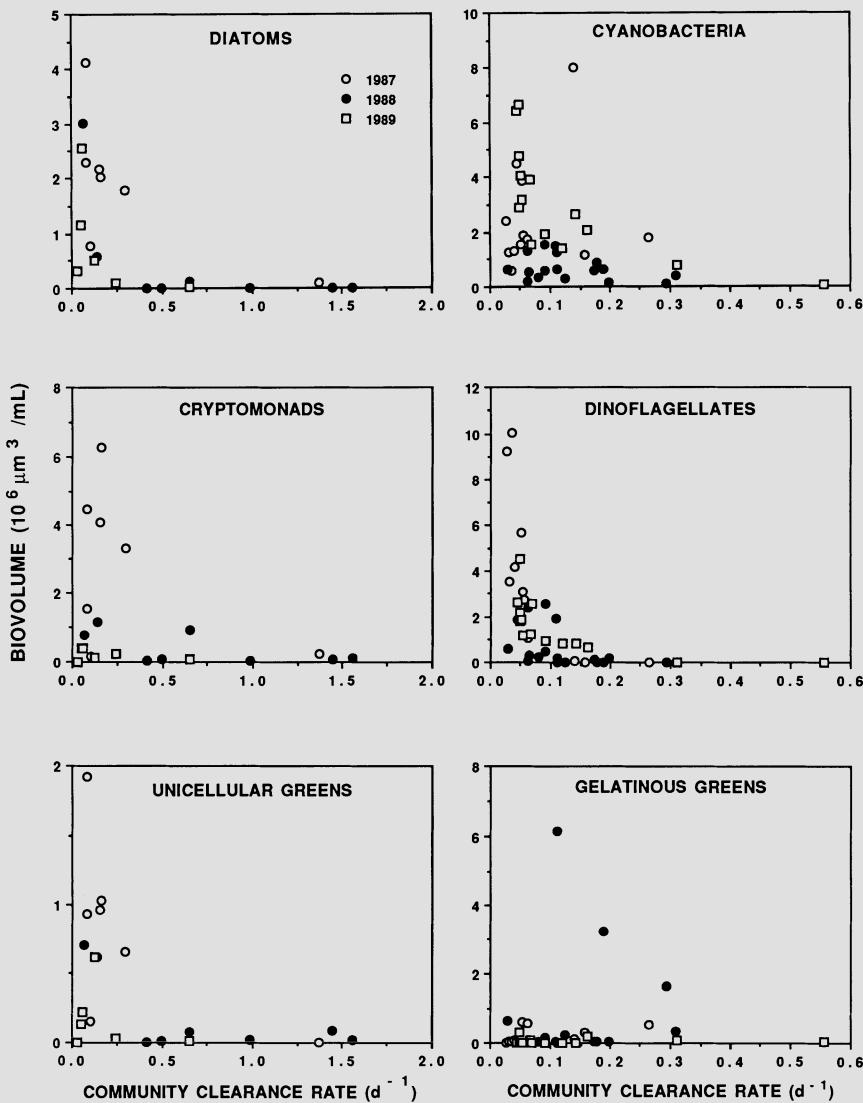
To further explore the relationship between herbivory and phytoplankton abundance during the three years, we plotted total phytoplankton biomass against community clearance rate (Figure 13.11). Each sampling date is represented by one data point. Total phytoplankton was negatively related to clearance rate in a nonlinear fashion (Figure 13.10). That is, a threshold clearance rate exists: at clearance rates above  $\sim 0.4 \text{ d}^{-1}$ , phytoplankton biovolume was always low ( $< 2 \times 10^6 \mu\text{m}^3 \cdot \text{mL}^{-1}$ ), while



**Figure 13-11.** Scatterplot of total phytoplankton biovolume versus community clearance rate in Lake Mendota, 1987–89. Each point represents one sample date.

at clearance rates below  $\sim 0.4 \text{ d}^{-1}$ , phytoplankton biovolume was quite variable (Figure 13.11). This threshold of  $\sim 0.4 \text{ d}^{-1}$  corresponds to roughly  $350 \mu\text{g Daphnia} \cdot \text{L}^{-1}$  (dry mass). Clearance rates  $\geq 0.4 \text{ d}^{-1}$  occurred only during the clear-water periods (Figure 13.6).

Similar plots were generated for individual phytoplankton groups. In these cases, datasets were restricted to periods of the year when each particular group is typically found in the lake. This reduces the frequency of zero values and also restricts analysis to periods when physicochemical conditions permit existence. For example, cyanobacteria are likely to be rare in spring because of cool temperatures, and diatoms are likely to be rare in summer because of low silica concentrations. Including spring dates for cyanobacteria, therefore, would tend to exaggerate any grazing effect of *Daphnia* because cyanobacteria would be rare at times when *Daphnia* were very abundant, even though factors other than grazing probably prevented cyanobacteria from dominating. Thus, analyses were restricted to spring dates for cryptomonads, diatoms, and unicellular green algae, and to summer dates for cyanobacteria, dinoflagellates, and gelatinous green algae. Scatterplots of these groups against community clearance rates in general show the same hyperbolic relationship as found between clearance rate and total phytoplankton biovolume (Figure 13.12). The hyperbolic pattern is less clear for cyanobacteria, and for gelatinous greens there may be a unimodal relationship between clearance rate and biovolume, a pattern that may arise through a combination of grazing and nutrient regeneration by zooplankton (Lehman and Sandgren 1985). The summer groups appear to have a lower “threshold”



**Figure 13-12.** Scatterplots of phytoplankton groups versus community clearance rate in Lake Mendota, 1987–89. Symbols as in Figure 13. 11. For each group, only dates during which physical conditions were conducive to growth were used; see text for details.

clearance rate than spring groups; that is, summer groups display low biovolumes ( $<2 \times 10^6 \mu\text{m}^3 \cdot \text{mL}^{-1}$ ) at lower clearance rates than spring groups. This may seem counterintuitive, given that summer taxa are generally less edible than spring taxa. However, summer taxa also have slower growth rates than spring taxa. Thus spring taxa can withstand a

relatively high herbivory rate and still maintain positive growth rates, while summer taxa, with low growth rates, cannot withstand these high herbivory rates.

### Prediction of Interyear Variation in Phytoplankton Biomass with Short-Term Grazing Experiments

In the short-term grazing experiments, gradients of zooplankton abundance were created and the response of phytoplankton observed. Because these experiments were conducted before the cisco mortality (1986 and 1987), and because they were conducted several times during the ice-free season, it is useful to assess whether these short-term experiments were good predictors of the phytoplankton response to cisco mortality and subsequent changes in herbivory from 1987 to 1988. We can distinguish three temporally separate phytoplankton assemblages, based on seasonal succession in the lake and response in grazing experiments: spring bloom, clear-water period, and summer assemblages. In short-term experiments, spring assemblages were vulnerable to grazing by copepods but more vulnerable to *Daphnia*, clear-water assemblages were vulnerable only to *Daphnia*, and summer assemblages were not vulnerable to copepods or *Daphnia*. Based on the results of these short-term experiments (Vanni and Temte 1990), one would predict that the increase in herbivory from 1987 to 1988 would greatly reduce spring phytoplankton biomass but have negligible effects on the clear-water and summer assemblages. The predicted lack of an effect during the clear-water period arises not because *Daphnia* cannot depress biomass of this assemblage, but because *Daphnia* was abundant at this time in both years. The predicted lack of effect on the summer assemblage arises from the negligible effect of *Daphnia* on biomass in short-term summer experiments.

As discussed above, phytoplankton biomass was apparently reduced in 1988 (compared to 1987) because of increased herbivory in spring and summer. If anything, phytoplankton were less limited by nutrients in summer 1988 than in summer 1987. Thus, the short-term experiments adequately predicted the response of the spring bloom assemblage to food web changes, but did not predict the observed decreased biomass of the summer assemblage.

### General Discussion

Lake Mendota exhibited a seasonal succession pattern typical of mildly eutrophic lakes in all years of this study. Based on the scheme presented by Reynolds (1984b), early spring phytoplankton represented a combination of assemblages B and C. The C assemblage consists of diatoms typical of eutrophic lakes, while the B assemblage consists of diatoms

typical of mesotrophic lakes. This was followed by a Y assemblage, consisting of cryptomonads, which typify spring assemblages in mesotrophic, eutrophic, and hypertrophic lakes. The clear-water period was dominated by Reynolds' assemblages F, G, and J, which consist of colonial green algae typical of late spring–early summer in mesotrophic, eutrophic, and hypertrophic lakes, respectively. The early summer assemblage was similar to Reynolds' assemblage H, characterized by filamentous, N-fixing cyanobacteria typical of eutrophic lakes, while the late summer assemblage was similar to assemblage M, represented by *Microcystis* and *Ceratium* and typical of eutrophic lakes. Thus, the overall successional sequence of assemblages was [B, C] → [Y] → [F, G, J] → [H] → [M], a pattern containing successional components “typical” of mesotrophic, eutrophic, and hypertrophic lakes.

Despite year-to-year similarities, substantial variation existed from 1987 to 1989. Such variation apparently arose in large part because of substantial variation in *Daphnia* abundance and nutrient loading rates.

The most dramatic among-years difference in phytoplankton was the decrease in phytoplankton biomass in 1988 and 1989 relative to 1987. This reduction in phytoplankton biomass followed the mass mortality of cisco (Luecke et al., Ch. 14), a dominant zooplanktivore, and it appears that cisco were ultimately responsible for the reduction in phytoplankton (Vanni et al. 1990a, 1990b). The patterns are especially evident with regard to spring phytoplankton biomass. Reduction in cisco biomass led to decreased zooplanktivory (Luecke et al., Ch. 14), and this in turn led to a replacement of the smaller *Daphnia galeata mendotae* by the larger *Daphnia pulicaria*. The two *Daphnia* species also displayed different phenologies. *D. pulicaria* became abundant earlier in the season in 1988 and 1989 than did *D. galeata mendotae* in 1987. This led to earlier maximum, and higher mean, spring clearance rates, and this in turn caused an earlier clear-water period and decreased mean spring phytoplankton biomass in 1988 and 1989 compared to 1987. In fact, the “typical” spring “bloom” was virtually nonexistent in 1988 and 1989 (Figure 13.1).

This shift in *Daphnia* biomass, species composition, and phenology parallels that which occurred in 1976–77 in Lake Mendota (Brock 1985; Vanni et al. 1990b; Lathrop and Carpenter, Ch. 8). In 1976 cisco were rare (as they had been for a number of previous years; Magnuson and Lathrop, Ch. 11), but in 1977 they had a strong year class. In 1976 *D. pulicaria* was dominant and became abundant relatively early in the season. In 1977 *D. pulicaria* declined to low levels and was subsequently replaced by *D. galeata mendotae*. In all years from 1978 to 1987, *D. galeata mendotae* was the dominant daphnid and became abundant relatively late in the spring. Presumably, these shifts in *Daphnia* biomass and species composition resulted in clearance rate shifts that parallel those in 1987–89. The duration of the spring clear-water period was longer in 1976 than in subsequent years, paralleling *Daphnia* phenologies. The

consistent results in response to changes in cisco populations in the 1970s and 1980s provide strong evidence that food web changes have pronounced effects on spring phytoplankton dynamics.

Nutrients do not limit phytoplankton in spring (Vanni and Temte 1990). Thus differences in spring phytoplankton biomass among the years from 1987 to 1989 cannot be attributable to differences in spring nutrient concentrations. In fact, spring nutrients, especially dissolved fractions, were highest in 1989 and lowest in 1987. Thus an inverse correlation existed between spring nutrients and phytoplankton biomass. In addition, maxima of  $\text{NH}_4\text{-N}$  and SRP coincided with maximum *Daphnia* biomass in 1987 and 1988. This suggests that in these two years, *Daphnia* grazing and subsequent regeneration of nutrients determined dissolved nutrient concentrations. Thus the effects of top predators can cascade not only to phytoplankton but all the way down to spring nutrient concentrations. In 1989 spring SRP and  $\text{NH}_4\text{-N}$  were much higher than in 1987 and 1988. Furthermore, no apparent relationship existed between *Daphnia* biomass and concentrations of these dissolved nutrients. Spring runoff was much higher in 1989 than in either 1987 or 1988 (Lathrop, Ch. 6). This suggests that high runoff, and associated high nutrient loading rate, can “swamp” food web effects on spring nutrient concentrations, although strong food web effects on spring phytoplankton were observed despite high nutrient loading in 1989.

With regard to spring phytoplankton biomass and nutrient concentrations, the following control mechanisms can be proposed. When *D. galeata mendotae* dominates the daphnid community, phytoplankton grow relatively unchecked in early spring, in response to abundant nutrients and increasing light. This results in a spring bloom consisting of diatoms, cryptomonads, and unicellular green algae. The spring bloom represents abundant high-quality food for zooplankton, whose biomass thus increases in response. Cyclopoid copepods (especially juvenile stages) become abundant early in spring, followed in late spring by *D. galeata mendotae*. Eventually *D. galeata mendotae* becomes abundant and community clearance rate exceeds growth rate of phytoplankton, producing the clear-water period. Reynolds (1984a; his Table 16) provides maximal growth rates of selected algal taxa under laboratory conditions of nutrient and light saturation. Cryptomonads and *Cyclotella* generally have maximal growth rates  $\leq 0.85 \text{ d}^{-1}$ , while *Chlamydomonas* can attain much higher growth rates ( $> 2 \text{ d}^{-1}$ ). Clearance rates in Lake Mendota exceeded  $0.85 \text{ d}^{-1}$  during maximal *Daphnia* abundance in 1987 and 1988 but never exceeded  $2.0 \text{ d}^{-1}$  in any year (Figure 13.6). This implies that the mortality rate of cryptomonads and *Cyclotella* could exceed the growth rate at times of maximal *Daphnia* abundance, but that mortality would never exceed growth of *Chlamydomonas*. However, the maximal growth rates presented in Reynolds (1984a) represent optimal laboratory conditions, and it is likely that growth rates in the lake do not approach these levels,

even during times of high nutrient availability. While phytoplankton are not nutrient limited in spring, they are probably not exposed to light-saturating conditions because the lake is isothermal and phytoplankton probably circulate to depths of suboptimal light. In addition, temperature may be less than optimal at these times. Thus phytoplankton growth rates are likely to be less than maximal, and at these times grazing may exceed growth. This results in greatly decreased phytoplankton biomass, causing the clear-water period.

The patterns and mechanisms outlined in the preceding paragraph support the Plankton Ecology Group (PEG) model of seasonal succession in eutrophic lakes (Sommer et al. 1986). However, succession deviated somewhat from this pattern in 1988 and 1989, after the cisco mortality and the subsequent dominance of spring zooplankton by *D. pulicaria*. When this species dominates, it appears early after ice-out and quickly reaches high densities. This leads to a greatly shortened and less intense spring "bloom," in which phytoplankton biomass is lower, and the clear-water period earlier, than in years when *D. galeata mendotae* dominates. Thus, while the general PEG model pattern of a spring bloom followed by increasing grazing and subsequent clear-water period is evident regardless of the structure of upper trophic levels, the relative duration and intensities of the various phases are greatly altered by variation in upper trophic levels.

While among-year differences in spring phytoplankton dynamics appear to be greatly influenced by variation in food web structure and little affected by variation in nutrient loading, summer dynamics are more complicated. Each of the three years yielded a distinct pattern of succession following the clear-water period, and it appears that both nutrient loading and food web structure affect the dynamics of summer assemblages. As with spring dynamics, summer 1987 represented a successional sequence "typical" of eutrophic lakes (Reynolds 1984b; Sommer et al. 1986), with filamentous, nitrogen-fixing cyanobacteria (*Aphanizomenon*) dominating soon after the clear-water period, succeeded by the cyanobacterium *Microcystis* and the dinoflagellate *Ceratium*. Phytoplankton biomass was high in summer 1987. Summer phytoplankton was much lower in 1988, after a short period of abundance of *Sphaerocystis*. However, in 1989 phytoplankton biomass was as high as in 1987, dominated by cyanobacteria and to a lesser extent *Ceratium*. Based on patterns in nutrient loading (runoff), nutrient concentrations, and herbivory, and on experimental investigations of nutrient limitation, the following mechanisms seem likely. Spring nutrient loading actually increased slightly from 1987 to 1988, and both years were below the long-term average (Lathrop 1990, Ch. 6). Phytoplankton were less nutrient limited in 1988 than 1987. These trends suggest that the decrease in summer biomass from 1987 to 1988 was not caused by decreased nutrient availability. Early summer clearance rates were much higher in 1988 than 1987

(Figure 13.7), and thus increased herbivory can potentially account for decreased summer phytoplankton biomass in 1988 compared to 1987. While clearance rates were clearly much lower in summer than spring in both years (Figure 13.6), phytoplankton growth rates were also much lower in summer and were similar in magnitude to clearance rates. Growth rates of typical summer taxa were generally  $<0.3\text{d}^{-1}$ , even in the absence of herbivores (Vanni and Temte, unpubl. data). An increase in clearance rate from 0.05 (typical of July 1987) to 0.15 (typical of July 1988) could have a large impact on phytoplankton growing at such low rates. Thus phytoplankton growth could potentially be balanced by a lower clearance rate in summer than spring.

Patterns of herbivory may help explain the dynamics of phytoplankton in summer 1989 as well. Herbivory declined at a slower rate in early summer in this year than in other years; the result was higher clearance rates in early to mid-June 1989 than 1987 or 1988 (Figure 13.7). The later decline in herbivory may explain the delayed increase in summer phytoplankton in 1989 compared to 1987 (Figure 13.1). When clearance rates finally did decline in 1989, they decreased to near 1987 levels, yielding similar rates in July–August 1987 and 1989. Phytoplankton biomass was also similar in July–August 1987 and 1989.

While herbivory may explain much of the interyear dynamics, clearly nutrient loading is important. It is probably no coincidence that relatively high nutrient loading rates in 1989 led to high phytoplankton biomass in summer 1989 (although an equally high biomass was attained in 1987 with much lower nutrient loading rates). In all likelihood, variations in nutrient loading and herbivory interact to produce among-year variation in phytoplankton abundance. Herbivory may have more effect on phytoplankton at low nutrient loading rates than at high nutrient loading rates. Such an interaction between grazing and nutrients has been advanced previously (McQueen et al. 1986; Carpenter, Ch. 21), although the mechanism for this interaction is not clear. One potential mechanism is simply that at high nutrient loading rates, phytoplankton growth rates are higher, thus requiring higher clearance rates to balance phytoplankton growth. Thus, higher phytoplankton biomass in late summer 1989 (compared to 1988) may have resulted from higher growth rates, despite similar herbivory rates between the two years during this period.

Finally, we may speculate on why the short-term summer experiments did not adequately predict the decrease in summer phytoplankton biomass from 1987 to 1988, while spring experiments were very good predictors of the decrease in spring phytoplankton biomass between these two years. The variation in predictive ability may be related to seasonal variation in the severity of nutrient limitation. In spring, when phytoplankton are not limited by nutrients, zooplankton affect phytoplankton in a simple way—through direct mortality. In such a situation, short-term experiments can adequately detect net grazing

effects. In summer, however, zooplankton affect phytoplankton through excretion of nutrients as well as through direct mortality. For example, *Daphnia* dominance may lead to increased N:P ratio excreted by the zooplankton community compared to that excreted by a small-species zooplankton community. Thus, *Daphnia* may feed on smaller, more edible phytoplankton and resupply nutrients at a higher N:P ratio than was in the water column previously. This may favor phytoplankton taxa other than cyanobacteria, thus enhancing further *Daphnia* survival and creating a positive feedback. If this is the case, the N:P ratio should increase during *Daphnia* dominance. In Lake Mendota, the N:P ratio increased seasonally in all three years despite substantial differences in *Daphnia* abundance. However, some support for this hypothesis is evidenced by more rapidly increasing N:P ratios in June–July 1988 and 1989, years of relative *Daphnia* dominance, than during the same period in 1987 (Figure 13.9). It is during this time period that nutrient limitation increased. Such complex mechanisms, while speculative at this time, may provide a key to understanding the means by which herbivores affect phytoplankton. If these mechanisms are important, short-term experiments may not be of long enough duration to discern the overall effects of zooplankton on phytoplankton.

Phytoplankton of Lake Mendota and other lakes are likely influenced by interactions of nutrient loading and herbivory. In particular, the success of a manipulation program designed to reduce phytoplankton biomass through food web alterations will likely depend on nutrient loading rates. As suggested by others (McQueen et al. 1986; Benndorf et al. 1988), the Lake Mendota data indicate that food web changes will be expressed more in phytoplankton communities at lower nutrient levels than at higher nutrient levels (but see Reinertsen et al. 1990). Thus, a combination of lowering nutrient loading rates and zooplanktivory rates may be the most effective means of reducing phytoplankton blooms in Lake Mendota and other eutrophic lakes.

## References

- Adrian R (1988) Untersuchungen zur herbivoren und carnivoren ernährungsweise von Cyclops kolensis und C. vicinus (Crustacea: Copepoda). Dissertation, Freien Universität, Berlin
- Benndorf J, Schultz H, Benndorf A, Unger R, Penz E, Kneschke H, Kossatz K, Dumke R, Hornig U, Kruspe R, Reichel S (1988) Food-web manipulation by enhancement of piscivorous fish stocks: Long-term effects in the hypertrophic Bautzen Reservoir. Limnologica 19:97–110
- Brock TD (1985) A eutrophic lake: Lake Mendota, Wisconsin. Springer-Verlag, New York
- Carpenter SR, Frost TM, Kitchell JF, Kratz TK, Schindler DW, Shearer J, Sprules WG, Vanni MJ, Zimmerman AP (1991) Patterns of primary production

- and herbivory in 25 North American lake ecosystems. In Cole J, Findlay S, Lovett G (eds) Comparative analysis of ecosystems: Patterns, mechanisms and theories, Springer-Verlag, New York, pp 67–96
- Carpenter SR, Kitchell JF (1988) Consumer control of lake productivity. *Bioscience* 38:764–769
- Carpenter SR, Kitchell JF, Hodgson JR (1985) Cascading trophic interactions and lake productivity. *Bioscience* 35:634–639
- Elser JJ, Elser MM, MacKay NA, Carpenter SR (1988) Zooplankton-mediated transitions between N and P-limited algal growth. *Limnol. Oceanogr.* 33:1–14
- Hessen DO (1990) The algal–grazer interface: Competitive feedback mechanisms linked to nutrient cycling. Paper presented at Vth International Ecological Congress, Yokohama, Japan, August 1990
- Lathrop RC (1990) Response of Lake Mendota (Wisconsin, U.S.A.) to decreased phosphorus loadings and the effect on downstream lakes. *Verh. Internat. Verein. Limnol.* 24:457–463
- Lehman JT (1980) Release and cycling of nutrients between planktonic algae and herbivores. *Limnol. Oceanogr.* 25:620–632
- Lehman JT, Sandgren CD (1985) Species-specific rates of growth and grazing loss among freshwater algae. *Limnol. Oceanogr.* 30:34–46
- Leibold MA (1989) Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *Am. Nat.* 134:922–949
- McQueen DJ, Post JR, Mills EL (1986) Trophic relationships in freshwater pelagic ecosystems. *Can. J. Fish. Aquat. Sci.* 43:1571–1581
- Moegenburg SM, Vanni MJ (1991) Nutrient regeneration by zooplankton: Effects on nutrient limitation of phytoplankton in a eutrophic lake. *J. Plankton Res.* 13:573–588.
- Peters RH, Downing JA (1984) Empirical analysis of zooplankton filtering and feeding rates. *Limnol. Oceanogr.* 29:763–784
- Reinertsen H, Jensen A, Koksvik JI, Langeland A, Olsen Y (1990) Effects of fish removal on the limnetic ecosystem of a eutrophic lake. *Can. J. Fish. Aquat. Sci.* 47:166–173
- Reynolds CS (1984a) The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge, England
- Reynolds CS (1984b) Phytoplankton periodicity: The interactions of form, function and environmental variability. *Freshwat. Biol.* 14:111–142
- Roughgarden J, Diamond J (1986) Overview: The role of species interactions in community ecology. In Diamond J, Case TJ (eds) Community ecology, Harper and Row, New York, pp 333–343
- Schindler DW (1977) Evolution of phosphorus limitation in lakes. *Science* 195:260–262
- Smith VH (1983) Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. *Science* 221:669–671
- Sommer U, Gliwicz ZM, Lampert W, Duncan A (1986) The PEG-model of seasonal succession of planktonic events in fresh water. *Arch. Hydrobiol.* 106:433–471
- Sterner RW (1989) The role of grazers in phytoplankton succession. In Sommer U (ed) Plankton ecology—succession in plankton communities, Springer-Verlag, Berlin, pp 107–170

- Sterner RW (1990) The ratio of nitrogen to phosphorus resupplied by herbivores: Zooplankton and the algal competitive arena. *Am. Nat.* 136:209–229
- U.S. Environmental Protection Agency (1979) Methods for chemical analysis of water and wastes. 2nd edn. U.S. EPA Report EPA-600/4-79/020
- Vanni MJ, Findlay DF (1990) Trophic cascades and phytoplankton community structure. *Ecology* 71:921–937
- Vanni MJ, Luecke C, Kitchell J, Allen Y, Temte J, Magnuson JJ (1990a) Effects on lower trophic levels of massive fish mortality. *Nature* 344:333–335
- Vanni MJ, Luecke C, Kitchell JF, Magnuson JJ (1990b) Effects of planktivorous fish mass mortality on the plankton community of Lake Mendota, Wisconsin: Implications for biomanipulation. *Hydrobiologia* 200/201:329–336
- Vanni MJ, Temte J (1990) Seasonal patterns of grazing and nutrient limitation of phytoplankton in a eutrophic lake. *Limnol. Oceanogr.* 35:697–709

# 14

## Interannual Patterns of Planktivory 1987–89: An Analysis of Vertebrate and Invertebrate Planktivores

Chris Luecke, Lars G. Rudstam, and Yvonne Allen

### Introduction

After a period of relative stasis, the crustacean zooplankton of Lake Mendota underwent a pronounced change in species composition between 1987 and 1988 (Lathrop and Carpenter, Ch. 8). This change was concordant with a dramatic die-off of cisco (Vanni et al. 1990; Rudstam et al., Ch. 12), indicating that changes in predation rates on different zooplankton groups may have been responsible for the observed shifts in zooplankton species composition. To determine the degree to which varying predation pressure resulted in changes in zooplankton abundance patterns, we examined the feeding relationships of the dominant zooplanktivores in the pelagic region of the lake and estimated the ability of these predators to regulate the dominant herbivorous zooplankton species. We were interested in determining the relative importance of various predators and in quantifying both interannual and seasonal dynamics of zooplanktivores and their prey.

Our approach was to assess the abundance and feeding habits of vertebrates and invertebrates that were known to consume zooplankton. From these potential zooplanktivores, we identified four species (*Leptodora kindtii*, *Mesocyclops edax*, yellow perch *Perca flavescens*, and cisco *Coregonus artedii*) that were likely to be the main predators on zooplankton in the lake. We estimated consumption rates of these four species, using either feeding experiments or bioenergetics simulations, and compared these population consumption estimates with the population dynamics of the dominant herbivorous zooplankton in the lake.

**Table 14-1.** Relationships used to estimate dry weight ( $\mu\text{g}$ ) of zooplankton from body length ( $L$  in mm). All equations are from Downing and Rigler (1984) except for *Daphnia* which are from Lynch et al. (1986).

Species	Equation
<i>Diaphanosoma</i>	$5.07463 L^{3.0468}$
<i>Bosmina</i>	$15.0533 L^{2.5294}$
<i>Daphnia pulicaria</i>	$10.674 L^{2.093}$
<i>Daphnia galeata</i>	$5.48 L^{2.200}$
Cyclopoda	$7.8279 L^{2.553}$
Calanoida	$3.4740 L^{2.2634}$
Nauplii	$2.0091 L^{0.469}$
<i>Leptodora</i>	$0.43955 L^{2.67}$

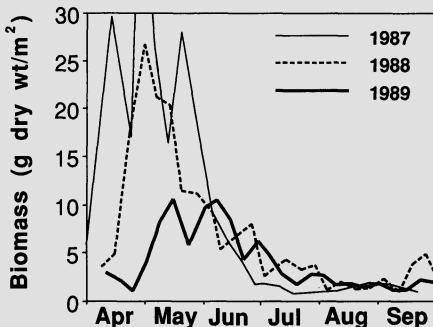
In this chapter we will describe changes in zooplankton species observed from 1987 to 1989, use a population dynamics model to examine the seasonality of birth and death in the dominant daphnid, and examine potential factors that may be responsible for the estimated birth and death rates. We focus on the sources of mortality, examining abundance patterns and feeding habits of the common zooplanktivores. Finally, we compare the rates of daphnid mortality with consumption rates of both vertebrate and invertebrate predators to determine the degree to which each of these predators potentially regulated daphnid abundance in Lake Mendota.

### Zooplankton Changes

Zooplankton were collected at three stations at approximately weekly intervals from April through September in 1987, 1988, and 1989. In this chapter we will examine changes in zooplankton in the pelagic region of the lake by comparing samples collected at the central station (23 m deep). Zooplankton were collected with a 125-mm diameter Clarke–Bumpus sampler equipped with a 130- $\mu\text{m}$  net by taking oblique tows from 20 m depth to the surface in 1989, or by pooling counts from depth-stratified oblique tows in 1987 and 1988. Additional details of the zooplankton collecting techniques can be found in Luecke et al. (1990). Entire zooplankton samples were scanned for rare taxa. Two or three 2% subsamples were enumerated for common taxa. Lengths of the first 30 individuals of a given taxon were measured with an ocular micrometer. Lengths were converted to dry mass using the relationships in Table 14.1.

The abundance and composition of zooplankton taxa in 1987 were similar to those that occurred between 1978 and 1986 (Pedros-Alio and Brock 1985; Lathrop and Carpenter, Ch. 8). Cyclopoid copepods, par-

**Figure 14-1.** Total biomass of zooplankton in Lake Mendota 1987, 1988, and 1989.

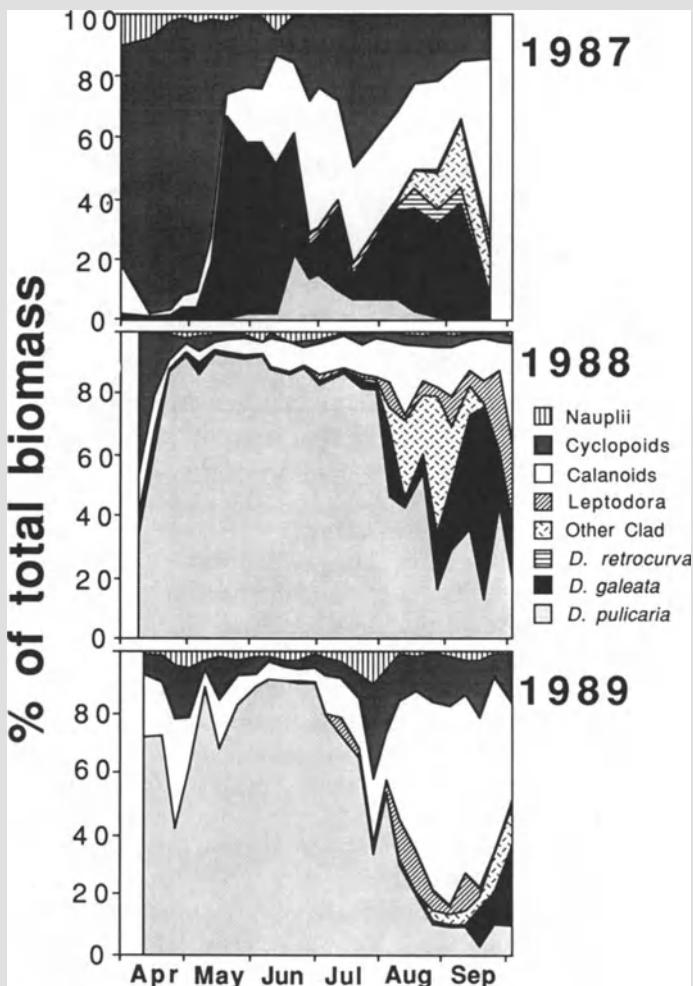


ticularly *Diacyclops thomasi*, dominated the crustacean biomass after ice-out, increased to peak biomass of  $30\text{ g dry weight m}^{-2}$  in early May, and then declined precipitously (Figures 14.1 and 14.2). This decline in *D. thomasi* appears to occur each year in early May and is likely caused by diapausing C-IV individuals (Brock 1985).

The decline in abundance of *D. thomasi* was quickly followed by a rapid increase in the abundance of *Daphnia galeata* in May of 1987. Populations of this cladoceran attained densities of 80 individuals per liter and biomass of  $20\text{ g m}^{-2}$  (Figures 14.1 and 14.2). In early June, abundances of *D. galeata* declined as the biomass of all crustaceans dropped to around  $2\text{ g m}^{-2}$  and remained there for the rest of the summer. From early July through September, the biomass of crustacean zooplankton was dominated by the calanoid copepods *Leptodiaptomus siciloides* and *Skistodiaptomus oregonensis*. The invertebrate planktivores *Leptodora kindtii*, *Mesocyclops edax*, and *Acanthocyclops vernalis* became more numerous during summer months.

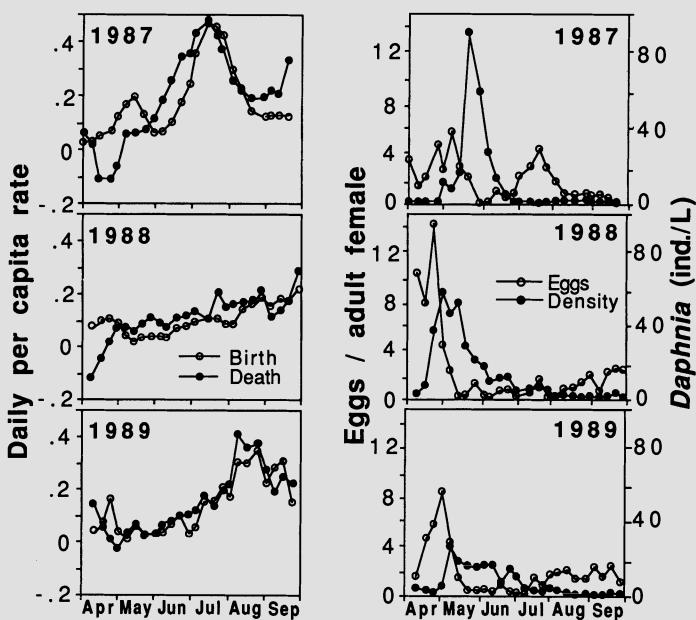
In contrast to the previous decade, the seasonal patterns of zooplankton succession in 1988 differed in two ways (Figure 14.2). First, *Daphnia pulicaria*, rather than *D. galeata*, became very abundant immediately after ice-out in 1988. Second, this large daphnid dominated the crustacean zooplankton throughout most of the spring and summer. In 1988 the biomass of *D. pulicaria* accounted for greater than 70% of crustacean biomass for over 100 days, whereas *D. galeata* accounted for a similar portion of the 1987 biomass for less than 7 days. In spite of the differences in relative biomass, the maximal biomass of both *D. galeata* in 1987 and *D. pulicaria* in 1988 was similar at around  $20\text{ g m}^{-2}$ . As in previous years, other cladocerans became more abundant during the late summer of 1988 (Figure 14.2).

In 1989 *D. pulicaria* again dominated the crustacean zooplankton during spring and summer but was less numerous than in 1988 (Figures 14.1 and 14.2). Maximal biomass attained only  $9\text{ g m}^{-2}$ , and copepod species were relatively more abundant than in the previous year. During September other cladocerans again became more numerous (Figure 14.2).



**Figure 14-2.** Species composition of zooplankton (by biomass) in Lake Mendota 1987, 1988, and 1989.

Analysis of birth and death rates of the dominant daphnid was conducted using an egg ratio analysis (Paloheimo 1974). Weekly changes in densities of the dominant daphnid were used to generate values of  $r$ , the instantaneous rate of increase (Figure 14.3). The number of eggs present in the population and mean temperature occupied by the *Daphnia* species were used to generate a per capita daily birth rate. Per capita daily mortality was derived by subtracting  $r$  from the estimated birth rate. In 1987 and 1989 birth rate was low after ice-out and gradually increased to a per capita rate of  $0.2\text{d}^{-1}$  in May and declined to near zero in June (Figure 14.3). In 1988 the number of eggs in the population and cor-



**Figure 14-3.** Left: Daily per capita birth and death rates of the dominant *Daphnia* species in 1987–89 as calculated using the egg-ratio method presented as a three-point moving average. Right: Density (individuals/L) and number of eggs per adult female of the dominant species of *Daphnia* in 1987–89. *D. galeata* was dominant in 1987, *D. pulicaria* in 1988 and 1989.

respondingly the birth rate were high immediately after ice-out and declined to low values in mid-May. In all three years, the birth rate was highest in late summer owing to faster egg development at relatively high water temperatures. The seasonal pattern of population mortality was similar in all years, with low (or even negative) death rates in early spring followed by increasing mortalities throughout the summer. Maximal per capita death rates occurred in late summer of each year, with estimates of  $0.4 \text{ d}^{-1}$  in 1987 and 1989 and  $0.3 \text{ d}^{-1}$  in 1988.

The differences in birth rates between years were likely due to differences in available food and/or water temperature. The correlation between edible phytoplankton biomass and the number of daphnid eggs per adult female was significant ( $r^2 = 0.301$ ,  $N = 61$ ,  $p < 0.001$ ) if egg ratio was lagged one sampling date (= 1 week) and correlated with  $\log_{10}$  of edible phytoplankton (Figure 14.4). Edible phytoplankton was defined as all phytoplankton excluding Cyanophyta, gelatinous green algae, and *Ceratium*. The direct correlation between edible phytoplankton and egg ratio was not significant ( $r^2 = 0.184$ ,  $N = 62$ ,  $p > 0.05$ ), but Matveev (1986) indicated a 1-week time lag is reasonable in that it takes daphnids several days to transform algal resources into egg production.

The variation in edible phytoplankton explained only 30% of the variation in egg number (Figure 14.4). This relatively weak relationship between egg production and food likely results from at least three circumstances. Different phytoplankton taxa provide different degrees of nutrition for cladocerans. Detrital carbon and bacterial food resources may have contributed to nutrition and subsequent production of daphnid eggs (Stockner and Porter 1989). Also, the presence of inedible filamentous algae may have inhibited the consumption of edible phytoplankton by daphnids (Gliwicz and Lampert 1990).

Differences in the death rates estimated for 1987–89 may be the result of variations in the abundances and feeding habits of predators. Several species that exist in Lake Mendota are known to prey on daphnids. The feeding habits of four predators were examined in detail because of their propensity to consume large numbers of daphnids in other lakes, and their high densities in Lake Mendota. These include two invertebrates, *Leptodora kindtii* and *Mesocyclops edax*, and two fish, perch and cisco.

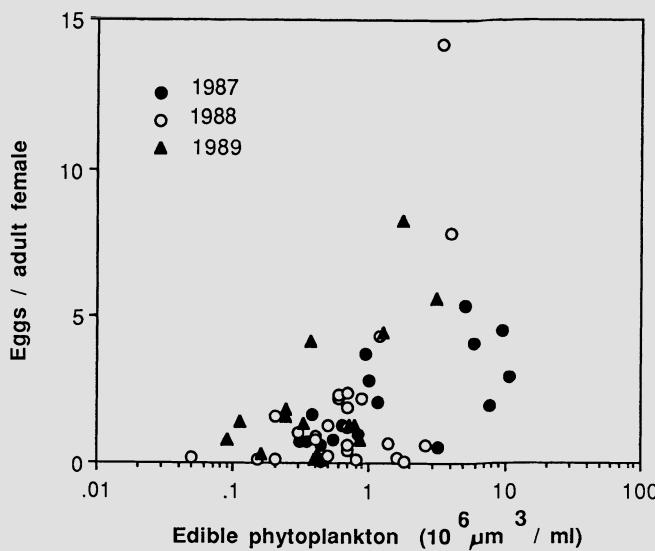
## Invertebrate Planktivores

### *Leptodora*

In 1987 we examined the potential for *Leptodora* to consume daphnids in a series of field predation trials. On four dates between July and September, a known number of adult *Leptodora* were placed in 21-L plastic containers with an ambient mixture of other zooplankton. After 48 h the zooplankton were counted and compared to the number of zooplankton remaining in similar containers with no *Leptodora* present. Differences in the number of different zooplankton taxa were attributed to predation by *Leptodora*. Details of these experiments can be found in Lunte and Luecke (1990).

Results of these experiments indicated that *Leptodora* consumed daphnids under a variety of conditions and consumed both *D. galeata* and *D. pulicaria*. The presence of *Leptodora* significantly reduced the abundance of four of the five cladocerans examined. The presence of *Leptodora* had no detectable effect on the abundance of cyclopoid or calanoid copepodites, but the rotifer *Conochilus* sp. decreased in containers with *Leptodora*. In these experiments *Leptodora* consumed both large and small daphnids. *Leptodora* was observed feeding on a 2.0-mm *D. pulicaria* in a laboratory feeding trial.

During these experiments, *Leptodora* fed on an average of 1.6 daphnids  $d^{-1}$  and exhibited an average clearance rate of  $0.088\text{ L} d^{-1}$  for daphnids (Table 14.2). Larger *Leptodora* had higher feeding rates than did small individuals. We generated an estimate of mortality of daphnids resulting from *Leptodora* by multiplying the density of *Leptodora*



**Figure 14-4.** Number of eggs per adult female of the dominant *Daphnia* plotted against the volume of edible phytoplankton present in the previous sample from 1987–89.

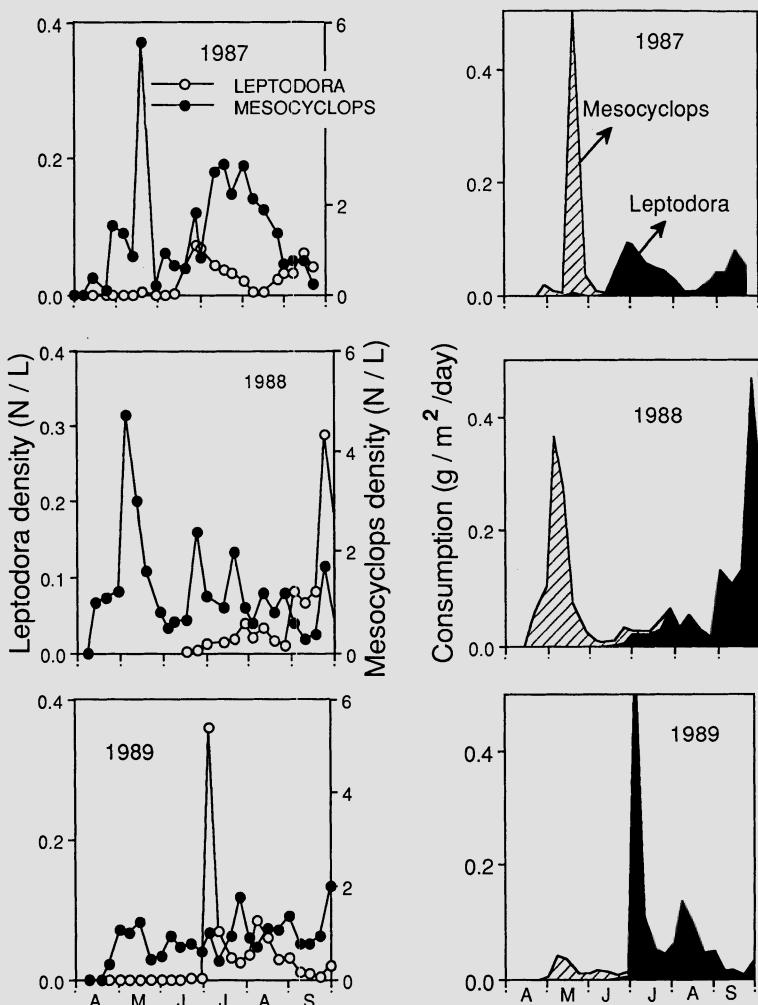
**Table 14-2.** Comparison of initial *Daphnia* density, *Leptodora* density, feeding rate (*N* prey/predator/d) and clearance rate (L/predator/d) derived from *Leptodora* field experiment conducted in August and September 1987.

Density			
<i>Daphnia</i>	<i>Leptodora</i>	Feeding rate	Clearance rate
36.6	1.2	2.3	0.063
18.5	1.4	1.6	0.086
18.5	1.7	2.1	0.114
4.5	1.8	0.39	0.087

by the average clearance rate and the density of daphnids in the water column. *Leptodora* was not present in the water column until June of each year (Figure 14.5), exhibiting peaks in biomass in July and again in September. Estimated *Leptodora* predation on daphnids was greatest in July and September. Rates of predation were greater in 1988 and 1989 than in 1987 when planktivorous fish abundance was high (Figure 14.5).

### Mesocyclops

Predation on daphnids by *Mesocyclops* was estimated using laboratory predation trials conducted in 0.47-L glass containers during the summer



**Figure 14-5.** Left: Density of *Leptodora* and *Mesocyclops* (*N/L*) in the water column at the main sampling station in 1987–89. Right: Potential predation on *Daphnia* by *Leptodora* and *Mesocyclops* in 1987–89. Mean clearance rates for *Leptodora* (0.088 L/predator/d) and *Mesocyclops* (0.014 L/predator/d) were multiplied by densities of *Daphnia* and the predator to generate potential predation estimates.

of 1989. In each of 10 containers, 30 neonate *D. galeata* and 30 neonate *D. pulicaria* were placed along with a mixture of green algae. Twenty adult *Mesocyclops*, which had been starved for 24 h, were added to half of the containers. The trials ran for 24 h. Predation rates were calculated by comparison of the number of daphnids remaining in predator and

predator-free containers. Clearance rates ( $L$  predator $^{-1}$  d $^{-1}$ ) were calculated according to Dodson (1975).

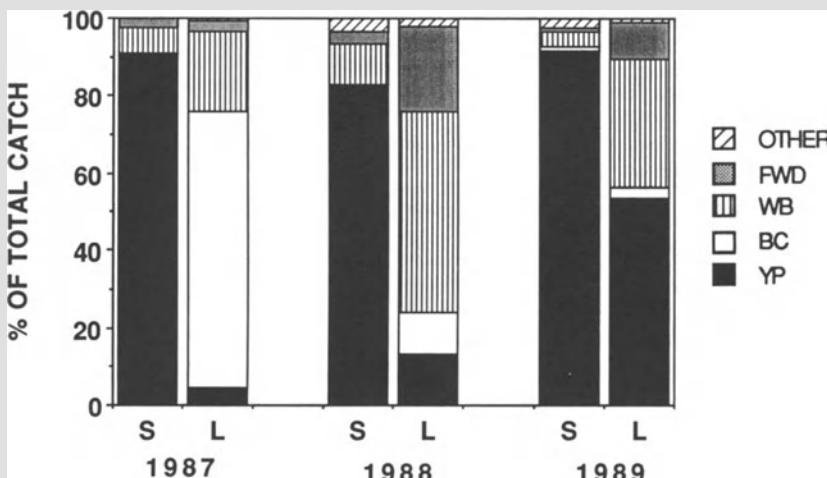
Results from these experiments indicated that individual *Mesocyclops* consumed 0.71 prey d $^{-1}$  and exhibited an average clearance rate of 0.0141 L d $^{-1}$ . No preference for either species of *Daphnia* was observed. Potential mortality on daphnids by *Mesocyclops* was calculated as for *Leptodora*. The clearance rates found in our experiments are similar to those reported by Schoeneck et al. (1990) for *Mesocyclops* feeding on small daphnids. Brandl and Fernando (1974, 1978) reported that cyclopoid copepods fed on small cladocerans at rates between 0.4 and 1.5 prey predator $^{-1}$  d $^{-1}$ .

Potential predation on *Daphnia* by *Mesocyclops* was higher than estimated predation by *Leptodora* in 1987 and 1988 (Figure 14.5). In 1989 daphnid mortality owing to these two invertebrates was similar except for one date when *Leptodora* were very abundant in zooplankton samples. The timing of potential predation impacts from these two invertebrates was similar in all three years (Figure 14.5). *Mesocyclops* predation peaked each spring when *Mesocyclops* abundance exceeded 1.0 L $^{-1}$ . During this period, abundance of *Daphnia* was also high, suggesting that *Mesocyclops* did not tightly regulate abundance patterns of daphnids in Lake Mendota. Predation by *Leptodora* peaked in late summer and fall when daphnid abundances were low.

## Vertebrate Planktivores

Relative abundances and diets of pelagic planktivorous fish were determined from samples taken in gill nets. A series of eight vertical gill nets (3 m wide, mesh sizes 19, 25, 32, 38, 51, 64, 89, and 127 mm stretch) were set at the central sampling station at monthly intervals during the period from April to September 1987–89. The nets were extended from the surface to the sediments (23 m depth) and generally set for 12 or 24 h. Additional details of the gill-netting methods can be found in Luecke et al. (1990).

A number of planktivorous fish species were captured in gill nets in the pelagic region of Lake Mendota. The catch of small planktivores (<250 mm) was dominated by yellow perch in all years (Figure 14.6). Small numbers of white bass, black crappie, and freshwater drum were also captured. The composition of larger planktivores (>250 mm) changed dramatically after the cisco die-off in the summer of 1987 (Figure 14.6). Cisco accounted for greater than 80% of the large planktivores caught in the early part of 1987 but less than 10% of the catch during 1988 and 1989. The catch of cisco declined from 1.27 to 0.044 fish set $^{-1}$  h $^{-1}$  during that period.

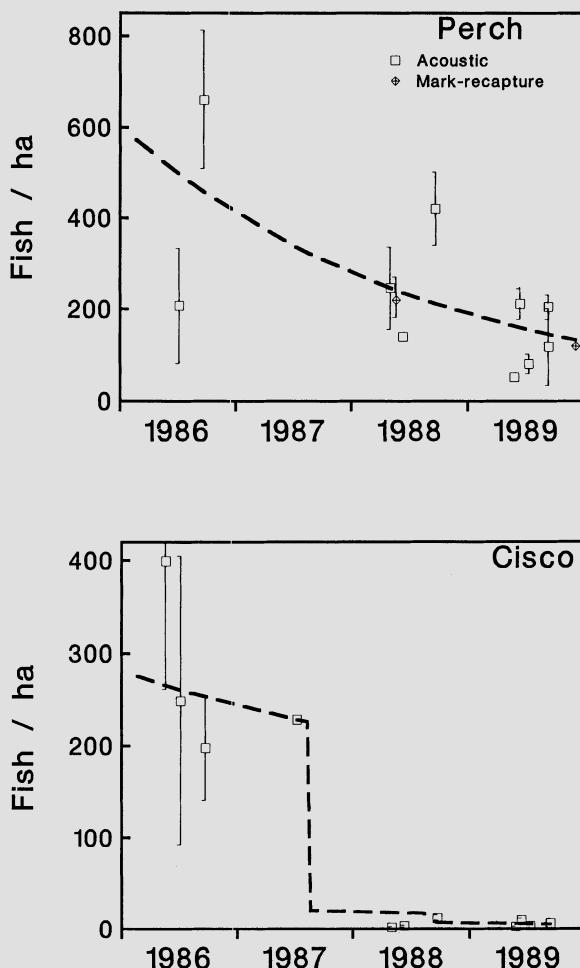


**Figure 14-6.** Species composition of small (S, less than 250 mm) and large (L, over 250 mm) fish in gill net catches from 1987, 1988, and 1989. Nets were set approximately monthly from April through September in all three years. FWD, Freshwater drum; WB, white bass; BC, black crappie; YP, yellow perch.

### Abundance Patterns

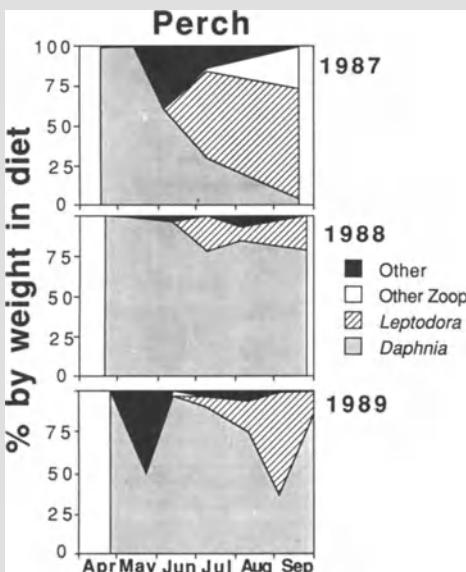
Total abundance of pelagic fishes was estimated using day and night hydroacoustics surveys with a 70-kHz echosounder (Rudstam and Johnson, Ch. 26). We include information from 1986 because of instrument problems in 1987. In all four years we surveyed one south–north transect and one east–west transect. These transects were duplicated in 1986 and 1987. In 1988–89 we surveyed additional transects following a zigzag pattern across the lake instead of repeating the same transects (Rudstam and Johnson, Ch. 26). The total amount of data corresponded to 3.5 to 4 h of recordings and a survey length of approximately 30 km in all four years. Estimates of variance were obtained by analyzing the total dataset over distances of 6–8 km, yielding three to four estimates of fish abundances in the lake for each sampling occasion. Water depths shallower than 5 m were not sampled.

The acoustic signals were converted to fish abundances using analysis of echo peaks from single fish echoes. The 1987 data were analyzed using the deconvolution method (Clay 1983; Rudstam et al. 1987). The 1986, 1988, and 1989 data were analyzed using the HADAS program (Lindem 1983). These two methods give the same fish abundances for fish densities below 8,000 fish ha<sup>-1</sup> (Rudstam et al. 1988). Both methods yield a distribution of target strengths that can be used to determine the abundance of different size groups (Lindem and Sandlund 1984; Rudstam et al. 1987). For Lake Mendota, we chose two size groups: (1) fish larger than



**Figure 14-7.** Abundance of perch and cisco from acoustic surveys in 1986 through 1989. Bars are 2 SE calculated from dividing the 30-km acoustic survey into four parts (6–8 km long). A population estimate for adult perch obtained with mark-recapture in 1988 and a population estimate based on this mark-recapture estimate and harvests (from creel surveys) for the end of 1989 are included in the perch graph. The line represents the assumed development of perch and cisco populations used in the bioenergetics calculations.

25 cm (targets larger than  $-40$  dB, primarily cisco before the 1987 summer kill and cisco, larger perch, white bass, and drum after the summer kill); (2) fish between 12 and 25 cm (targets between  $-46$  and  $-40$  dB, primarily perch). Depth from the surface to 2 or 3 m depth (depending on weather conditions) cannot be sampled with acoustics, and this layer is not included in our estimates. However, few fish were caught in the top



**Figure 14-8.** Seasonal changes in the diet of yellow perch collected in vertical gill nets at the central sampling station 1987–89.

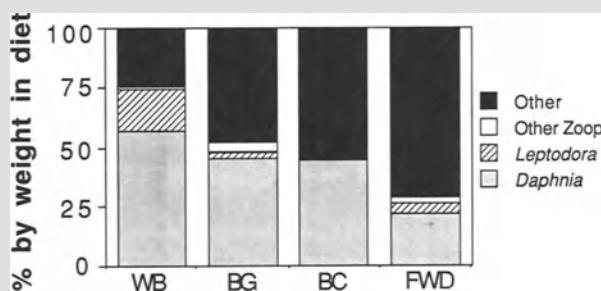
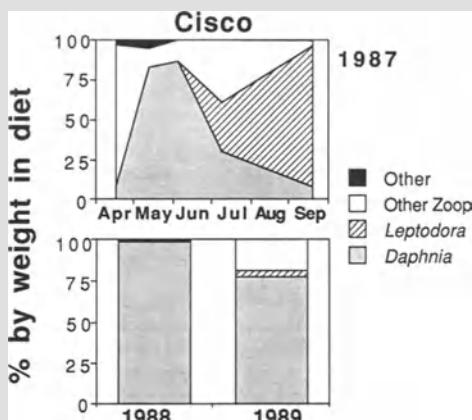
3 m in the vertical gill nets in 1987 to 1989. We used both day and night surveys for the larger fish (cisco) and only day surveys for the medium-size fish (perch). See Rudstam and Johnson (Ch. 26) for an elaboration of the acoustic methods and for solutions to lake-specific sampling problems.

Estimates of the abundance of cisco from these surveys indicated that the summer kill resulted in a 90% reduction of the cisco population (Figure 14.7). Densities of cisco declined from over 200 fish  $\text{ha}^{-1}$  in 1986 and early 1987 to less than 5 fish  $\text{ha}^{-1}$  in 1989. Hydroacoustics surveys also indicated that the abundance of perch declined over that same period (Figure 14.7). Densities of perch declined from 500 to 100 fish  $\text{ha}^{-1}$  from 1986 to 1989. These acoustic density estimates for perch agree well with a population estimate of yellow perch conducted in 1988 and with a calculated decrease in the perch population from fishing (creel survey results) through 1989 (Figure 14.7; Rudstam and Johnson, Ch. 26).

### Feeding Habits

The feeding habits of fish collected in vertical gill nets indicated that the diets of most species consisted primarily of zooplankton, with the exception of freshwater drum, which fed primarily on benthic invertebrates (Figures 14.8–10). Over 50% of the diets of the other fishes were composed of daphnids and *Leptodora*. We examined the diets of perch and cisco in more detail, given the high relative abundance and/or biomass of these two species in gill net catches.

**Figure 14-9.** Diet composition of cisco collected in vertical gill nets at the central sampling station 1987–89. Too few fish were collected in 1988 and 1989 to assess seasonal changes.



**Figure 14-10.** Diet composition of other planktivores collected in vertical gill nets at the central sampling station 1987–89. WB, White bass; BG, bluegill; BC, black crappie; FWD, freshwater drum.

Perch diets consisted almost entirely of *Daphnia* in the spring of 1987, when the abundance of *D. galeata* in the water column was high. After *D. galeata* declined and *Leptodora* became present, perch fed mainly on *Leptodora* (Figure 14.8). In 1988 and 1989, when the larger *D. pulicaria* was relatively common throughout the stratified season, perch fed predominantly on this species (Figure 14.8). Although the abundance of *Leptodora* was similar in all three years, the proportion of *Leptodora* in the diet of perch was lower in 1988 and 1989.

The feeding habits of cisco exhibited the same general trend as perch in 1987, in that daphnids were fed on extensively in spring, but *Leptodora* contributed a large portion of the diet in summer and fall (Figure 14.9). Cisco made more extensive use of copepods and smaller cladocerans than did perch. The number of cisco captured in 1988 and 1989 was small, but stomach contents suggest that the diet of cisco consisted mostly of *D. pulicaria* in these years.

**Table 14-3.** Mean standardized forage ratio for yellow perch in 1987–89 and cisco in 1987. *Leptodora* was not present in water column samples collected in April and May. Prey types: D, *Daphnia*; L, *Leptodora*; C, copepod. Between two and four sampling dates were pooled to generate the ratio. The value for neutral selection is 0.5 for April–May and 0.33 for June–September.

	April–May			June–Sept.		
	D	L	C	D	L	C
1987						
Perch	0.99	–	0.01	0.07	0.93	0
Cisco	0.91	–	0.09	0.33	0.62	0.05
1988						
Perch	0.99	–	0.01	0.33	0.67	0
1989						
Perch	0.90	–	0.01	0.46	0.54	0

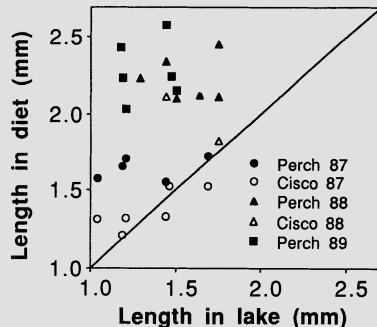
Both perch and cisco selectively consumed larger zooplankton species. Perch were more selective planktivores than cisco in terms of both size and species of zooplankton consumed. Standardized forage ratios (SFR, Chesson 1983) were calculated for perch and cisco from the numbers of each zooplankton species in stomach and lake samples (Table 14.3). Perch exhibited a consistently higher SFR for *Leptodora* and daphnids than did cisco. As the mean length of daphnids in the lake increased from 1987 to 1989, the SFR of perch for daphnids increased. In 1989, the year with the largest daphnids, perch SFRs were similar for *Daphnia* and *Leptodora*.

Perch selectively consumed the larger size classes of daphnids in the lake, whereas cisco exhibited no selection for larger individuals (Figure 14.11). An analysis of covariance (ANCOVA) of mean daphnid length in stomachs of these two species, using mean length of daphnids in the lake as a covariate, indicated that perch consumed larger daphnids than did cisco ( $F_{1,22} = 17.6$ ,  $p < 0.001$ ).

### Energetics Simulations

The consumption dynamics of perch and cisco were investigated using bioenergetics models. These models can be used to calculate the consumption rates necessary to account for observed growth, and they require input of fish growth, occupied temperature, diet, and energetic content of fish and their prey (Hewett and Johnson 1987). For perch we used the model developed by Kitchell et al. (1977), and for cisco we used a model developed for bloater (*Coregonus hoyi*) in Lake Michigan (Table 14.4; Rudstam et al., in prep). The perch were modeled as four separate

**Figure 14-11.** Mean length of *Daphnia* in the lake and in stomach contents of perch and cisco in 1987–89. The diagonal line represents the 1:1 relationship indicating no size selectivity.



**Table 14-4.** Parameter values for the coregonid model used to calculate cisco consumption in Lake Mendota (Rudstam et al., in prep). The equation for temperature dependence of maximum consumption follows Kitchell et al. (1977). Consumption parameters are based on experiments with bloater, metabolism parameters on experiments with whitefish (*Coregonus clupeaformis*) by Bernatchez and Dodson (1985), swimming speed parameters on Rudstam et al. (1984), excretion on Guissani and DeBernardi (1977) and Rösch (1985), and egestion on Stewart and Binkowski (1986). The specifics of these equations and of the bioenergetics approach in general are discussed in detail by Kitchell (1983) and Hewett and Johnson (1987).

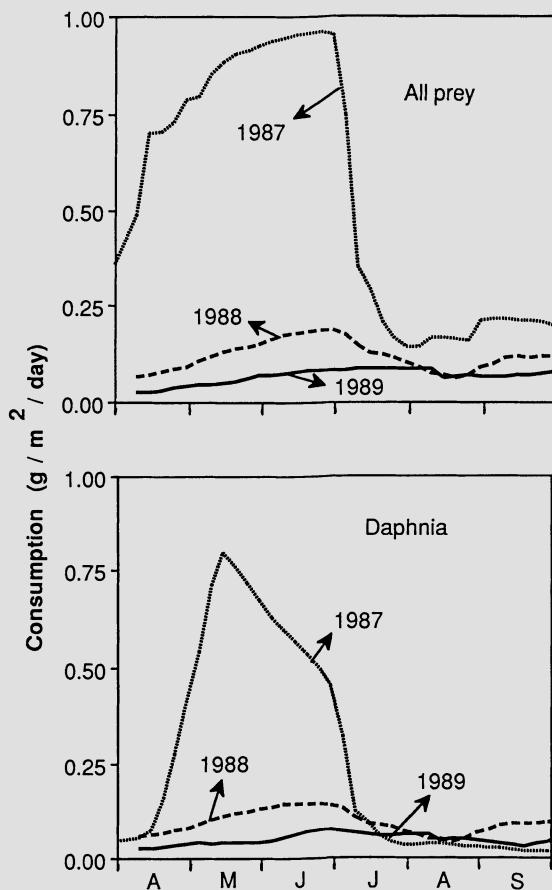
Symbol	Parameter description	Value
Consumption, $C$ ; $C = P \cdot a \cdot W^b \cdot f(T)$		
$P$	Fitted parameter	
$a$	Intercept: $C$ at $T_{\text{opt}}$	1.57
$b$	Coefficient: $C$ versus weight	-0.523
$T_{\text{opt}}$	Optimum temperature: $C$ (°C)	15.8
$T_{\text{max}}$	Maximum temperature: $C$ (°C)	26
$Q$	Slope for temperature dependence: $C$	4.04
$W$	Weight in grams	
Metabolism, $R$ ; $R = \alpha \cdot W^\beta \cdot \exp(\gamma \cdot T) \cdot \exp(n \cdot U)$ ; SDA = SDA( $C - F$ )		
$\alpha$	Intercept: $R$	0.0018
$\beta$	Coefficient: $R$ versus weight	-0.12
$\gamma$	Coefficient: $R$ versus temperature	0.047
$n$	Coefficient: $R$ versus swimming speed	0.025
SDA	Coefficient: specific dynamic action	0.17
Swimming speed, $U$ ; $U = w \cdot W^\delta$		
$w$	Intercept: $U$ (in cm/s)	7.09
$\delta$	Coefficient: $U$ versus weight	0.25
Egestion and excretion, $F$ and $E$ ; $E/F = f \cdot C$ ; $E = \epsilon(C - F)$		
$f$	Proportion of consumed food egested	0.25
$\epsilon$	Proportion of assimilated food excreted	0.10

**Table 14-5.** Cohort structure and weight change of perch and cisco in Lake Mendota between 1987 and 1989. These data were used in bioenergetic simulations of planktivory by perch and cisco from 1 May to 1 October each year.

Age class	I+	II+	III+	IV+ & older
<i>Age structure (%)</i>				
Perch	1987	2	63	22
	1988	26	16	49
	1989	2	8	36
Cisco	1987–89			55
				100
<i>Change in weight (g)</i>				
Perch	1987	12–72	56–109	120–140
	1988	13–82	72–118	109–152
	1989	13–52	82–125	118–139
Cisco	1987			150–173
	1988			140–157
	1989			152–172
				600–630
				630–750
				750–820

age classes (age 1 to 4); cisco were considered one age class, as the majority of the fish were from the 1977 cohort (Rudstam et al., Ch. 12). Fish diet and abundance have been presented above. Occupied temperatures were assumed to be the closest water temperatures to the respective preference temperature of cisco ( $16^{\circ}\text{C}$ ) and perch ( $23^{\circ}\text{C}$ ) available (oxygen content above 4 ppm). This simple assumption yielded similar temperatures to the temperature of the median distribution of respective species in vertical gill nets. Growth was calculated as the average size of a cohort in the September and May gill net samples (Table 14.5). Age of the fish was based on scale readings. Energy content of the fish was obtained from bomb calorimetry. Five perch caught in November 1987 had energy contents of  $1,180 \text{ cal g}^{-1}$  wet weight ( $\text{SE} = 37$ ). The energy content of cisco decreased from  $2,125 \text{ cal g}^{-1}$  wet weight ( $\text{SE} = 53, N = 5$ ) for fish caught 21 August 1987, to  $1,818 \text{ cal g}^{-1}$  wet weight ( $\text{SE} = 65, N = 8$ ) for fish caught in the middle of September and beginning of December 1987. The fish also lost weight during August 1987, probably as a result of high temperatures. Only one simulation was used for the period April through October. The resulting seasonal growth trajectories of cisco and perch were comparable to the observed changes in weight obtained from monthly gill net samples.

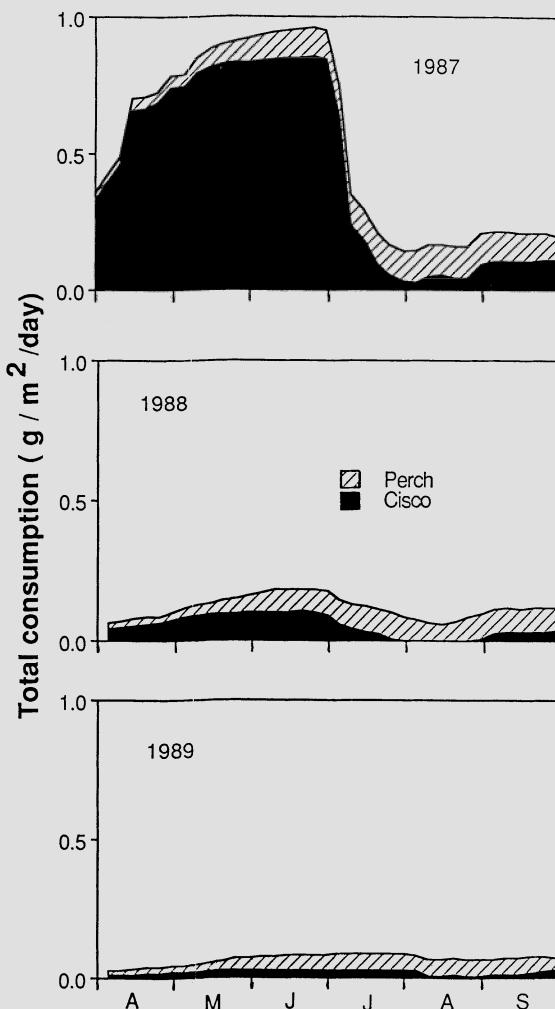
The total consumption of all prey by perch and cisco in 1987 was approximately five times as great as in 1988, and 10 times the values for 1989 (Figure 14.12). This change results almost entirely from the catastrophic die-off of cisco that occurred in late August of 1987. The reduction in cisco abundance resulted in a qualitative shift in the species



**Figure 14-12.** Top: Total consumption of all prey by perch and cisco in 1987–89 as estimated from bioenergetics analyses. Bottom: Consumption of *Daphnia* by perch and cisco in 1987–89.

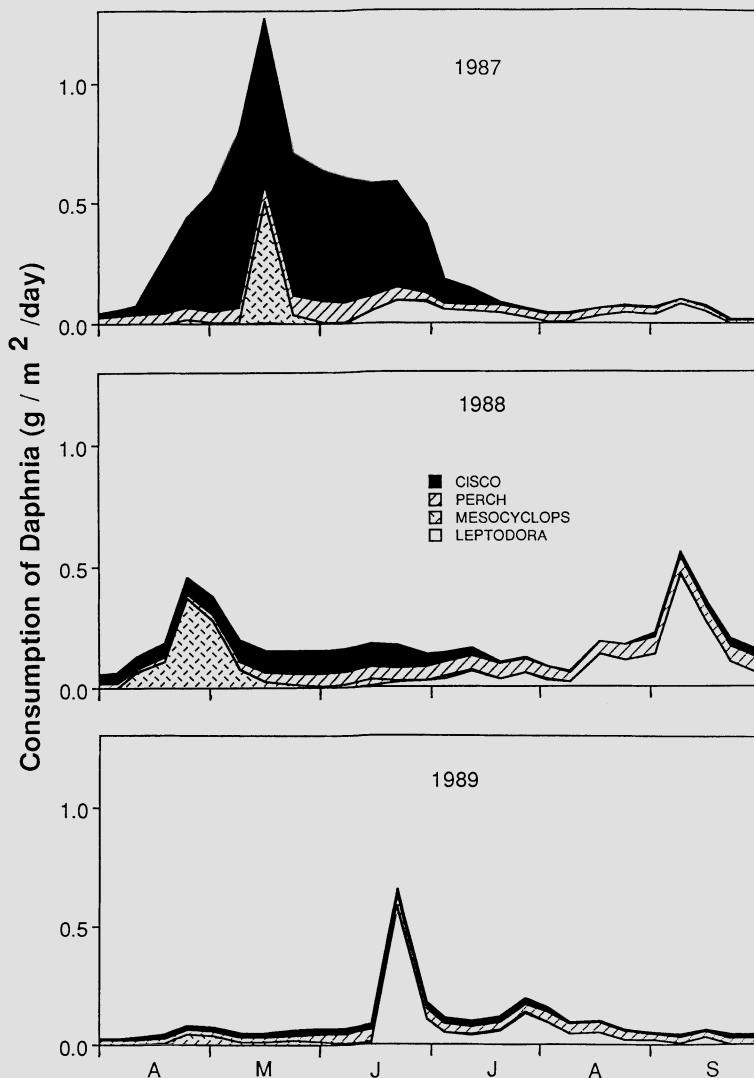
of planktivores responsible for zooplankton consumption. In 1987 consumption by perch accounted for less than 30% of estimated fish consumption, but that proportion increased to over 90% by 1989 (Figure 14.13).

These qualitative changes in the composition of planktivorous fish resulted in pronounced differences in the intraannual patterns of zooplankton consumption (Figure 14.14). These intraannual differences result from the temperature dependence of the consumption dynamics of perch and cisco; perch exhibit maximal consumption at 23°C (Kitchell et al. 1977) and coregonids at 16°C (Table 14.4). Coregonid consumption at low temperatures is also relatively high.



**Figure 14-13.** Seasonal consumption patterns of perch and cisco in 1987–89. All prey types are included.

In 1987 consumption by cisco increased with temperature in spring and peaked when temperatures reached 16°C in early June. As oxygen content became depleted in deep, cooler waters, cisco were forced to move into the epilimnion where temperatures exceeded 20°C. At these higher temperatures cisco consumption was greatly reduced (Figure 14.13). In 1988 and 1989, when perch were the dominant planktivorous fish, seasonal changes in total consumption were reduced. Total consumption of zooplankton by perch and cisco increased as the lake warmed



**Figure 14-14.** Consumption of *Daphnia* by perch, cisco, *Leptodora*, and *Mesocyclops* in 1987–89.

in spring, but no large reduction in consumption was noted during midsummer.

Between-year differences in *Daphnia* consumption follow consumption patterns of all zooplankton (Figure 14.12). Energetics analyses indicated that many more daphnids were consumed in 1987 than in 1988 and 1989. Differences in intraannual patterns of daphnid consumption among years

are also apparent. In 1987 seasonal variations in daphnid consumption were especially pronounced, in that both perch and cisco fed extensively on *Leptodora* once this large invertebrate appeared in the water column. In 1988 and 1989 the abundance of *D. pulicaria* remained relatively high throughout the summer, allowing planktivorous fish to continue feeding on this species while feeding less frequently on *Leptodora*.

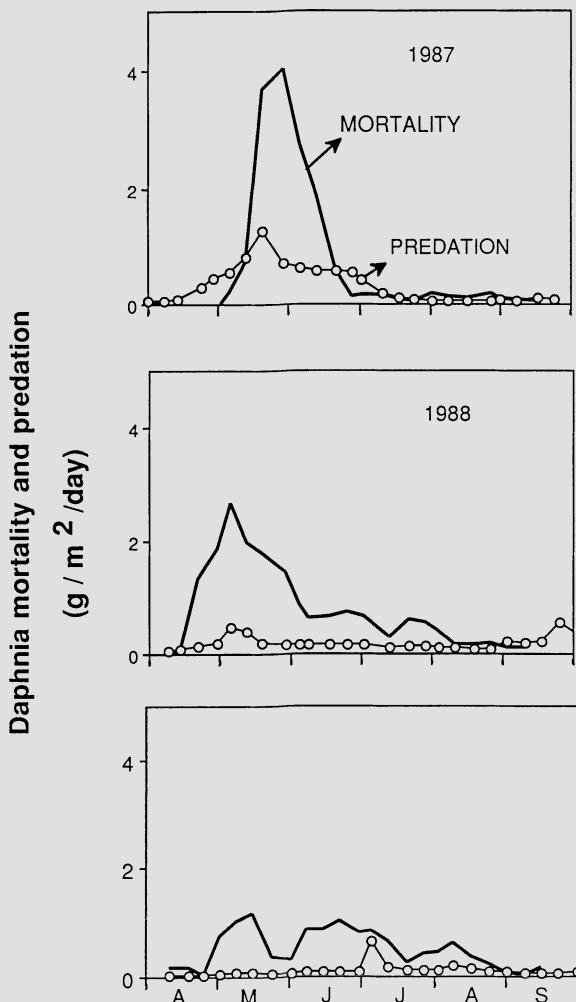
### Comparison of Fish and Invertebrate Planktivory

By combining results from the bioenergetics analysis with our extrapolations of feeding experiments using *Leptodora* and *Mesocyclops*, we can compare the relative importance of these vertebrate and invertebrate predators to daphnid population dynamics (Figure 14.14). In 1987 planktivorous fish dominated the consumption of daphnids, accounting for 50–95% of estimated total consumption throughout most of the year. In 1988 and 1989 the reduction in cisco abundance resulted in lower overall consumption estimates as well as a change in the relative importance of the invertebrate predators. In 1988 invertebrate planktivores dominated the consumption patterns in spring, whereas consumption by fish was more important during summer months. In 1989 the further reductions in perch and cisco abundance allowed the invertebrate planktivores to account for most of the daphnid consumption from May to September (Figure 14.14).

### Comparison of Daphnid Mortality and Planktivore Consumption

The egg-ratio population analysis provides an estimate of total daphnid mortality which can be compared to estimates of daphnid consumption by vertebrate and invertebrate predators. The egg-ratio analysis does not allow estimates of size-specific mortality of *Daphnia*. We know from analysis of fish stomachs that the planktivorous fish fed selectively on large daphnids. Our comparison of daphnid mortality with consumption of daphnids assumes that all predators consumed daphnids of the mean body length present in the lake at any given time period. Estimations of the errors associated with our estimates of predator consumption are likely to be closely related to the degree of error associated with the estimation of abundances of fish and invertebrate planktivores. Our acoustics estimates have a precision of  $\pm 30\%$  and our estimates of invertebrate abundance have a precision of  $\pm 20\%$  (Luecke et al. 1990).

Our analyses indicated that combined predation by fish and invertebrates on daphnids declined about eightfold from 1987 to 1989 (Figure 14.14). When these summed predation rates are compared to estimates of



**Figure 14-15.** Comparison of estimated consumption (predation) by fish and invertebrate predators with estimated total mortality of the dominant *Daphnia* species in 1987–89.

total mortality of the daphnid populations as measured using egg-ratio analyses (Figure 14.15), two conclusions emerge. First, the ability of estimated predation to account for the observed daphnid mortality varies considerably from year to year. Second, a large proportion of total daphnia mortality in each year is not accounted for in our analysis of the four most important predators.

The year-to-year differences in the degree to which predation appears to explain daphnid mortality are striking. In 1987 estimated predation

accounted for almost all observed mortality in April, July, August, and September. In 1988 and 1989, September is the only month in which predation accounts for such a high degree of total daphnid mortality. Tenfold decreases in consumption of daphnids by cisco in April in 1988 and 1989 likely account for the changes in total abundance, the timing of peak abundance, and the species composition of *Daphnia* of 1987–89 (Figure 14.15). The consumption dynamics of this cold-water planktivore appear crucial in establishing spring zooplankton assemblages. The relatively high consumption rate of cisco at temperatures present just after ice-out appears to preclude the immediate population expansion of *Daphnia* in years when cisco are abundant (1987, for example). The high level of spring consumption in 1987 likely delayed the expansion of *D. galeata* until warmer temperatures allowed daphnid birth rates to climb. The reduced spring fish planktivory in 1988 and 1989 allowed *D. pulicaria* to become abundant more rapidly. The dominance of *D. galeata* in 1987 likely resulted from the earlier age at first reproduction exhibited by this species and the fitness advantage accrued from this trait (Taylor 1980). The dominance of *D. pulicaria* in 1988 and 1989 likely resulted from potential competitive superiority (Lynch et al. 1986; Leibold 1989) under conditions of low mortality from predators. Our zooplankton samples from 1990 indicate that at ice-out, *D. pulicaria* was producing four times as many eggs per adult female as *D. galeata*. Also, the lower food threshold of *D. pulicaria* (Gliwicz and Lampert 1990) allows this species to survive during the clear-water phase when food resources become scarce. In addition to these arguments, paleoecological analyses (Kitchell and Sanford, Ch. 4), historical records (Lathrop and Carpenter, Ch. 8), and simulation modeling (Luecke et al., Ch. 20) strongly suggest that the abundance of cisco regulates the species composition of daphnids in Lake Mendota.

The late-summer increase in the degree to which predators account for the mortality patterns of *Daphnia* in all three years suggests that these predators tightly regulate daphnid populations during this period. In fact, cladoceran assemblages typically become much more diverse in late summer, including a variety of small-bodied and/or evasive species (Lathrop and Carpenter, Ch. 8).

Mortality that cannot be accounted for with our estimates of predation likely results from several sources. Other species of planktivorous fish and invertebrates, although small in number, do consume daphnids and could account for a small portion of the observed mortality. The seasonal pattern of this additional mortality, however, argues against the importance of supplementary planktivores, which are relatively rare. In 1987 this unaccounted-for mortality occurred almost entirely during the end of the clear-water phase when food resources were extremely low. Luecke et al. (1990) concluded that starvation was the most likely cause of

the high mortalities of *D. galeata* observed in that year. Low food levels (Lampert and Schober 1980) may also have contributed to the unaccounted-for mortality during 1988 and 1989. Threlkeld (1985) and Hovenkamp (1990) indicate that starvation can be an important source of mortality for cladocerans in lakes. Gilbert (1990) reports that the presence of Cyanophyta can result in direct mortality of daphnids. Also, few daphnids are known to survive longer than 30 days at summer epilimnetic temperatures (McCauley et al. 1990). The reduced number of predators in 1988 and 1989 may have allowed a higher portion of daphnids to senesce during the summers of these two years.

## General Discussion

The interannual variation in total zooplankton consumption, and specifically in the consumption of *Daphnia*, closely followed the observed variation in planktivorous fish biomass from 1987 to 1989. Interestingly, compensatory changes in the behavior or production of planktivores in Lake Mendota did not negate the impacts of the cisco die-off, as has been suggested by some authors (Benndorf 1987; Vadas 1989). At least three mechanisms could compensate for reduced consumption of *Daphnia* resulting from the catastrophic reduction of cisco in Lake Mendota: (1) the diets of the remaining fishes could shift toward greater dominance of daphnids (DeBernardi and Giussani 1975); (2) increased growth and production of remaining fishes could occur, amplifying existing feeding habits (Gophen and Pollingher 1985); (3) increases in abundance of other planktivores could augment consumption of daphnids (Langeland 1982; Benndorf et al. 1988).

Each of these three mechanisms appears to have occurred in Lake Mendota in 1988 and 1989, but only to a limited degree. The proportion of *Daphnia* in the diets of perch and remaining cisco increased, particularly in summer months. This increased feeding on *Daphnia* resulted in similar estimates of daphnid consumption by fish in late summer and fall of each year. The growth rates of different cohorts of perch increased only slightly in 1988 and 1989, and bioenergetics analyses indicate that these small increases in growth resulted in small increases in individual consumption of *Daphnia*. Also, the greater food availability for planktivorous fishes in 1988 did not allow strong year-class formation for any of the species. In 1989 larval density of several species of fish was greater than in 1988 (Post et al., Ch. 15). Interestingly, this increased abundance of larvae did not result in major changes in zooplankton species composition. Finally, although the relative importance of invertebrate planktivores increased after the cisco mortality, the absolute abundance of *Leptodora* and *Mesocyclops* increased only slightly in 1988

and 1989. Results from modeling simulations (Luecke et al., Ch. 20) and other studies (Benndorf 1988) suggest that this third mechanism can be important and may become more prominent in future years.

As the piscivore enhancement continues into the 1990s, the potential for these compensatory mechanisms to moderate the changes in zooplanktivory observed during 1987–89 will increase (Reinertsen and Langeland 1982). Continued examination of food web structure will be fruitful, particularly in three areas. (1) The ability of stocked piscivores to reduce recruitment of planktivorous fish remains unknown. Strong recruitment events appear to be uncommon among Lake Mendota fishes. The most recent strong recruitment years were 1977 for cisco and 1985 for perch. We do not currently know how growth and survivorship of a large young-of-year (YOY) cohort would fare under conditions of both high levels of daphnid food resources and high levels of piscivory (Post and Rudstam, Ch. 19), and it may take a number of years before the appropriate sequence of events occurs. (2) Species of invertebrate planktivores that currently are not present or present at low levels could become abundant and exert stronger control of zooplankton populations. *Chaoborus punctipennis* is presently rare in Lake Mendota but occurred in large numbers in the 1940s (Lathrop, Ch. 10). Chaoborids are known to influence zooplankton species composition (Pastorok 1980; Luecke and Litt 1987). (3) Finally, if levels of planktivory remain similar to levels observed in 1988 and 1989, the year-to-year variation in nutrient input will allow evaluation of the effects of resources on determining species composition and abundance patterns of zooplankton populations in Lake Mendota.

**Acknowledgments.** We thank Lance Gardner, Steve Anglea, Paul Jacobson, Denise Schael, Terry Schenk, Cindy Lunte, and Stan Dodson for helping with field collections and experiments. Peter Leavitt, Mike Vanni, and John Post provided many helpful suggestions on earlier drafts of the manuscript. This study was supported by the Federal Aid in Sport Fish Restoration Act under Project F-95-P, The WDNR, and the Swedish Forestry and Agricultural Research Council (to L.G.R.).

## References

- Benndorf J (1987) Food web manipulation without nutrient control: A useful strategy in lake restoration? Schweiz. A. Hydrobiol. 49:237–248
- Benndorf J, Schultz H, Benndorf A, Unger R, Penz E, Kneschke H, Kossatz K, Dumke R, Hornig U, Kruspe R, Reichel S (1988) Food-web manipulation by enhancement of piscivorous fish stocks: Long-term effects in the hypereutrophic Bautzen Reservoir. Limnologica 19:97–110

- Bernatchez L, Dodson JJ (1985) Influence of temperature and current speed on the swimming capacity of lake whitefish (*Coregonus* sp.) and cisco (*C. artedii*). *Can. J. Fish. Aquat. Sci.* 42:1522–1529
- Brandl Z, Fernando CH (1974) Feeding of the copepod *Acanthocyclops vernalis* on the cladoceran *Ceriodaphnia reticulata* under laboratory conditions. *Can. J. Zool.* 52:999–105
- Brandl Z, Fernando CH (1978) The impact of predation by the copepod *Mesocyclops edax* (Forbes) on zooplankton in three lakes in Ontario, Canada. *Can. J. Zool.* 57:940–942
- Brock TD (1985) A eutrophic lake: Lake Mendota, Wisconsin. Springer-Verlag, New York
- Chesson J (1983) The stimulation and analysis of preference and its relationship to foraging models. *Ecology* 64:1297–1304
- Clay CS (1983) Deconvolution of the fish scattering PDF from the echo PDF for a single transducer sonar. *J. Acoust. Soc. Am.* 73:1989–1994
- DeBernardi R, Giussani G (1975) Population dynamics of three cladocerans of Lago Maggiore related to predation pressure by a planktivorous fish. *Verh. Internat. Verein. Limnol.* 19:2906–2912
- Dodson, SI (1975) Predation rates of zooplankton in arctic ponds. *Limnol. Oceanogr.* 24:940–949
- Downing JA, Rigler FH (1984) A manual on methods for the assessment of secondary productivity in fresh waters. Blackwell Scientific, Oxford
- Gilbert JJ (1990) Differential effects of *Anabaena affinis* on cladocerans and rotifers: Mechanisms and implications. *Ecology* 71:1727–1740
- Gliwicz ZM, Lampert W (1990) Food thresholds in *Daphnia* species in the presence and absence of blue-green filaments. *Ecology* 71:691–702
- Gophen M, Pollingher U (1985) Relationships between food availability, fish predation, and the abundance of the herbivorous zooplankton community in Lake Kinneret. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 21:397–405
- Giussani G, DeBernardi R (1977) Food selectivity of *Coregonus* sp. of Lago Maggiore: an energetical approach. *Mem. Ist. Ital. Idrobiol.* 34:121–130
- Hewett SW, Johnson BL (1987) A generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin Sea Grant Institute Technical Report WIS-SG-87-245, Madison
- Hovenkamp W (1990) Instar-specific mortalities of coexisting *Daphnia* species in relation to food and invertebrate predation. *J. Plankton Res.* 12:483–495
- Kitchell JF (1983) Energetics. In Webb PW, Weihs D (eds) *Fish biomechanics*, Praeger Press, New York, pp 312–338
- Kitchell JF, Stewart DJ, Weininger D (1977) Applications of a bioenergetic model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *J. Fish. Res. Board Can.* 34:1922–1935
- Lampert W, Schober U (1980) The importance of “threshold” food concentrations. *Am. Soc. Limnol. Oceanogr. Spec. Symp.* 3:264–267
- Langeland A (1982) Interactions between zooplankton and fish in a fertilized lake. *Holarct. Ecol.* 5:273–310
- Leibold M (1989) Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *Am. Nat.* 134:922–949

- Lindem T (1983) Successes with conventional *in situ* determinations of fish target strength. In Nakken O, Venema SC (eds) Symposium on fisheries acoustics, Bergen, Norway, 21–24 June 1982, FAO Fish. Rep. 300:104–111
- Lindem T, Sandlund OT (1984) New method in assessment of pelagic freshwater fish stocks—coordinated use of echosounder, pelagic trawl and pelagic nets (in Norwegian with English summary). Fauna 37:105–111
- Luecke C, Litt AH (1987) Effects of predation by *Chaoborus flavicans* on crustacean zooplankton of Lake Lenore, Washington. Freshwat. Biol. 18:185–192
- Luecke C, Vanni MJ, Magnuson JJ, Kitchell JF, Jacobson PJ (1990) Seasonal regulation of *Daphnia* populations by planktivorous fish: Implications for the clearwater phase. Limnol. Oceanogr. 35:1718–1733
- Lunte CC, Luecke C (1990) Trophic interactions of *Leptodora* in Lake Mendota. Limnol. Oceanogr. 35:1091–1100
- Lynch M, Weider LJ, Lampert W (1986) Measurement of the carbon balance in *Daphnia*. Limnol. Oceanogr. 31:17–33
- Matveev VF (1986) Long-term changes in the community of planktonic crustaceans in Lake Glubokoe in relation to predation and competition. Hydrobiologia 141:33–43
- McCauley E, Murdoch WW, Nisbet RM, Gurney WSC (1990) The physiological ecology of *Daphnia*: Development of a model of growth and reproduction. Ecology 71:703–715
- Paloheimo JE (1974) Calculation of instantaneous birth and death rate. Limnol. Oceanogr. 19:692–694
- Pastorok RA (1980) Selection of prey by *Chaoborus* larvae: A review and new evidence for behavioral flexibility. Am. Soc. Limnol. Oceanogr. Spec. Symp. 3:538–555
- Pedros-Alio C, Brock TD (1985) Zooplankton dynamics in Lake Mendota: Short-term versus long-term changes. Freshwat. Biol. 15:89–94
- Reinertsen H, Langeland A (1982) The effect of a lake fertilization on the stability and material utilization of a limnetic ecosystem. Holarct. Ecol. 5:311–324
- Rösch R (1985) Nahrungsauaufnahme und Nahrensausnutzung von Sandfelchen (*Coregonus lavaretus* L.) bei Fütterung mit Lebendplankton (*Daphnia pulicaria*). Ph.D. Dissertation, Albert-Ludwigs-Universität, Freiburg, Germany
- Rudstam LG, Binkowski FP, Miller MA (in prep.) Bioenergetics model for analysis of food consumption by bloater in Lake Michigan
- Rudstam LG, Clay CS, Magnuson JJ (1987) Density and size estimates of cisco, *Coregonus artedii* using analysis of echo peak PDF from a single transducer sonar. Can. J. Fish. Aquat. Sci. 44:811–821
- Rudstam LG, Lindem T, Hansson S (1988) Density and *in situ* target strength of herring and sprat: A comparison between two methods of analyzing single-beam sonar data. Fish. Res. 6:305–315
- Rudstam LG, Magnuson JJ, Tonn WT (1984) Size selectivity of passive fishing gears: A correction for encounter probability applied to gill nets. Can. J. Fish. Aquat. Sci. 41:1252–1255
- Schoeneck LJ, Williamson CE, Stoeckel ME (1990) Diel periodicity and selectivity in the feeding rate of the predatory copepod *Mesocyclops edax*. J. Plankton Res. 12:29–40

- Stewart DJ, Binkowski FP (1986) Dynamics of consumption and food conversion by alewives: An energetic-modeling synthesis. *Trans. Am. Fish. Soc.* 115:643–661
- Stockner JG, Porter KG (1989) Microbial food webs in freshwater planktonic ecosystems. In Carpenter SR (ed) *Complex interactions in lake communities*, Springer-Verlag, New York, pp 80–97
- Taylor BE (1980) Size-selective predation on zooplankton. *Am. Soc. Limnol. Oceanogr. Spec. Symp.* 3:377–387
- Threlkeld ST (1985) Resource variation and the initiation of midsummer declines of cladoceran populations. *Ergeb. Limnol.* 21:333–340
- Vadas RL, Jr (1989) Food web patterns in ecosystems: A reply to Fretwell and Oksanen. *Oikos* 56:339–343
- Vanni M, Luecke C, Kitchell JF, Magnuson JJ, Allen Y, Temte J (1990) Cascading trophic interactions and phytoplankton abundance: Effects of massive fish mortality. *Nature* 344:333–335



**Plate 5.** Purse seining for larval fishes in University Bay.

# 15

## Pelagic Planktivory by Larval Fishes in Lake Mendota

**John R. Post, Lars G. Rudstam, Denise M. Schael,  
and Chris Luecke**

### Introduction

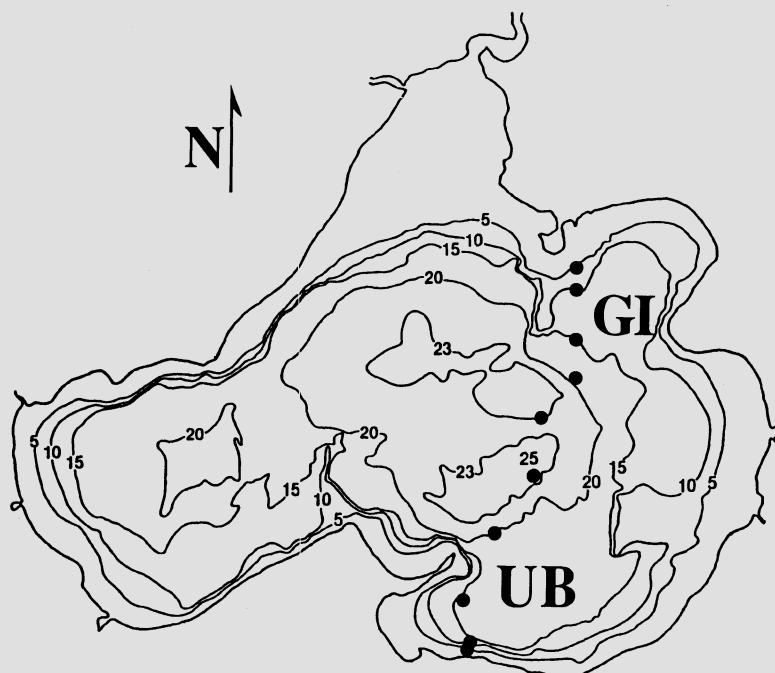
The influx of large numbers of recently hatched fish larvae into the pelagic zone of freshwater lakes can have a significant impact on the zooplankton communities on which they feed (Mills et al. 1987; Post and McQueen 1987; Whiteside 1988; Hewett and Stewart 1989). Fish larvae can have daily consumption rates which exceed their own biomass (Post 1990; Houde 1989), and therefore the potential for predatory impacts, intra- and interspecific competition, and density-dependent growth is high (Post 1990). Through these mechanisms, the interactions between larval fishes and their zooplankton prey can be pivotal in larval growth, survival, recruitment, and food web structure (Houde 1987; Rice et al. 1987; Post and Prankevicius 1987; Post and Rudstam, Ch. 19).

This study is part of a whole-lake experiment designed to test the strengths of trophic interactions in the “trophic cascade” (Kitchell, Ch. 1). The goal of the larval fish component of the study is to assess the significance of larvae as pelagic planktivores in Lake Mendota, Wisconsin. We will examine temporal patterns in consumption rates by pelagic larval fishes, describe their diets, and relate these patterns to temporal patterns in planktivory by adult fish and to zooplankton biomass dynamics. This study is complementary to the empirical study of planktivory by adult fishes and invertebrates (Luecke et al., Ch. 14), the modeling synthesis of planktivory by all age classes of fish and invertebrates (Luecke et al., Ch. 20), and the modeling synthesis of competition, predation, and recruitment dynamics in fishes (Post and Rudstam, Ch. 19).

## Distribution and Abundance

The pelagic larval fish in Lake Mendota were sampled in the spring and summer of 1988 and 1989. A fine-mesh ( $1 \text{ mm}^2$ ) purse seine (30 m long, 9 m deep) similar to those described by Evans and Johannes (1988) and Post and Evans (1989) was used (Plate 5). The area sampled by the net was approximately  $74 \text{ m}^2$ . Sampling was conducted at 1- to 3-week intervals for a total of six sampling dates in 1988 and nine sampling dates in 1989. Sampling sites were located along a transect drawn from University Bay to Governors Island (Figure 15.1) at 5, 10, 15, and 20 m depths at each end of the transect, and at a single central site over approximately 25 m of water. Therefore, on each sampling date a total of nine purse seine samples were taken representing habitats ranging from nearshore to offshore.

Since the net had a fine mesh, samples also often included large numbers (as much as 5–10 L) of large-bodied zooplankton from which the



**Figure 15.1.** Map of Lake Mendota, Wisconsin, with the purse seining sample sites marked. Sites were selected along a transect from University Bay (UB) in the south to Governors Island (GI) in the north and were placed at intervals of 5 m water depth from nearshore to offshore at either end of the transect.

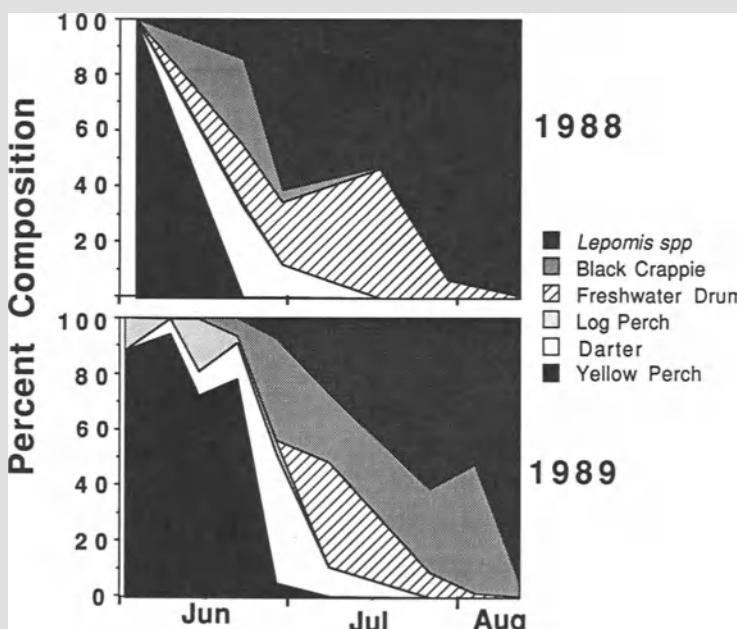
larval fish had to be sorted. Occasionally the net also captured juvenile and adult yellow perch and white bass. A similar net fished in other lakes was effective for capturing pelagic larvae, juveniles, and adults of a number of species (Evans and Johannes 1988; Johannes et al. 1989; McQueen et al. 1989). Whole-lake population estimates based on density in repeated purse seine catches did not differ from mark-recapture estimates for fish up to approximately 15 cm in length (M.R.S. Johannes and J.R. Post, unpubl. data). It was therefore assumed that the efficiency of the net for the capture of larval fish was 100% and was not size biased. Thus our samples should be representative of the larval and juvenile fish in the upper half of the epilimnion (0–6 m) in Lake Mendota. Sonar data (200 kHz) showed 44% (on 12 June 1989) and 72% (on 10 July 1989) of the small targets to be in the 2–6 m depth strata during the day (Rudstam, unpubl. data).

Larvae were preserved in 95% ethanol and stored for analysis. In the laboratory they were identified to species where possible or to genus using the keys of Auer (1982). All larvae, up to a maximum of 50 per species per sample, were measured for total length and 10 subsampled for weight.

**Table 15-1.** Family, genus, species and common name of larval and juvenile fishes captured in our pelagic purse seining sampling in Lake Mendota in 1988 and 1989. The relative abundance of the various species is indicated as either common (C) or rare (R).

Family	Genus/species	Common name	Abundance
Percidae	<i>Perca flavescens</i>	Yellow perch	C
	<i>Etheostoma</i> spp.	Darters	C
	<i>Percina caprodes</i>	Logperch	C
	<i>Stizostedion vitreum</i>	Walleye	R
Centrarchidae	<i>Lepomis</i> spp.	Sunfish	C
	<i>Pomoxis nigromaculatus</i>	Black crappie	C
	<i>Micropterus salmoides</i>	Largemouth bass	R
	<i>Ambloplites rupestris</i>	Rock bass	R
Cyprinidae	<i>Cyprinus carpio</i>	Carp	R
	<i>Pimephales notatus</i>	Bluntnose minnow	R
		Misc. minnows	R
Sciaenidae	<i>Aplodinotus grunniens</i>	Freshwater drum	C
Percichthyidae	<i>Morone chrysops</i>	White bass	R
Cottidae	<i>Cottus</i> spp.	Sculpins	R
Atherinidae	<i>Labidesthes sicculus</i>	Brook silverside	R
Catostomidae	<i>Catostomus</i> spp.	Suckers	R
Ictaluridae	<i>Ictalurus</i> spp.	Bullhead	R

Magnuson and Lathrop (Ch. 11) list 40 species of fish that are known to have occurred in the 1980s in Lake Mendota. Of these, 17 taxa of larval fish were captured in the pelagic zone of Lake Mendota during the spring and summer of 1988 and 1989 (Table 15.1). Of these taxa, six were sufficiently common to describe temporal distribution patterns, consumption rates, and diet. These common groups were yellow perch (*Perca flavescens*), darters (*Etheostoma* spp.), logperch (*Percina caprodes*), *Lepomis* spp., black crappie (*Pomoxis nigromaculatus*), and freshwater drum (*Aplodinotus grunniens*) (Table 15.1). Other taxa not represented in our sampling either do not have pelagic larvae or were too rare to be captured in our sampling regime. Cisco, *Coregonus artedii*, spawn in early December in Lake Mendota and the eggs hatch in April. Larval cisco were present in the pelagic zone in the spring of both 1988 and 1989 (a total of 12 fish caught on 12 and 26 April and 17 May 1988, and a total of 33 fish caught between 5 and 24 May 1989). These samples were taken with a neuston net which samples the top 20 cm of the water column (Rice et al. 1987). No larval cisco were caught in purse seines in June, July, or August. During the summer young-of-year (YOY) cisco may move inshore (observed for other *Coregonus* spp., Naesje et al. 1986) or



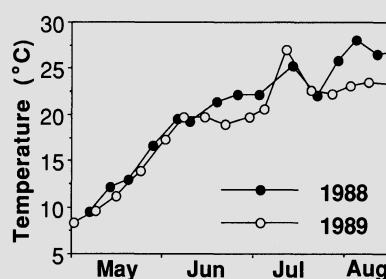
**Figure 15-2.** Seasonal succession of pelagic larval fish in Lake Mendota in 1988 and 1989.

move to the bottom of the epilimnion (8–10 m depth), which we do not sample with the purse seine.

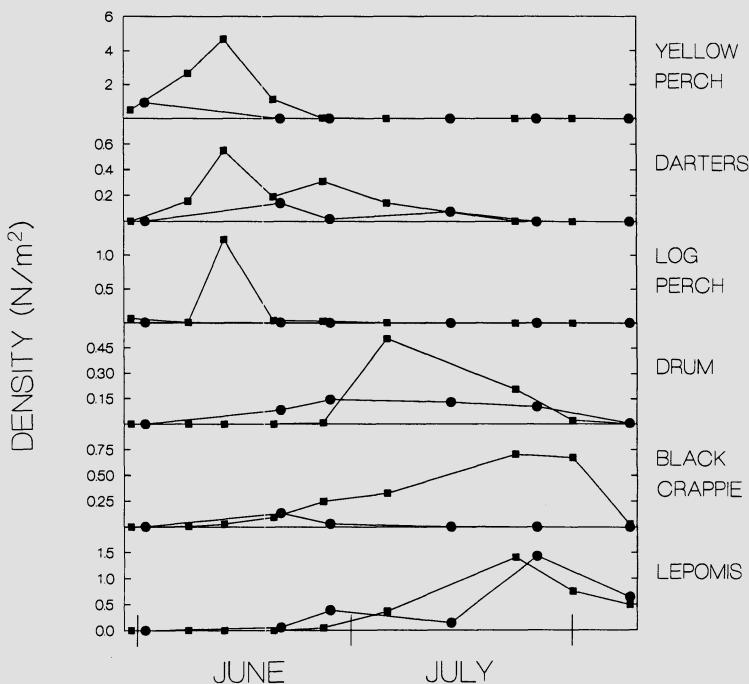
The seasonal succession of the 6 common taxa was similar in 1988 and 1989 (Figure 15.2). Yellow perch were the main pelagic larvae early in June, followed by the two other percids, darters and logperch. Of the centrarchids, black crappie were abundant in early summer to mid-summer and *Lepomis* spp. were the predominant pelagic larvae late in the summer. Freshwater drum were a substantial component of the pelagic fish larvae in midsummer. The timing of these patterns shows that the successional events were advanced in 1988 when compared to 1989. This is probably due to the earlier spring warming in 1988 than in 1989 (Figure 15.3). It is not surprising that temperature would have this effect, since spawning, egg incubation rate, and larval growth rates are strongly temperature dependent processes (Scott and Crossman 1973; Shuter et al. 1980; Gregory and Powles 1985).

The patterns in the abundance of the three percids and two centrarchids in the pelagic zone are consistent with their known spawning habits. The percids generally have a discrete spawning period which produces a discrete pulse of larvae to the pelagic zone. On the other hand, the centrarchids tend to have a more protracted spawning period and therefore dominate the larval fish community for a longer time. Although not fully understood, the offshore migration of larvae hatched in the littoral zone and the later return to this zone are probably a function of body size and/or age (see Post and McQueen 1988 for a review of migration patterns in *Perca* spp.). In this study we focus only on the time window encompassing the pelagic phase of early life history.

The abundances of the three percid larvae appear to have been higher in 1989 than in 1988 (Figure 15.4), although the temporal scale of the 1988 sampling regime may not have been fine enough to establish the dynamics observed with more frequent sampling in 1989. Yellow perch and logperch showed narrow peaks in abundance probably associated with discrete spawning periods and a short pelagic residence time. In contrast, the darters had a bimodal distribution in time in both years,

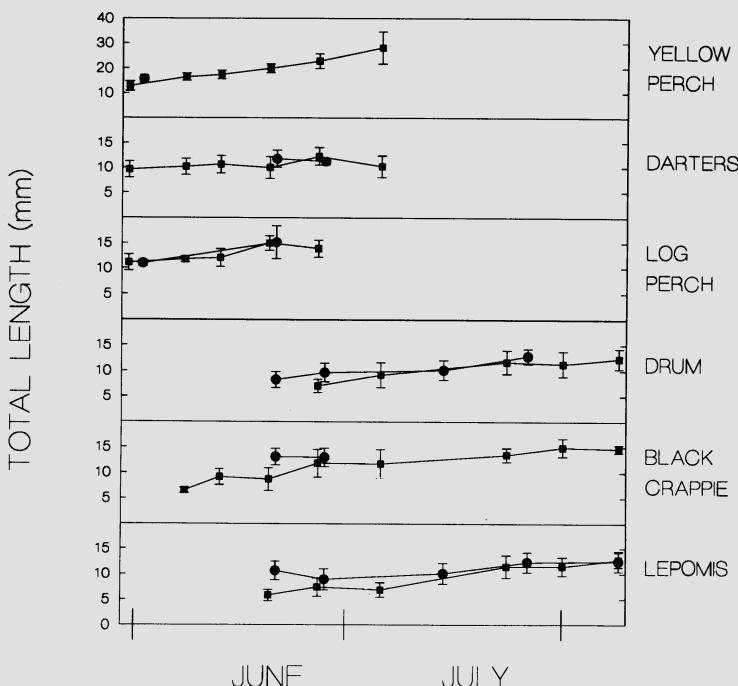


**Figure 15-3.** Mean epilimnetic temperature of Lake Mendota in the spring and summer of 1988 and 1989.



**Figure 15-4.** Density of pelagic larval fish in Lake Mendota in 1988 (circles) and 1989 (squares). The areal density is based on the top 6 m of the water column.

with greater abundance in 1989 than 1988. The bimodal pattern may reflect differences in spawning time between Johnny and Iowa darters, the two species common in Lake Mendota (Lyons 1989). The Iowa darter typically spawns at somewhat cooler temperatures in the spring (Becker 1983). The temporal distribution of freshwater drum was substantially different in the two years (Figure 15.4). In 1988 with earlier spring warming, freshwater drum larvae were found in open water earlier than in the cooler spring of 1989, but abundances were higher in 1989 than in 1988. There were dramatic differences in the timing and densities of black crappie larvae in the two years (Figure 15.4). The peak densities of black crappie larvae were about five times higher and 1 month later in 1989 than in 1988. On the other hand, the temporal pattern and densities of *Lepomis* spp. larvae were almost identical in 1988 and 1989 (Figure 15.4). The observation that abundances of five of the six taxa examined were higher in 1989 than in 1988 suggests that the same mechanisms may limit year class strength of fishes with pelagic larvae. Estimates of cisco density from the neuston sampling in April–May also show greater year class



**Figure 15-5.** Mean total length and 95% confidence intervals of pelagic larval fish in Lake Mendota in 1988 (circles) and 1989 (squares).

strength in 1989 than in 1988. This is further supported by the observation that of the five strong year classes of yellow perch in Lake Mendota in the last 15 years (1977, 1981, 1982, 1983, 1985), three were accompanied by strong year classes of cisco (1977, 1982, 1985) (L.G. Rudstam and R. Lathrop, unpubl. data).

There was little change in mean length of larvae in the pelagic zone through the spring and summer for all taxa but yellow perch (Figure 15.5). This suggests that the pelagic larvae caught were those of the particular size or age associated with the pelagic developmental stage rather than sequential sampling of the same larvae. The biomass of the pelagic larvae, required for estimating consumption, was calculated from these density estimates (Figure 15.4), mean length (Figure 15.5), and length versus weight regressions (Table 15.2).

The temporal patterns in the density of pelagic larvae for all taxa but *Lepomis* spp. differed between 1988 and 1989. Higher rates of spring epilimnetic water warming in 1988 probably induced earlier spawning, shorter incubation times, and earlier hatch. Five of the six common taxa

**Table 15-2.** Length versus weight regressions for Lake Mendota larvae where WEIGHT =  $a * \text{TOTAL LENGTH}^b$ . Weight is in grams and total length (TL) is in millimeters. Regressions for all species except cisco were calculated from specimens collected in purse seines in 1988. The cisco specimens were collected in a neuston net in 1987.

Species	$a$	$b$	$r^2$	$n$	Range in TL (mm)
Yellow perch	$3.16 \times 10^{-7}$	4.07	0.76	137	12–28
<i>Lepomis</i> spp.	$5.25 \times 10^{-8}$	4.75	0.76	210	5–17
Logperch	$7.76 \times 10^{-6}$	3.04	0.82	9	10–22
Freshwater drum	$1.95 \times 10^{-6}$	3.43	0.64	171	4–14
Darters	$2.57 \times 10^{-7}$	4.04	0.50	77	7–20
Black crappie	$1.41 \times 10^{-5}$	2.63	0.78	56	10–20
Cisco	$3.17 \times 10^{-7}$	3.82	0.95	86	14–27

were more abundant in 1989 than in 1988, although *Lepomis* spp. were equally abundant in the two years. Mean densities of all taxa combined were approximately seven times higher in the spring of 1989 than in 1988 and approximately 50% higher in the summer of 1989 than in 1988.

### Diet and Consumption Estimates

Ontogeny of diet was determined from the contents of the entire digestive tract from 10–16 larval yellow perch, freshwater drum, black crappie, and *Lepomis* spp. from each sample site on the University Bay end of the transect, including the Deep Hole site.

Adult and immature stages of calanoid and cyclopoid copepods were the dominant prey of these four species (Table 15.3). The data do not indicate strong ontogenetic shifts in prey taxa selection, but an analysis of size selectivity shows increasing selectivity for larger prey by larger larvae (Schael et al., in press). Measurements of gape size predicted the upper limit of prey sizes ingested and some of the variability in mean size of ingested prey, but the relationships differed between species (Schael et al., in press).

Consumption rates by the community of larval fish were estimated using a general empirical relationship derived by Houde in a survey of larval fish energetics. Houde (1989) described general linear relationships between growth and temperature ( $r^2 = 0.57$ ) and ingestion and growth ( $r^2 = 0.80$ ) and calculated the relationship between ingestion and temperature:

$$\text{INGESTION} = -0.125 + 0.0326 * \text{TEMPERATURE}$$

**Table 15-3.** Percent composition by number in the diet of Lake Mendota larval fish. Calanoid and cyclopoid copepodites and nauplii were not differentiated. The total number of prey identified and counted and the number of stomachs examined for each fish species on each sample day are indicated.

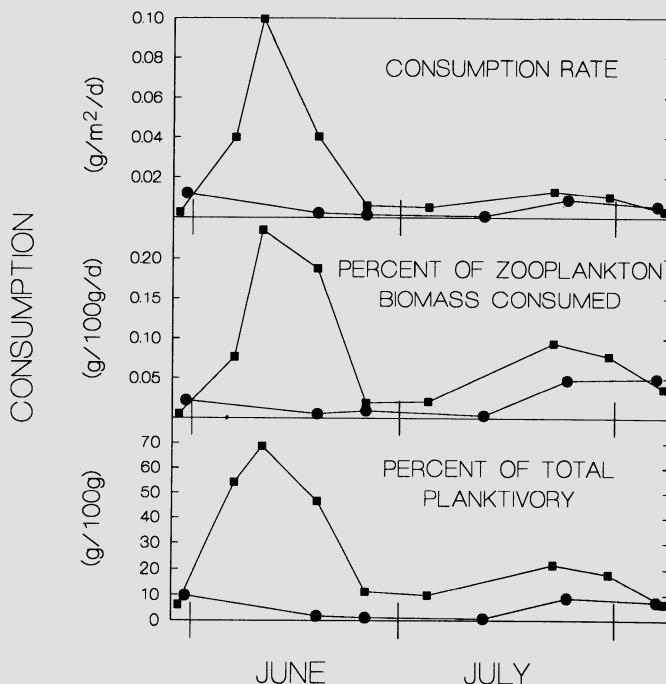
**Table 15-3. Continued**

Date	<i>Daphnia</i>	Calanoid copepod	Cyclopoid copepod	Copepodite nauplii	Other	N prey	N stomachs
<i>Lepomis</i> spp.							
1988 June 27	1	3	31	65	0	0	36
July 14	19	0	15	66	0	<1	35
July 26	9	0	46	26	0	19 <sup>a</sup>	44
August 8	26	0	49	0	0	25 <sup>a</sup>	44
1989 June 27	8	27	44	13	8	0	41
July 6	3	5	19	55	17	<1	13
July 24	0	0	1	12	87	0	50
August 1	4	4	12	78	2	0	29
August 9	96	4	0	0	0	0	30
						169	30

<sup>a</sup> Primarily *Diaphanosoma*.

where INGESTION is in grams consumed per gram of fish per day and TEMPERATURE is in degrees centigrade. The total biomass of larval fishes was calculated by summing across taxa. The temperature used in the model was the mean temperature in the top 5 m of the water column (Figure 15.3). Houde's model does not incorporate either the allometry of consumption or the effects of prey availability on consumption, but the advantages of his model are that it is general across species and does not require growth estimates. Growth could not be estimated from our dataset because the larvae are only temporary residents of the pelagic zone and their migrations in and out of the pelagic zone are size related. Therefore our sampling captures larvae of a particular size but does not follow the growth of individuals. Houde's model predictions are similar to those yielded by the more comprehensive model of Post (1990) for larval yellow perch of intermediate body size and prey availability.

Mean pelagic daily consumption rates by the larval fish community were approximately an order of magnitude higher in the spring than in the summer of both years (Figure 15.6). The consumption rates were



**Figure 15-6.** Daily consumption rate in  $\text{gm}^{-2} \text{d}^{-1}$  of the pelagic larval fish community, percent of the zooplankton biomass consumed daily, and larval fish consumption as a percent of total vertebrate planktivory in Lake Mendota in 1988 (circles) and 1989 (squares).

substantially higher in 1989 than in 1988 due to the higher larval fish densities in 1989. The maximum proportion of zooplankton biomass consumed by pelagic larval fish was 0.25% per day (Figure 15.6). In June 1989, when larval fish abundance was the highest, planktivory by larval fish accounted for 70% of total vertebrate planktivory, partly as a result of very low adult biomass of cisco and yellow perch (Rudstam et al., Ch. 12; Luecke et al., Ch. 14). The larvae of a strong year class comparable to that of the yellow perch of 1985 would be the main planktivores in Lake Mendota throughout the year.

Since strong zooplankton–phytoplankton interactions are expected only when there are abundant large *Daphnia*, and since *Daphnia* were at most times a small component of the diet of Lake Mendota fish larvae, larval fish were probably not major players in the trophic cascade in either 1988 or 1989. On the other hand, there is the potential for impacts on copepod population dynamics, because they are a larger component of larval fish diets and also because their turnover rates are lower than for cladocera (Allan 1976).

## General Discussion

A number of studies have shown significant effects of planktivory by larval and juvenile fishes (Cryer et al. 1986; Mills et al. 1987; Post and McQueen 1987; Whiteside 1988; Hewett and Stewart 1989), which is counter to our conclusions for Lake Mendota. But the year class strength of fish is extremely variable (Sissenwine 1984), and the year class strength of yellow perch in Lake Mendota has been low since 1985 (Johnson et al. 1992). The 1985 year class may have been 50 times higher than the 1988 and 1989 cohorts (Johnson et al. 1992), and larval perch would have been a major planktivore in the lake that year.

In the later half of the 1980s the yellow perch population in Lake Mendota was dominated by the 1985 cohort. Predation by stocked walleye and pike (Johnson et al., Ch. 16) and cannibalism by perch are potential explanations for poor year class strength since 1985. Adult and larval perch do overlap substantially, both spatially and temporally. Analysis of adult perch stomachs has not identified larval perch as significant components of their diet (Luecke et al., Ch. 14), but larval fish are digested so rapidly that this is not surprising (Brandt et al. 1987; Rice et al. 1987). The adult perch population has been declining during the later half of the 1980s (Rudstam et al., Ch. 12) because of poor recruitment and high harvest rates (Johnson and Staggs, Ch. 17). This is a population dynamics scenario explored by Post and Rudstam (Ch. 19), and their model predicts that as the adult yellow perch population

declines, cannibalism rates will decline and the probability of one or more strong cohorts will increase. This scenario suggests a very dynamic system with a periodicity of approximately the life span of yellow perch (4–5 years). The implications of this annual variability to rates of planktivory by larval fish are substantial. We expect one or more strong year classes of perch early in the 1990s and predict lower zooplankton biomass associated with these abundant year classes.

**Acknowledgments.** We thank Brett Johnson, Chuck Madenjian, and Jim Kitchell for constructive comments on an earlier draft of the chapter. We also thank all of those who helped with the arduous task of purse seining, including Terry Schenk, Jo Temte, Steve Anglea, Deborah Shostek, and Lance Gardner. Special thanks to Yvonne Allen for her help in all aspects of this study. John Post was supported by a Natural Science and Engineering Research Council of Canada Postdoctoral Fellowship. Lars Rudstam was supported by a Postdoctoral Fellowship from the Swedish Council for Forestry and Agricultural Research. Denise Schael and Chris Luecke were supported by a Federal Aid in Sport Fish Restoration Act under Project F-95-P and the Wisconsin Department of Natural Resources (WDNR).

## References

- Allan JD (1976) Life history patterns in zooplankton. *Am. Nat.* 110:165–180
- Auer NA (1982) Identification of larval fishes of the Great Lakes Basin with emphasis on the Lake Michigan drainage. Great Lakes Fishery Commission Special Publication 82–3, Ann Arbor, Michigan
- Becker GC (1983) Fishes of Wisconsin. University of Wisconsin Press, Madison
- Brandt SB, Mason DM, MacNeill DB, Coates T, Gannon JE (1987) Predation by alewives on larvae of yellow perch in Lake Ontario. *Trans. Am. Fish. Soc.* 116:641–645
- Cryer M, Peirson G, Townsend CR (1986) Reciprocal interactions between roach, *Rutilus rutilus*, and zooplankton in a small lake: Prey dynamics and fish growth and recruitment. *Limnol. Oceanogr.* 31:1022–1038
- Evans DO, Johannes PR (1988) A bridle-less trawl and fine-mesh purse seine for sampling pelagic coregonine larvae with observations of spatial distribution and abundance. Ontario Fisheries Technical Report Series No. 27
- Gregory RS, Powles PM (1985) Chronology, distribution, and sizes of larval fish sampled by light traps in macrophytic Chemung Lake. *Can. J. Zool.* 63:2569–2577
- Hewett SW, Stewart DJ (1989) Zooplanktivory by alewives in Lake Michigan: Ontogenetic, seasonal and historical patterns. *Trans. Am. Fish. Soc.* 118:581–596

- Houde ED (1987) Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. 2:17–29
- Houde ED (1989) Comparative growth, mortality and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish. Bull. U.S. 87:471–495
- Johannes MRS, McQueen DJ, Stewart TJ, Post JR (1989) Golden shiner (*Notemigonus crysoleucas*) population abundance: Correlations with food and predators. Can. J. Fish. Aquat. Sci. 46:810–817
- Johnson BM, Luecke C, Stewart RS, Staggs MD, Gilbert SJ, Kitchell JF (1992) Forecasting effects of harvest regulations and stocking on prey fish communities in a eutrophic lake. N. Am. J. Fish. Manage. (in press)
- Lyons J (1989) Changes in the abundance of small littoral-zone fishes in Lake Mendota, Wisconsin. Can. J. Zool. 67:2910–2916
- McQueen DJ, Johannes MRS, Post JR, Stewart TJ, Lean DRS (1989) Bottom-up and top-down impacts on freshwater pelagic community structure. Ecol. Monogr. 59:289–309
- Mills EL, Forney JL, Wagner KJ (1987) Fish predation and its cascading effect on the Oneida Lake food chain. In Kerfoot WC, Sih A (eds) Predation: Direct and indirect effects on aquatic communities, University Press of New England, Hanover, New Hampshire, pp 118–131
- Naesje TF, Sandlund OT, Jonsson B (1986) Habitat use and growth of age-0 whitefish, *Coregonus lavaretus*, and cisco, *C. albula*. Environ. Biol. Fish. 15:309–314
- Post JR (1990) Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): In situ estimates and bioenergetic models. Can. J. Fish. Aquat. Sci. 47:554–560
- Post JR, Evans DO (1989) Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): Laboratory, in situ enclosure, and field experiments. Can. J. Fish. Aquat. Sci. 46:1958–1968
- Post JR, McQueen DJ (1987) The impact of planktivorous fish on the structure of a plankton community. Freshwat. Biol. 17:79–89
- Post JR, McQueen DJ (1988) Ontogenetic changes in the distribution of larval and juvenile yellow perch (*Perca flavescens*): A response to prey or predators? Can. J. Fish. Aquat. Sci. 45:1820–1826
- Post JR, Prankevicius AB (1987) Size-selective mortality in young-of-the-year yellow perch (*Perca flavescens*): Evidence from otolith microstructure. Can. J. Fish. Aquat. Sci. 44:1840–1847
- Rice JA, Crowder LB, Holey ME (1987) Exploration of mechanisms regulating larval survival in Lake Michigan bloater: A recruitment analysis based on characteristics of individual larvae. Trans. Am. Fish. Soc. 116:703–718
- Schael DM, Rudstam LG, Post JR (1991) Gape limitation and prey selection in larval yellow perch (*Perca flavescens*), freshwater drum (*Aplodinotus grunniens*) and black crappie (*Pomoxis nigromaculatus*). Can. J. Fish. Aquat. Sci. (in press)
- Scott WB, Crossman EJ (1973) Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184
- Shuter BJ, MacLean JA, Fry FEJ, Regier HA (1980) Stochastic simulation of temperature effects on first-year survival of smallmouth bass. Trans. Am. Fish. Soc. 109:1–34

- Sissenwine MP (1984) Why do fish populations vary? In May RM (ed) Exploitation of marine communities, Springer-Verlag, Berlin, pp 59–94
- Whiteside MC (1988) O+ fish as major factors affecting abundance patterns of littoral zooplankton. Verh. Internat. Verein. Limnol. 23:1710–1714



**Plate 6.** Fingerling walleyes typical of the sizes stocked in Lake Mendota.

# **16**

## **Piscivores and Their Prey**

**Brett M. Johnson, Stephen J. Gilbert,  
R. Scot Stewart, Lars G. Rudstam, Yvonne Allen,  
Don M. Fago, and David Dreikosen**

### **Introduction**

Not surprisingly, Lake Mendota's fishes have been the subject of a multitude of studies since the days of Birge and Juday. However, these studies have focused almost entirely on yellow perch (*Perca flavescens*), white bass (*Morone chrysops*), and cisco (*Coregonus artedii*), probably because of their abundance or importance to the fishery. When this study began, relatively little was known about Lake Mendota's piscivore community, including abundance, reproductive success, growth rates, diet, and distribution. Hence, we had some fundamental questions that needed to be addressed before we could predict the course of the biomanipulation experiment. Among our questions were:

- Would piscivores, especially walleye, inhabit the open water?
- What biomass of piscivores could be gained and maintained by stocking and fishing regulations?
- What are the dominant species in the prey assemblage?
- Do piscivores feed on target planktivore species?
- Which piscivore species is most suited to biomanipulation?
- What effect will piscivores have on prey populations?

The goal of this chapter is to present our best answers to these questions. We will give estimates of piscivore demographics, distribution, food habits, and food consumption generated during 1987–89. These data will be used to compare the utility of walleye, northern pike, and bass for biomanipulation in Lake Mendota. We will present a more comprehen-

sive examination of the prey fish assemblage than has been previously attempted. And finally, we will use piscivore population statistics to model piscivore biomass and forecast the short-term impacts of piscivory on selected prey species.

## Methods

### Assessing the Fish Populations

*Piscivore Populations.* A variety of sampling gear and assessment techniques were used to gather fish population data. Sampling began at ice-out, when 20 fyke nets (32-mm stretch mesh, 15-m lead, 0.9 × 1.8-m frame, 0.9-m diameter hoops) were fished daily for about 4 weeks. Piscivores captured in fyke nets were measured and weighed. We took scale samples from at least 10 fish of each species and sex per 25-mm size class to determine growth rates. Piscivores larger than a species-specific minimum length (Johnson et al. 1992b) were tagged with T-bar anchor tags and finclipped to quantify tag loss rate.

Beginning in the first week of May for 1 month, we used a standard three-person Wisconsin Department of Natural Resources (WDNR) electrofishing boat (300V pulsed DC, 2.5 A mean amperage; Novotny and Priegel 1974) to shock about 2.5 laps (62–94 km) of the shoreline. A similar amount of electrofishing effort was used in the fall. The main objective of electrofishing was to make mark–recapture population estimates. Piscivores less than approximately age 4 were marked with a temporary finclip; randomly selected recapture transects were shocked after each marking period to compute Petersen abundance estimates. The entire spring shocking period served as the recapture sample of fish marked in fyke nets and as an additional recapture sample of fish marked in the previous fall. Fall mark–recapture work was concentrated on estimating growth, abundance, and survival of young-of-year (YOY) piscivores.

Experimental gill nets were fished during May–August 1987, and June–August 1988 and 1989 to recapture piscivores for population estimates, to determine piscivore depth distribution and thermal history, and to collect summer diet data. These data were required for bioenergetics modeling of piscivore consumption.

All nets were constructed of five panels of different mesh sizes, each panel either 3 or 7.6 m in length. Meshes ranged from 25 to 76 mm, 64 to 114 mm, or 102 to 203 mm (stretch measure). Nets were either 0.9 or 1.8 m high; 0.9-m nets were set in depths of 1.8–2.5 m. We set nets out to the maximum depth with at least 2.0 mg/L dissolved oxygen; by July this was a depth of about 9 m. In August 1988 we set 1,486 m of gill net at randomly selected open-water locations. These nets were suspended

above the thermocline to sample pelagic walleyes with the bottom of each net 8 m below the surface in water deeper than 9 m. In most months we set nets at about 18 locations per day, and the nets fished for 24 h. Population estimates were computed using experimental gill nets fished during June–August to obtain a recapture sample of fishes marked in spring fyke netting and spring electrofishing. Size-specific estimates were corrected for growth occurring after marking.

An access point creel survey (Johnson and Staggs, Ch. 17) was used to estimate the harvest of all sport fishes. The ratio of total annual harvest to population estimates computed before the fishing season began gave harvest mortality rates. The creel clerk examined all harvested piscivores for marks; thus, the creel survey also provided an independent recapture sample of piscivores marked in spring fyke nets and electrofishing.

*Prey Populations.* To characterize the prey assemblage during 1987–89, we gathered data from a variety of fish sampling efforts conducted during this project. We distinguish three classes within the prey assemblage because prey fish size relates to vulnerability to sampling gear and to predation. “Small prey fishes” are those species that remain vulnerable to predation throughout their life and reach an adult body length of less than 120 mm. “Large prey fishes” exceed 120 mm before age 2 and include fishes such as cisco, perch, bluegill, crappie, and white bass. This class of prey is divided into juveniles and adults. Juvenile abundance varies independently of adult abundance, and generally only juveniles are vulnerable to predation.

A catamaran trawl was used to sample larval fishes in May–July 1987. This trawl has a 1-m<sup>2</sup> opening and is suspended between two boats; it can be depressed to a depth of 3 m. A fine-mesh purse seine (Post et al., Ch. 15) was used in May–July 1988 and 1989. Shoreline seines (7.6-m beach seine, 3.2-mm mesh) and mini-fyke nets (4.8-mm mesh, 7.6-m lead, 0.6 × 0.9-m frame, 0.6-m diameter hoops) were used to index year class strength of prey. We sampled 20 sites per month during July and August. Sites included a variety of substrates and macrophyte densities. Seine hauls were made perpendicular to shore from a depth of 1.0 m. The average area seined was about 100 m<sup>2</sup>. Catch per unit effort (CPUE) of prey was computed in August when YOY of all prey species were fully recruited to the mini-fyke nets and seines. These annual CPUE data were then relativized to 1.0 for each species, because density estimates among species are not directly comparable owing to gear selectivities.

Once per week during spring fyke netting for piscivores, we computed CPUE for all nonpiscivore species caught in fyke nets, and we measured a random subsample of each species. These nets probably selected for adults of large prey species because of mesh size and behavior differences between adults and juveniles. Adult prey fish abundance was also determined from hydroacoustic surveys in conjunction with vertical gill net

sampling at 2, 12, and 22 m. Vertical gill nets were of eight mesh sizes ranging from 19 to 127 mm and were deployed once per month during May–September 1987–89. Methods are presented by Rudstam and Johnson (Ch. 26). Creel survey data were used to compile species composition of the angler catch of large prey fishes. This serves as an index of relative abundance of prey species caught by anglers if one assumes equal vulnerability to angling.

In 1988 we computed a mark–recapture population estimate for adult yellow perch. Using fyke nets set during 21 April to 6 May we captured and finclipped 22,632 yellow perch larger than 180 mm. Marked perch were released at sites widely scattered around the lake. During 6 June to 20 July we used experimental gill nets (25- to 102-mm stretch mesh) to collect recapture samples and compute the population estimate. A known angler harvest also allowed us to compute fishing mortality rate for the yellow perch population.

### Determining Distribution and Diet of Piscivores

Information on the distribution and diet of piscivores is required to use bioenergetics models for quantifying piscivory. Depth distributions are important to bioenergetics estimates of consumption because they correspond with estimates of thermal history. Diet data are required to make species-specific estimates of consumption.

Our efforts to quantify depth distribution of piscivores focused on the June–August period. During this period piscivore consumption rates are high, and the lake is thermally stratified with a range of temperatures available to the fish. We used two methods to determine piscivore distribution: radio telemetry (walleyes only) and experimental gill nets (all piscivores).

On 12 and 17 April and 24 May 1989, radio transmitters were implanted into 12 walleye ranging in weight from 704 to 3,400 g (Fago 1990). Each two-stage transmitter had a unique frequency between 49.000 and 50.999 MHz and a battery life of 150 to 500 days. The transmitters weighed 11 or 45 g depending on battery size. Fish to be radiotagged were captured in fyke nets at four locations around the lake and were anesthetized prior to surgery. The incision was closed with sutures and the fish was returned to the same part of the lake that it was caught.

Movements of these fish were tracked using a scanning receiver from a boat equipped with Yagi and hand-held antennas, and from an airplane equipped with a dipole antenna. Fish were located one to three times per week. Each time a fish was located from the air, its location, date, and time were recorded on a 7.5-min topographic map. Whenever possible, the tracking boat would then determine the exact location of the fish and record its latitude and longitude using LORAN-C. Latitude and longitude

were used for plotting and computing minimum and average distance traveled between observations.

Summer depth distributions of each piscivore population were determined by multiplying gill net CPUE within 3-m depth strata by the proportion of the lake's surface area contained within each stratum (from Brock 1985). Each product was then relativized to the sum of these products for all strata, giving the proportion of the lakewide population inhabiting each depth stratum during each sampling period. These proportions as weighting factors, plus observed temperature profiles, then served to compute mean population thermal histories for use in bioenergetic computations. In this analysis, we assumed that gill net CPUE was proportional to number of fish per unit area within each stratum.

Piscivores were collected for stomach analysis during the growing season. We collected fish primarily by electrofishing in spring (April and May) and fall (September, October, November), and by experimental gill nets in summer (June, July, August). Fish captured in fyke nets were not used because of the potential bias introduced if netted piscivores preyed on other fish within the fyke net. Stomach samples were obtained by gastric lavage (Gilbert and Johnson, 1992) on large piscivores during electrofishing; stomachs were excised from piscivores sampled in gill nets. Large-piscivore stomach contents and whole, small piscivores were preserved in a 10% formalin solution until samples were analyzed. Fish prey in guts were identified to the lowest taxonomic level possible using structures resistant to digestion. Vertebral column lengths were recorded for all identifiable prey fishes. Vertebral column lengths were converted to wet weights using regressions from Wahl (1982) or by converting vertebral length to total length (Knight et al. 1984) and total length to wet weight (Carlander 1977). Diet composition was expressed as the proportion of each prey species consumed, based on wet weight.

## The Piscivore Assemblage

### Walleye

In the 10 years preceding the biomanipulation, fingerling walleye (Plate 6) were stocked only in 1977, 1985, and 1986 (Table 16.1). Electrofishing surveys detected naturally produced YOY walleye only in 1978–79, but 1980–84 year classes were represented in the population-age frequency in 1987, indicating that some natural reproduction occurred during these years as well. However, natural reproduction alone has not been sufficient to maintain a satisfactory population, with only 3,951 adult (age-3 and older walleyes; 1.1 kg/ha) present in the lake in 1987. Contrast this

**Table 16-1.** Piscivores stocked in Lake Mendota during the 1980s. Fry are usually 2-day-old larvae. Fgl = fingerling; walleye fingerlings averaged about 50 mm in length, northern pike fingerlings averaged 200–250 mm.

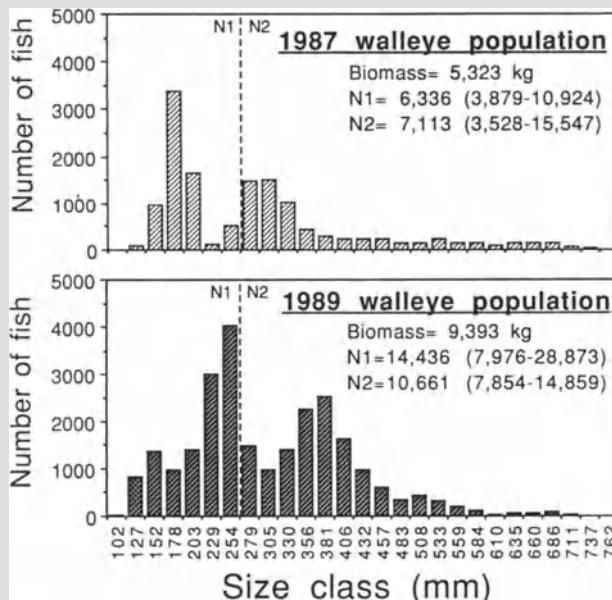
Year	Species	Size	Number stocked
1980	Hybrid muskellunge	fgl	3,610
1981	Northern pike	fgl	3,860
	Hybrid muskellunge	fgl	10,000
	Largemouth bass	fgl	1,000
1982	Northern pike	fry	2,005,000
		fgl	10,260
1983	Northern pike	fgl	5,357
1984	Northern pike	fgl	2,910
1985	Walleye	fgl	106,200
	Northern pike	fgl	2,500
	Hybrid muskellunge	fgl	3,312
1986	Walleye	fry	20,000
		fgl <sup>1</sup>	57,662
	Northern pike	fry	56,000
		fgl	2,274
	Hybrid muskellunge	fgl	1,500
1987	Walleye	fry	20,100,000
		fgl <sup>2</sup>	647,540
	Northern pike	fry	10,760,000
		fgl	23,434
1988	Walleye	fry	26,865,000
		fgl	500,986
	Northern pike	fry	9,923,000
		fgl	2,520
1989	Walleye	fry	20,000,000
		fgl	500,038
		fgl <sup>3</sup>	10,000
	Northern pike	fry	10,000,000
		fgl	22,732

<sup>1</sup>Raised and stocked by Lake Mendota Fishing Association.

<sup>2</sup>68,600 raised and stocked by Lake Mendota Fishing Association.

<sup>3</sup>Large walleye fingerlings, about 180 mm TL.

with adult biomass in two well-known walleye lakes: Escanaba Lake, Vilas County, Wisconsin, had a walleye biomass that varied from 4.2 to 20.7 kg/ha (Kempinger and Carline 1977), and in Oneida Lake, New York, biomass varied from 18.5 to 30.1 kg/ha (Forney 1967). An important difference between Lake Mendota and many high-density walleye lakes is that a large proportion (64%) of Lake Mendota's surface area is deeper than 10 m, and our sampling showed few piscivores inhabiting



**Figure 16-1.** Size structure, abundance, and biomass of the Lake Mendota walleye population in 1987 and 1989. Petersen mark-recapture population estimates were computed for two size classes (<279 mm for N1, and ≥279 mm for N2).

these areas. During summer there is less than 2 ppm dissolved oxygen below 10 m, thus excluding fishes.

Beginning in 1987, we stocked  $2.0 \times 10^7$  fry and about  $5.0 \times 10^5$  fingerling [50 mm total length (TL)] walleye per year for 3 years (Table 16.1). In 1987, walleyes stocked by the WDNR were supplemented with 68,600 fingerlings raised by the Lake Mendota Fishing Association, a group of local walleye enthusiasts. The survival of stocked walleye fry was assumed to be negligible because larval fish sampling conducted after fry stocking captured no walleye fry in 1987 and 1988, and only 23 walleye fry (80 fry/ha; 15.8 mm TL) in 1989. Survival of fingerlings from stocking in June to October was similar in 1987–89 (3.2%, 3.6%, and 1.6%, respectively), but survival to the following May declined from 2.0% in 1987 to 0.11% in 1989. The first-year survival of the 1986 year class (assuming no natural reproduction in 1986) was 10.4%. Thus, overwinter survival has decreased each year since 1986.

Declining first-year survival of stocked walleye fingerlings during 1986–89 suggests that a negative feedback may undermine efforts to enhance piscivore populations by stocking. Fish surviving the initial stockings may cannibalize subsequently stocked fingerlings. Diet sampling in spring 1989

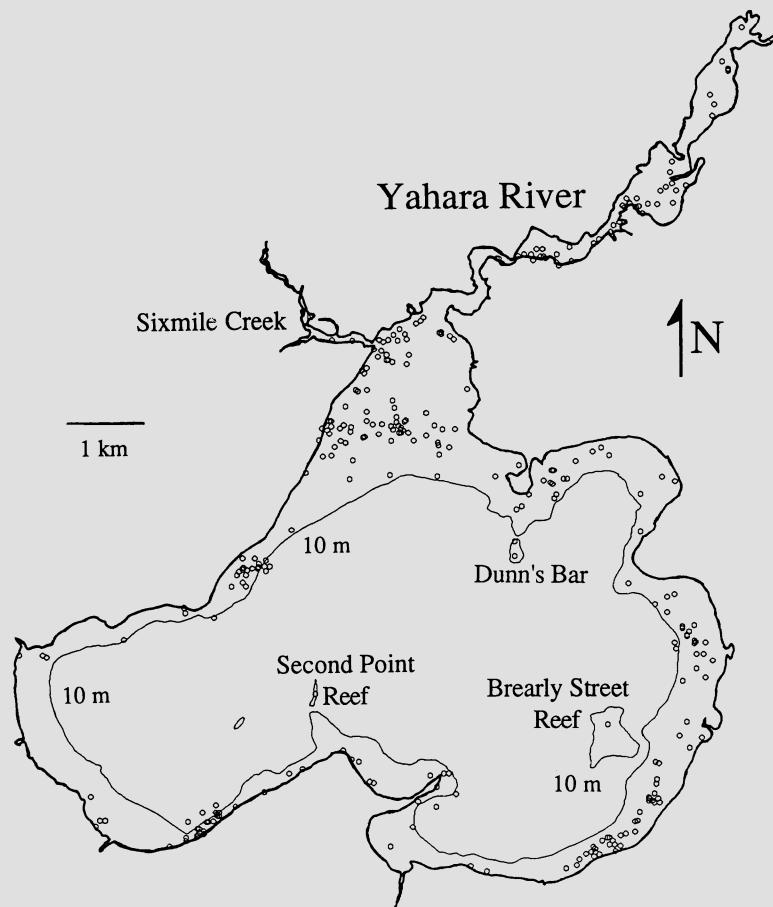
**Table 16-2.** Length (mm) and weight (g) at age of Lake Mendota piscivores, estimated from scale samples taken during 1987–89. Sexes of bass and age-1 and age-2 walleyes were indistinguishable.

Age	Mean length	N	Mean weight	N	Mean length	N	Mean weight	N
Female walleye								
1	177	45	67	30	177	45	67	30
2	276	21	262	20	276	21	262	20
3	409	3	591	3	356	76	416	74
4	427	20	1,148	19	400	45	620	44
5	541	27	1,706	27	427	55	872	52
6	569	26	2,071	25	474	35	1,160	34
Male walleye								
1	348	9	216	8	332	35	173	34
2	493	111	857	104	437	178	524	171
3	589	108	1,433	93	549	97	1,003	91
4	724	75	2,579	59	594	44	1,271	40
5	785	48	3,481	48	640	42	1,535	38
6	808	45	3,733	38	673	19	1,789	19
Female northern pike								
Male northern pike								
1	137	37	36	22	114	25	19	12
2	226	71	186	57	203	58	114	33
3	292	70	416	66	284	59	372	50
4	353	62	738	60	353	43	716	41
5	401	46	1,121	38	409	16	1,196	12
6	432	25	1,458	34	447	11	1,634	11
All largemouth bass								
All smallmouth bass								
1	137	37	36	22	114	25	19	12
2	226	71	186	57	203	58	114	33
3	292	70	416	66	284	59	372	50
4	353	62	738	60	353	43	716	41
5	401	46	1,121	38	409	16	1,196	12
6	432	25	1,458	34	447	11	1,634	11

revealed small walleyes in both walleye and northern pike stomachs. Using the bioenergetics model, we estimated that 33% of the mortality of fingerlings from October 1988 to May 1989 could be accounted for by walleye and northern pike predation just during April and May 1989.

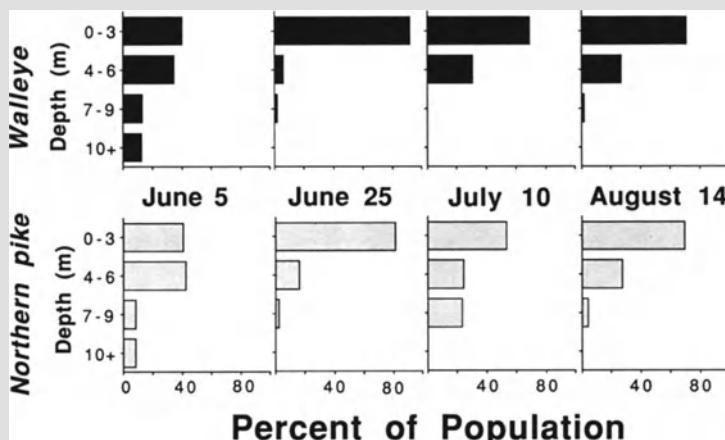
Largely as the result of stocking in 1986 and 1987, the abundance of all sizes of walleye had increased from 13,449 fish in 1987 to 25,097 fish in 1989 (Figure 16.1). Walleye biomass increased from 5,323 kg (1.33 kg/ha) to 9,393 kg (2.4 kg/ha) in 1989. With poorer survival of the 1988 and 1989 year classes, we expect declining walleye abundance after 1989. Walleye biomass may also decline if high exploitation rates observed in 1988–89 (Johnson and Staggs, Ch. 17) continue and recruitment continues to decline. Growth rates of age-2 and older walleye (Table 16.2) were similar to the Wisconsin statewide average (Klingbeil 1990a).

During the growing season, walleyes inhabit the littoral zone. In August 1988 we set 1.5 km of suspended gill nets in the pelagic and



**Figure 16-2.** Cumulative plot of all walleyes located by radio telemetry during summer 1989. Inner line is the 10-m depth contour.

caught no walleyes. Cumulative plots of all radio-tracking locations also show walleyes inhabiting depths less than 10 m, and some use of the Yahara River (<2 m deep) upstream from Lake Mendota (Figure 16.2). During June–August, most of the walleyes in Lake Mendota can be found in depths of 0–3 m (Figure 16.3). The population is most dispersed in early June, before hypolimnetic anoxia begins (Figure 16.3). After anoxia limits fish to depths above the thermocline, their exact depth distribution has little consequence for thermal histories, since temperatures where >95% of the fish were found varied by less than a degree across depth strata in each period.



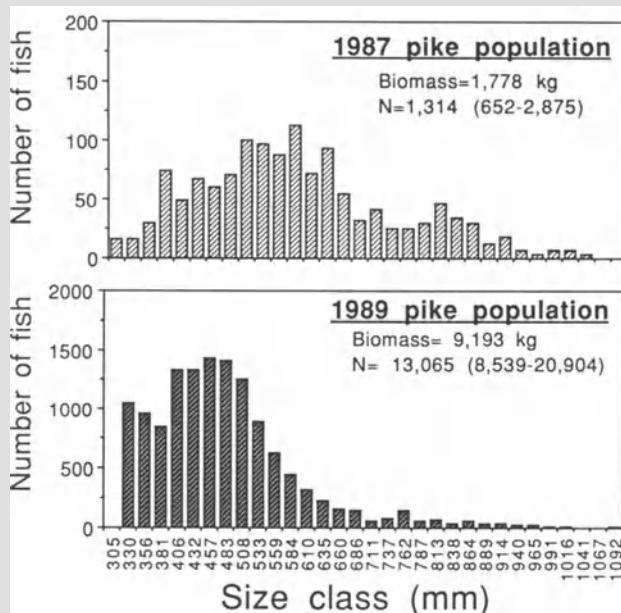
**Figure 16-3.** Depth distribution of walleyes and northern pike larger than 250 mm during summer 1989 in Lake Mendota, computed from experimental gill net CPUE and lake bathymetry.

### Northern Pike

Lake Mendota's northern pike population has suffered from recruitment problems during the 1970s and 1980s. Johnson and Staggs (Ch. 17) believe this has been due to the degradation of northern pike spawning habitat. Regardless of the cause, CPUE of pike in WDNR fyke net surveys declined from 12.0 pike/net-day in the late 1960s to 0.5 pike/net-day in 1987 (Johnson et al. 1992b). This was despite regular WDNR fingerling stockings of 2,300–10,300 fish per year since 1981 (Table 16.1). Once the dominant piscivore, the pike population in 1987 was estimated at less than 1,400 fish (Figure 16.4). In addition to increasing total piscivore biomass for the biomanipulation, our program of increased stocking, restrictive harvest regulations, and higher springtime lake levels was aimed at rehabilitating the pike population and restoring adequate natural reproduction (Johnson and Staggs, Ch. 17).

During 1987–89 we stocked about  $1.0 \times 10^7$  northern pike fry each year. Fingerling (ca. 250 mm TL) stockings varied (Table 16.1), with 23,434 fingerlings stocked in 1987, 2,500 in 1988, and 22,732 in 1989. By 1989 the cohort stocked in 1987 had fully recruited to spring fyke nets. Survival of pike fingerlings stocked in 1987 was excellent and at least 20 times greater than survival of 50-mm walleye fingerlings. Only 23,000 pike fingerlings were planted in 1987, and 2 years later about 5,600 remained.

The number of pike larger than 305 mm increased by a factor of 10 from 1,314 in 1987 to 13,065 in 1989, primarily due to the 1987 (stocked)



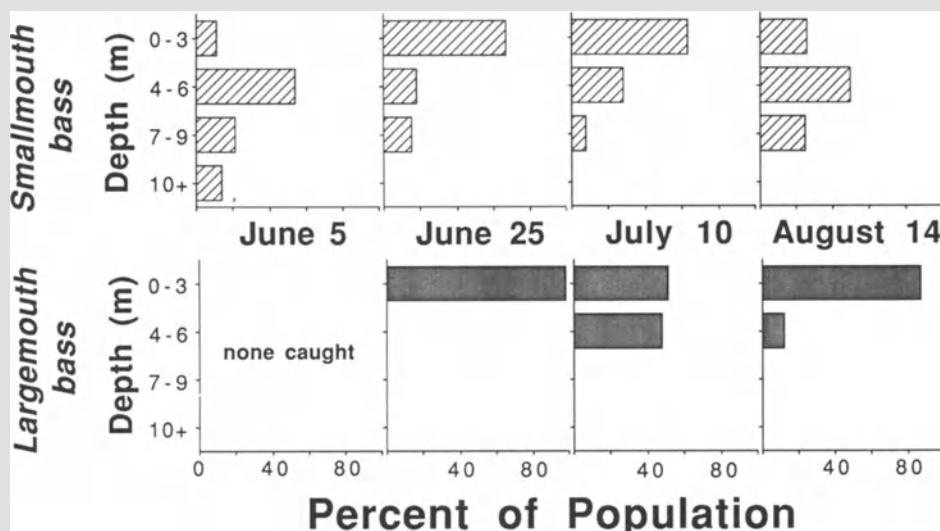
**Figure 16-4.** Size structure, abundance, and biomass of the Lake Mendota northern pike population in 1987 and 1989. Note that the scale on the Y-axis is 10 times greater in 1989.

and 1986 (mostly native) year classes (Figure 16.4). In just 2 years, pike biomass nearly equaled walleye biomass, reaching 2.3 kg/ha by spring 1989. Pike grow rapidly here, with female pike reaching 2 kg in under 4 years (Table 16.2). Unlike walleyes, northern pike growth rates in Lake Mendota exceed statewide averages (Klingbeil 1990a).

Northern pike depth distribution during summer was very similar to that of walleye, with a majority of the population found in the 0- to 3-m stratum (Figure 16.3). As with walleye, northern pike were dispersed over a greater range of depths in early June, when the largest segment of the population was found in 4–6 m (Figure 16.3).

### Smallmouth and Largemouth Bass

Lake Mendota has always had self-sustaining smallmouth and largemouth bass populations (Magnuson and Lathrop, Ch. 11). Although smallmouth bass proved difficult to sample with standard assessment methods, creel survey data suggest that they are more abundant than largemouth bass. Both species are probably equally desirable and vulnerable to anglers, and smallmouth bass have outnumbered largemouth bass in creel surveys during 1952, 1973–74, 1982 (Lathrop et al., 1992) and in the current



**Figure 16-5.** Depth distribution of largemouth and smallmouth bass larger than 200 mm during summer 1989 in Lake Mendota, computed from experimental gill net CPUE and lake bathymetry.

study, where they outnumbered largemouth bass by 2:1 (Johnson and Staggs, Ch. 17). Largemouth bass abundance has remained relatively stable during 1987–89 at about 0.53 bass/ha. Fyke net CPUE has remained constant for both black basses during 1987–89 (Johnson et al. 1992a). Assuming a smallmouth:largemouth bass abundance ratio suggested by creel surveys, the total black bass density in Lake Mendota would be 1.7 bass/ha or 1.2 kg/ha each year, which is about half of 1989 pike or walleye biomass. Growth of both species is above average for Wisconsin waters (Klingbeil 1990a), due in part to Lake Mendota's location in the southern third of the state.

Smallmouth and largemouth bass depth distributions were quite dissimilar. On average, largemouth bass inhabited shallower water than pike and walleye, and smallmouth bass were found in deeper water than the other piscivores (Figure 16.5). This deeper distribution of smallmouth bass could explain the paucity of smallmouth bass in our fyke net and electrofishing sampling.

### Other Piscivores

Over the past 20 years, hybrid muskellunge fingerlings have been stocked only in 1980, 1981, 1985, and 1986 and in low numbers (Table 16.1). Currently they are not abundant (less than 1.0% of fyke net catches), but

**Table 16-3.** Ranked relative abundance of small prey fishes<sup>a</sup> observed in all piscivore guts during 1987–89, and in beach seine catches during July and August 1987 and 1989. Adult length (mm) from Becker (1983).

Common name	Scientific name	Adult length	Rank	
			Piscivore guts	Beach seine
Brook silverside	<i>Labidesthes sicculus</i>	51–76	1	1
Logperch	<i>Percina caprodes</i>	94	2	3
Darters <sup>b</sup>	<i>Etheostoma</i> spp.	51	3	4
Bluntnose minnow	<i>Pimephales notatus</i>	64	4	2
Spottail shiner	<i>Notropis hudsonius</i>	51–76	5	5
Golden shiner	<i>Notemigonus crysoleucas</i>	102	6	—

<sup>a</sup>Those species with a maximum adult body length of 120 mm or less.

<sup>b</sup>Johnny darter (*Etheostoma nigrum*) and Iowa darter (*Etheostoma exile*).

all of the above year classes are represented in the fyke net catch. With low WDNR hatchery supply of esocids, our current management plans call for concentrating northern pike in Lake Mendota and providing a muskellunge fishery in the lower Yahara lakes, rather than spreading out both species at low numbers in all the area lakes. Bowfin (*Amia calva*) inhabit the Lake Mendota drainage; however, we only captured them in spring fyke nets, and only in those set in wetland areas of the lake and its tributaries. Their impact on lake planktivores is probably minimal. Longnose gar (*Lepisosteus osseus*) are present in Lake Mendota, and individuals more than 1.0 m long are occasionally captured in our experimental gill nets. The state record longnose gar (6.2 kg) was taken by spearfishing in Lake Mendota in 1988.

### The Prey Assemblage

Our knowledge of the composition of the prey assemblage is less quantitative than that of the piscivore assemblage. Prey populations are notoriously difficult to sample quantitatively, in part because of gear selectivity, habitat constraints, and high intersample variation (Johnson et al. 1988). Here we draw on several lines of evidence to characterize the prey assemblage. Magnuson and Lathrop (Ch. 11) present relative abundance of all Lake Mendota fishes during the 1980s, which they assembled from a variety of data sources. In general, the relative abundance of prey fishes in our sampling in 1987–89 was quite similar to that estimated by Magnuson and Lathrop (Ch. 11) for the entire 1980s.

### **Small Prey Fishes**

By definition, important prey species are revealed in piscivore diets. Based on diet sampling, small prey fishes (Table 16.3) are an important food source at certain times of the year, particularly in spring before YOY panfish appear. Annually, these fishes comprised about 10% of the total prey biomass consumed. The diversity and abundance of small littoral zone fishes in Lake Mendota have declined dramatically since 1990 (Lyons 1989; Magnuson and Lathrop, Ch. 11) due to a variety of factors, including perhaps increased piscivory by stocked gamefishes during the 1960s through the 1980s (Magnuson and Lathrop, Ch. 11). Still, some purse seine hauls in early summer capture larval darters and logperch (Post et al., Ch. 15), suggesting that some species remain. In general, the species composition of small prey fishes in beach seine hauls in July and August 1987 and 1989 was similar to that in piscivore guts (Table 16.3).

### **Large Prey Fishes—Juveniles**

Annual consumption estimates for piscivores (derived from diet sampling and bioenergetics modeling) show that YOY and juvenile bluegill, yellow perch, black crappie, and white bass contributed more than 60% of the biomass consumed. Because these fishes are consumed as subadults, the relative importance of these species in piscivore diets is not directly related to adult abundance, but rather to juvenile abundance. We have used CPUE in three gear types as an index of year class strength. Year class strength of these fishes has been variable during 1987–89, whether assessed in the pelagic region at the larval stage by trawls and purse seine (Post et al., Ch. 15) or in the littoral zone at the juvenile stage using minifyke nets and beach seine (Johnson et al. 1992b).

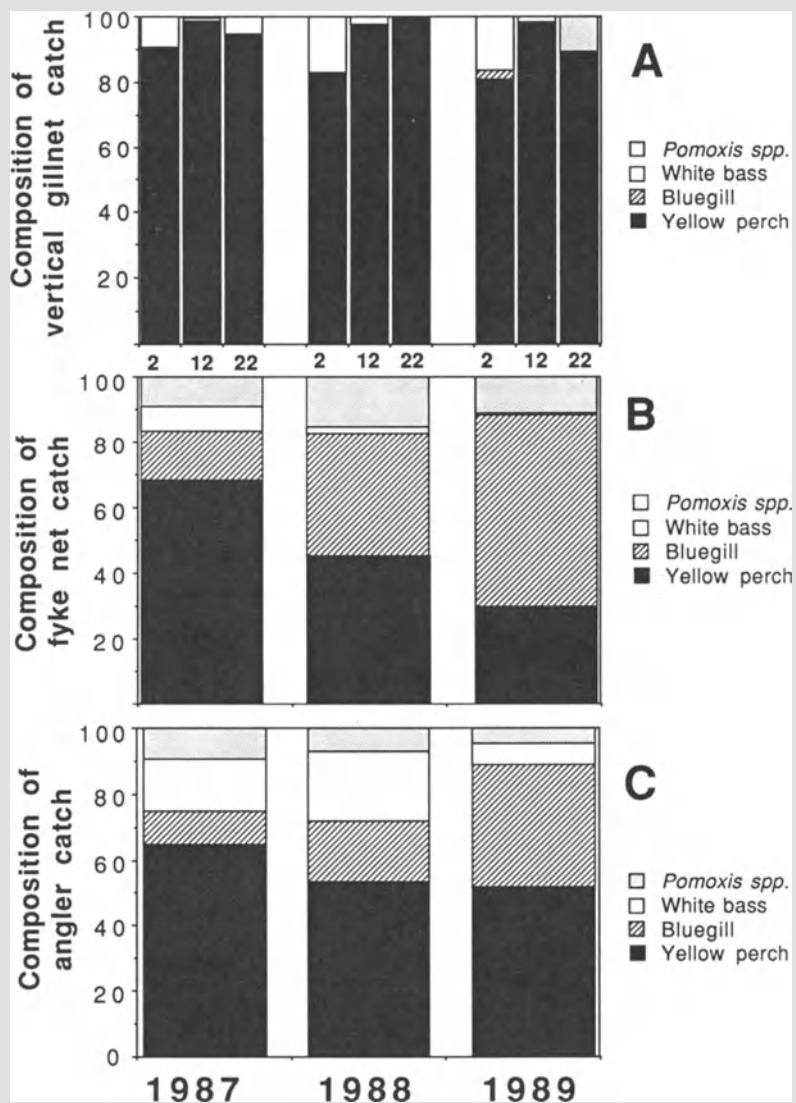
These three gear types gave consistent estimates of relative year class strength of yellow perch and bluegill. Yellow perch year class strength was greatest in 1987, slightly less in 1989, and in 1988 it was one-tenth or less of the 1987 level. And yet, yellow perch recruitment in 1987 was probably 20 times lower than the highest year class strength observed in the 1980s (Johnson et al., 1992a). Bluegill year class strength appears to have increased steadily during 1987–89, as CPUE in all gears increased each year. While estimates for crappies are inconsistent among gear types, year class strength appears to have been highest in 1987. As will be shown in the section on piscivory, variability in year class strength of large prey species is reflected in the summer and fall diet composition of piscivores. Although juvenile cisco are consumed by piscivores when they are available, recruitment of cisco has been poor since the 1987 die-off (Post et al., Ch. 15), and cisco only appeared in piscivore diets in spring 1987.

### Large Prey Fishes—Adults

Piscivores generally fed on prey smaller than 30% of their own length in Lake Mendota (Campbell 1989). Since adults of most large prey fishes were 170–250 mm in 1987–89, few piscivores were large enough to consume these prey. Only a few adult prey were found in large northern pike and walleye guts. However, this prey group is of interest because of the coupling with juvenile abundance through reproduction, and their contribution to angler catches. Further, the fishes in this group were the dominant planktivores in the lake in 1987–89 (Luecke et al., Ch. 14). Absolute abundance estimates of larger prey fishes were obtained by a mark–recapture study on perch during 1988 and by hydroacoustic surveys in all three years. Hydroacoustics can give abundance estimates in two to three broad size classes of fish. In Lake Mendota we could separate cisco (larger than 35 cm) from other large prey fishes (generally less than 25 cm, see Rudstam and Johnson, Ch. 26). But we could not distinguish species within the 12- to 25-cm size class. Hydroacoustics can only be used to estimate fish abundance in open water; areas close to the surface or bottom, and the littoral zone, cannot be examined. Hydroacoustics is particularly useful for cisco because cisco inhabit the open water, avoiding the littoral zone (Luecke et al. 1990). For other species we relied on other gear to establish the relative proportions of different large prey species. We have three sources of information: creel survey, spring fyke net catch, and monthly vertical gill net samples at 2-, 12-, and 22-m-deep water.

With the exception of cisco, adult large prey fishes are readily caught by anglers. Therefore, catch composition observed in the creel survey provides an estimate of the lakewide relative abundance of large adult prey fishes. The top four fishes caught by anglers in 1987–89 were yellow perch, bluegill, crappies, and white bass (Johnson and Staggs, Ch. 17). The relative composition of these species in spring fyke net sampling was similar to the annual creel catch (Figure 16.6). Despite the fact that fyke nets and anglers may have different species selectivities, some consistent patterns emerged from these data. Both samples indicate that adult yellow perch have declined each year. Crappie and white bass relative abundance have remained stable or have declined from 1987 to 1989, while bluegills have increased steadily in relative abundance (Figure 16.6).

Vertical gill nets, on the other hand, show perch to be the dominant large prey at all depths (excluding cisco, Figure 16.6). Centrarchids are probably underrepresented in gill net samples because their body shape makes them much less vulnerable to capture in gill nets. Even so, the abundance estimates of perch from the mark–recapture study (860,000 perch) and the abundance of “perch-size” targets from acoustics (1,100,000) were close (Rudstam and Johnson, Ch. 26), suggesting that perch was the primary pelagic planktivore in 1988.



**Figure 16-6.** Composition of catch by various methods of four large prey species (larger than 120 mm) in Lake Mendota. Vertical gill nets were set at 2, 12, and 22 m of water.

Of the three gears, the 1987–89 trend in spring fyke net catch most closely follows the trend in estimated perch abundance (approximately 500, 250, and 125 fish/ha in 1987, 1988, and 1989, respectively) computed by Luecke et al. (Ch. 14). Assuming that the different species are equally

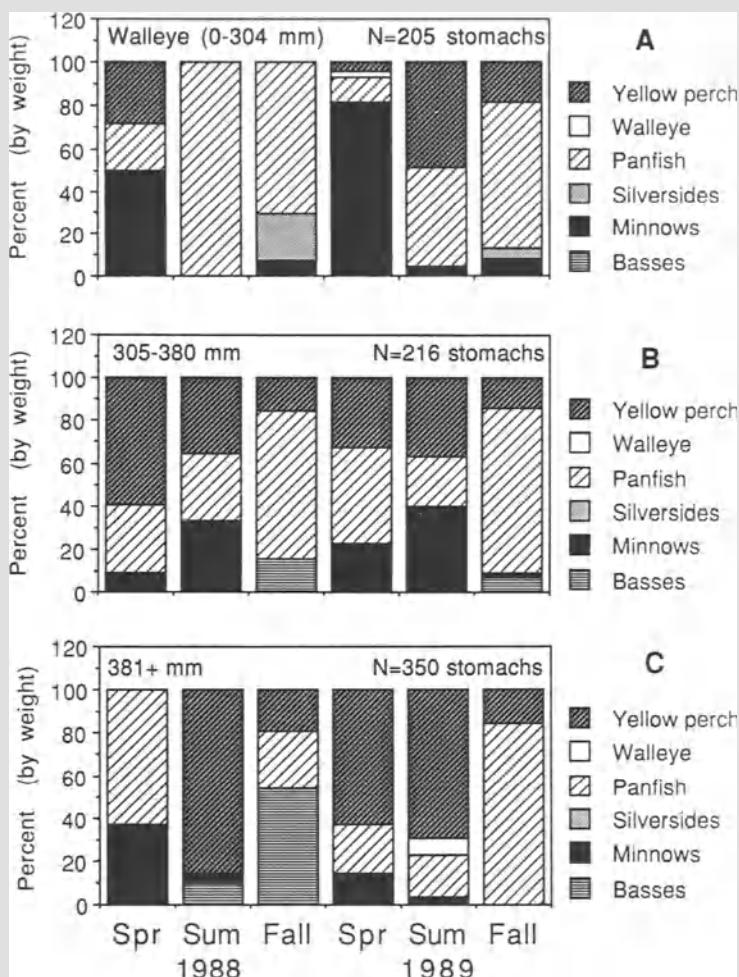
vulnerable to spring fyke nets, we calculate bluegill abundances of 110, 210, and 250 fish/ha. This increase in bluegill abundance is also evident in the angler catch (Figure 16.6) and the establishment of a large winter fishery for bluegill along the shores of Lake Mendota in January 1990. With the decline of the perch population in the lake, bluegills have become the most abundant littoral fish species and perhaps the numerically dominant planktivore in the lake.

## Piscivore Diets

### Walleye Diet

Walleye diet composition was quantified for three size classes in 1988–89. The 0- to 304-mm size class corresponds to walleyes less than age 2, 305–380 roughly corresponds to ages 2–3, and the larger than 381 mm size class was mainly walleyes older than age 4. The largest size class comprised those walleyes vulnerable to anglers. Small walleyes (Figure 16.7A) consumed mostly small littoral-zone fishes (minnows and darters) in spring of both years, when YOY fishes were not available. They consumed YOY panfish other than perch (small centrarchids and percichthyids) in summer 1988, when yellow perch recruitment was poor. They consumed a combination of yellow perch and centrarchid panfish in summer 1989, when there was a moderate perch year class. In fall of both 1988 and 1989, small walleyes ate mostly YOY panfish, but minnows and darters and silversides were also eaten, perhaps as appropriately sized YOY panfish became scarcer. In fall 1989 about 20% of the diet of small walleyes was YOY yellow perch.

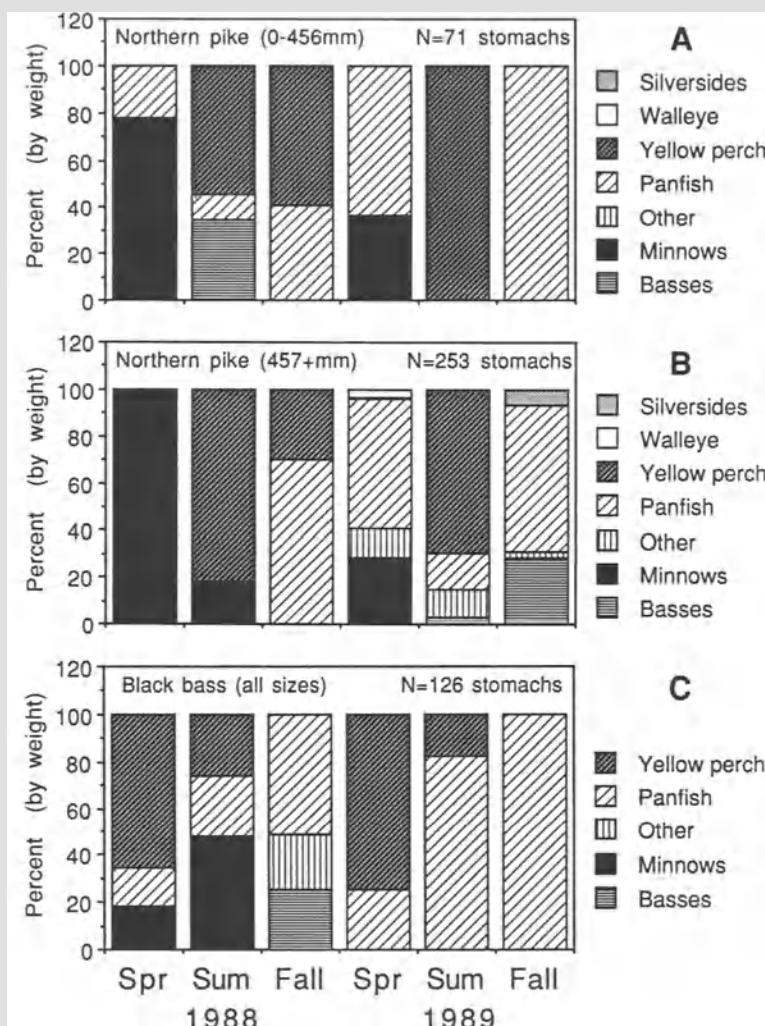
The diet of 305- to 380-mm walleyes in each season did not change between years (Figure 16.7B). Their diet in spring and summer was composed of yellow perch, panfish, and minnows and darters. In fall the diet was composed mostly of panfish, but with about 15% yellow perch and 15% YOY black bass. Large walleye diet (Figure 16.7C) was similar to that for 305- to 380-mm walleyes, but the larger walleyes consumed a greater proportion of yellow perch in most seasons and years. In 1988, when there appeared to be a large hatch of both black basses (based on mini-fyke net CPUE), about half of the diet of large walleyes in the fall was composed of basses. However, black bass did not appear in stomachs of large walleyes in 1989, as they did for 305- to 380-mm walleyes. Cannibalism by walleyes was rarely observed; about 2% of the diet of age-1 walleyes in spring 1989 (Figure 16.7A) and 5% of the diet of age-4 and older walleyes in summer 1989 (Figure 16.7C) consisted of young walleyes. However, as presented above (Piscivore Assemblage), consumption of walleyes under 200 mm by larger walleyes in early spring



**Figure 16-7.** Composition (percent by weight) of the walleye diet in Lake Mendota during 1988–89. Panfish are percichthyids and centrarchids other than *Micropterus* spp.; Minnows are minnows, shiners, and darters (*Percina* and *Etheostoma* spp.); Basses are *Micropterus* spp. N is the number of stomachs examined.

1989 was almost 20% of the young walleye biomass lost overwinter. Thus, cannibalism could be an important constraint on walleye recruitment.

Although we had fewer diet data in 1987 (181 stomachs analyzed), some general differences in walleye diet were apparent. In spring 1987 about 20% of the walleye diet was cisco. Cisco did not appear in walleye guts after spring 1987, presumably because the massive cisco summer kill



**Figure 16-8.** Composition (percent by weight) of the northern pike and black bass (smallmouth and largemouth bass) diet in Lake Mendota during 1988–89. Panfish are percichthyids and centrarchids other than *Micropterus* spp.; Minnows are minnows, shiners, and darters (*Percina* and *Etheostoma* spp.); Other includes bullheads and freshwater drum; Basses are *Micropterus* spp. N is the number of stomachs examined.

of 1987 precluded any substantial cisco recruitment in 1988–89. Perch year class strength was moderate in 1987, and about a third of the diet of all sizes of walleyes in that summer was yellow perch. The remainder was centrarchid panfish (about 60%) and minnows and darters (7%).

### Northern Pike and Bass Diet

Northern pike and bass are probably gape limited to a lesser degree than walleyes, because piscivore gape is a function of total length. Because northern pike grow faster, a 2-year-old pike is as long, and thus can probably ingest the same size fish, as a 5-year-old walleye. Black basses, with a steeper gape:length relationship, should also show a different seasonal pattern of prey choice than the more gape-limited walleye. This suggests that pike and bass should be less dependent upon YOY fishes than are walleyes because they can consume a broader range of sizes of prey. In fact, small northern pike (0–456 mm, age 1) consumed more yellow perch (Figure 16.8A) than same-age walleyes, but pike also relied heavily on small littoral zone fishes in spring when YOY fish of larger species were absent. Age-2 and older pike (larger than 457 mm; Figure 16.8B) had a similar diet to small pike, but large pike consumed more prey types including freshwater drum, bullheads, silversides, and walleye. Based on the diet and bioenergetics modeling, pike predation on small walleyes accounted for 14% of the total overwinter mortality of small walleye in 1989.

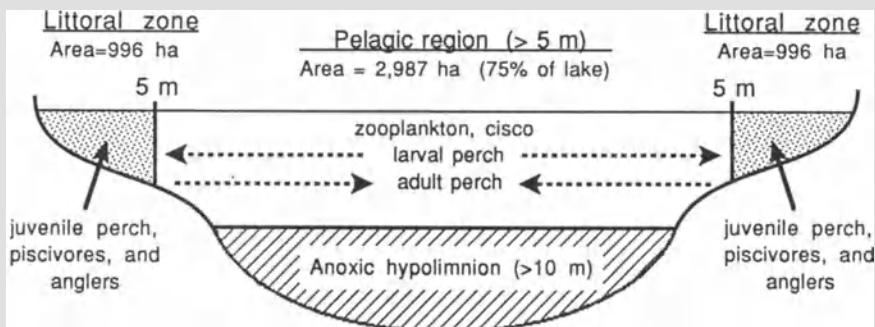
Recent pike diet differs from that observed in the earlier part of the century. During the spring and summer of 1915 and 1916, Lake Mendota pike consumed 66% yellow perch, 17% largemouth bass, and 17% minnows (Pearse 1918). Thus, at this earlier time pike were consuming more yellow perch and no centrarchid panfish. This is not entirely surprising, given that the prey community in Lake Mendota during the early part of the century was dominated by an abundant, slow-growing yellow perch population (Pearse and Achtenburg 1920) and the minnow community was much more diverse (Lyons 1989).

Black basses (smallmouth and largemouth bass) consumed a higher proportion of yellow perch in spring than other piscivore species (Figure 16.8C). The proportion of yellow perch in their diet in summer was similar in 1988 and 1989, regardless of the different year class strengths of perch observed in the two years. Black basses did not consume any yellow perch in the fall (Figure 16.8C), consuming a large proportion of panfish instead.

### Piscivore–Planktivore Interactions

#### Spatial Distribution Patterns

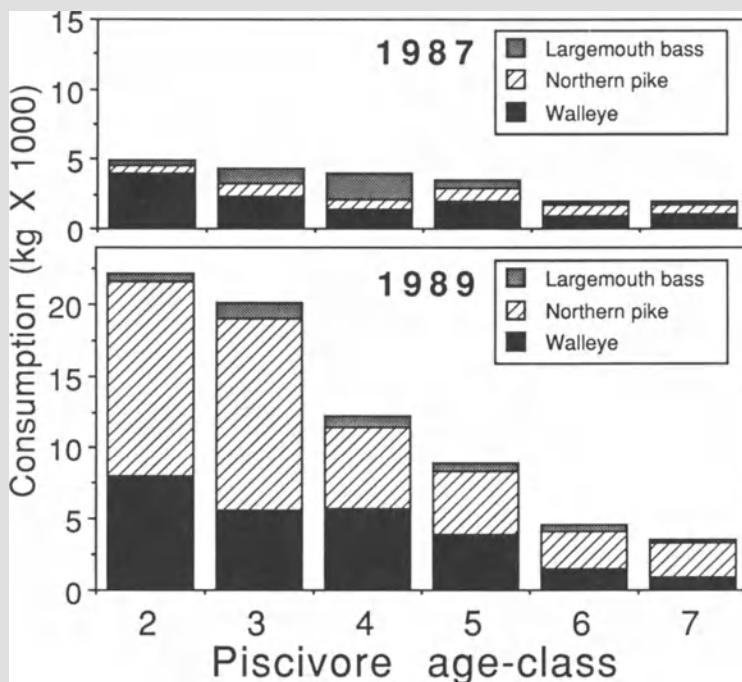
Lake Mendota's primary planktivores, cisco and yellow perch, inhabit the pelagic region during the growing season (Luecke et al., Ch. 14). Originally, walleyes were stocked because they were expected to act as pelagic predators, feeding on these planktivores suspended above the



**Figure 16-9.** Schematic of Lake Mendota during summer. Here we define the littoral zone as 0–5 m.

thermocline in waters greater than 10 m deep. However, gill net sampling and radio telemetry suggest that walleyes (and other piscivores) are not pelagic during summer and mainly inhabit depths less than 5 m. The spatial disassociation of piscivores and the main pelagic planktivores could imply an uncoupling of piscivory and planktivory. However, at least in the case of yellow perch, only the larvae and adults are pelagic. The juveniles inhabit the littoral zone (McCarty 1990), where they coincide with piscivores. The littoral zone is also a nursery area for primarily littoral planktivores such as bluegill and crappies. Because of their lower temperature preference, all ciscos remain pelagic at the coolest temperature with sufficient dissolved oxygen. The spatial distribution of Lake Mendota's piscivore–planktivore community in summer is illustrated in a schematic of the lake (Figure 16.9). This distribution pattern, in which juvenile perch, piscivores, and anglers are restricted to the littoral zone, has a number of implications for predator–prey interactions.

First, most of the lake's piscivores are confined to a zone that is 25% of the lake's surface area. Thus, compared to lakes with an equal lake-wide piscivore density and more free-ranging piscivores or a larger littoral:pelagic area ratio, piscivory in the littoral zone is up to four times more intense in Lake Mendota. Small littoral zone fishes (*sensu* Lyons 1989) could be subjected to intense predation pressure in spring before YOY of large prey species appear, or when year class strength of large prey species is poor. Magnuson and Lathrop (Ch. 11) suggest that piscivory could be a cause of the documented decline in small littoral zone fishes. Second, cisco have a refuge from predators in the part of the lake where their food resources, zooplankton grazers, are most available. Prospects for top-down effects would be poor if there had not been a cisco summer kill in 1987. Third, angler catch rates should respond more rapidly to increases in lakewide density of piscivores because of a smaller



**Figure 16-10.** Total consumption by three Lake Mendota piscivore populations in 1987 and 1989, computed from measured population parameters using a bioenergetics model.

area of the lake anglers need to search. Piscivory by anglers is an important component of Lake Mendota's food web (Johnson and Staggs, Ch. 17).

Given our findings about the spatial distribution of piscivores and planktivores, the importance of the littoral zone in lake food web interactions initially may have been underestimated. However, a new collaborative project between the WDNR and the University of Wisconsin (UW) Center for Limnology (Littoral Zone Fisheries Project) is just beginning. This project fills many of the gaps in our continuing study of the Lake Mendota food web.

#### Biomass Consumed and Piscivore Utility

A fishery model [Generalized Inland Fishery Simulator (GIFSIM); Taylor 1981] was used to forecast piscivore population biomass under various harvest regulations and stocking scenarios. Estimates of future consumption by piscivore populations were generated by projecting popula-

**Table 16-4.** Criteria for evaluating candidate piscivores to be used in biomanipulation. Availability for stocking is specific to Wisconsin and is based on current WDNR hatchery priorities and production capabilities. Post-stocking survival is based on results from standard WDNR stocking practices that differ among species. Black basses (smallmouth and largemouth bass) are only raised for special situations and are not sufficiently available to be considered as a stocked piscivore.  $T_{\text{Opt}}$  is optimum temperature for consumption (Hewett and Johnson 1987).

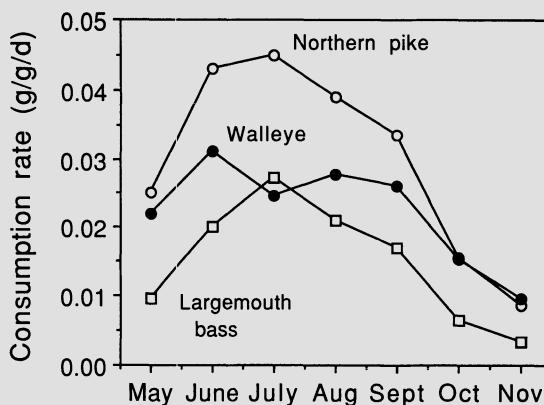
Piscivory criterion	Walleye	Northern pike	Black bass
Availability for stocking	High	Low	Low
Post-stocking survival	Low	High	Low
Angler harvest demand	High	Low	Low
Trophy regs. acceptable?	Maybe	Yes	Probably
Hooking mortality	Low	High?	Low
Natural mortality	Low	High?	Low
Growth rate (in weight)	Low	High	Low
$T_{\text{Opt}}$ for consumption	22.0	24.0	27.5
Planktivores in diet?	Yes	Yes	Maybe

tion size and age structure with the fishery model, and using these as inputs to a bioenergetics model (see Johnson and Staggs, Ch. 17).

To compute biomass of prey consumed by each piscivore population, field estimates of abundance, growth, diet, and thermal history were used in the Hewett and Johnson (1987) bioenergetics model. Mortality rates were also required for this analysis; total mortality rates were generated from known fishing mortality rates (Johnson and Staggs, Ch. 17) and assumed age- and species-specific annual natural mortality rates of between 0.10 and 0.25. Combining these two modeling approaches allowed us to forecast changes in piscivore populations resulting from management efforts and to assess how these changes would affect predation pressure by piscivores.

Total prey biomass consumed by age-2 and older piscivores increased substantially between 1987 and 1989 (Figure 16.10). Between 1987 and 1989, total consumption by walleyes increased 120%. Bass biomass remained relatively stable during the period, and thus so has bass consumption. Consumption by northern pike increased from 1987 to 1989 by a surprising 780%, overtaking total consumption by the walleye population.

Exploring the reasons for interspecies differences in the dynamics of piscivory points out important differences in the utility of each species in biomanipulations (Table 16.4). Rapid individual growth of pike relative to other Lake Mendota piscivores (Table 16.2), and high survival of stocked fingerlings, suggests a fast-acting piscivore. Predatory inertia

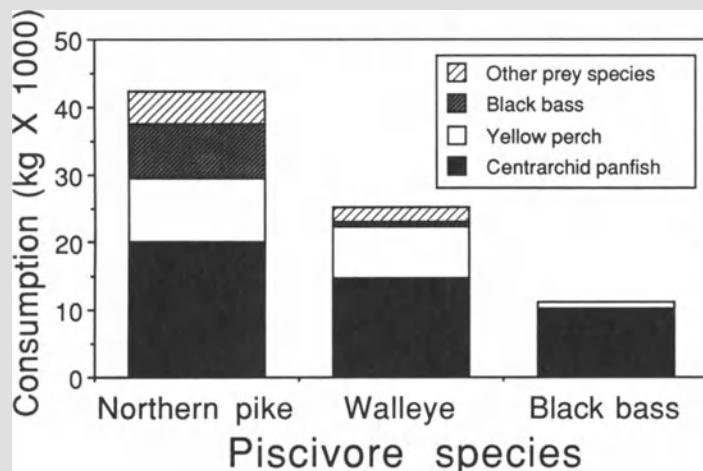


**Figure 16-11.** Maximum consumption rate of 1-kg piscivores computed with a bioenergetics model from water temperatures observed in Lake Mendota in summer 1989.

(Stewart et al. 1981) of pike may be low, however, if stocking is discontinued, hooking and/or natural mortality is high, or fishing mortality is not controlled through regulations. Because of their rapid growth, “trophy” harvest regulations may be required if pike are to remain in the lake for a sufficient period of time to maximize consumption. Natural mortality of northern pike appears to be high and density dependent in some northern Wisconsin lakes (Snow 1974, 1978; Kempinger and Carline 1978).

Northern pike fingerlings are usually stocked in September in Wisconsin at a much larger size than walleye or bass fingerlings (Klingbeil 1990b), and their survival in Lake Mendota has been about 20 times higher than for walleye. Piscivory by walleye may be slower to develop because of low survival of stocked fingerlings and a lower individual growth rate. Walleyes are highly prized by anglers for food, and thus restrictive harvest regulations may be difficult to institute. Black bass are not raised in hatcheries to any significant extent in Wisconsin. The growth rate of largemouth bass in Lake Mendota is lower than that of walleye. Low availability for stocking and low growth rate make largemouth bass the least desirable candidate for biomanipulation in Wisconsin.

Bioenergetically, northern pike are superior to walleye and largemouth bass at the Lake Mendota thermal regime. Northern pike have a higher maximum consumption rate (Figure 16.11) and an optimum temperature for consumption better suited to water temperatures common to Lake Mendota (Table 16.4). Largemouth bass consumption rate is limited by cool temperatures, and walleye maximum consumption rate undergoes a midsummer depression because of high temperatures.

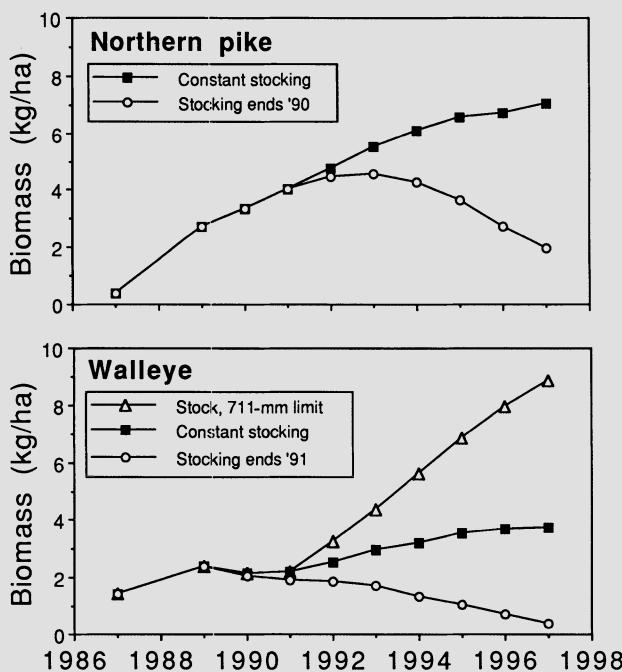


**Figure 16-12.** Total consumption of various prey types by three Lake Mendota piscivore populations in 1989, computed from measured population parameters using a bioenergetics model. Centrarchid panfish are centrarchids other than *Micropterus* spp. Black bass are *Micropterus* spp. Other prey species includes minnows, shiners, darters, silversides, bullheads, and freshwater drum.

Prey selection should also be considered when judging utility of piscivores for biomanipulation experiments. In 1989, when total piscivory was greatest, age-2 and older northern pike consumed a slightly higher biomass of centrarchid panfish and yellow perch than did age-2 and older walleyes (Figure 16.12). All piscivores fed on the dominant planktivores in the lake: mostly centrarchid panfish, followed by yellow perch. However, black bass consumed almost entirely centrarchids, and walleye ate proportionally less bass and other prey than did northern pike.

### Predation Inertia

Consumption by either the 1989 walleye or northern pike population alone was greater than that by all piscivores combined in 1987 (Figure 16.10). These increases arose primarily from recruitment of fish from the 1986–87 pike and 1985–87 walleye year classes. Thus, at present, lakewide piscivory is dominated by a few young age classes of mostly stocked walleye and northern pike. Of course, we expect further increases in piscivore consumption as 1988, 1989, and later stocked year classes grow and the biomass of populations increases. However, projected increases in walleye biomass are not as great as predicted in 1987 (Johnson et al., 1992a). On the other hand, northern pike biomass and consumption responded more strongly to management than initially pre-



**Figure 16-13.** Biomass of age 1–9 northern pike and age 1–10 walleyes in Lake Mendota projected with the GIFSIM fishery model (Taylor 1981). “Constant stocking” means stocking continues at 1987–89 rates. Northern pike simulations assume an 813-mm minimum size limit starting in 1988. “Stock, 711-mm limit” refers to the simulation with constant stocking and a 711-mm minimum size limit established in 1991. Other walleye simulations assume a 381-mm minimum size limit during 1988–90 and a 457-mm size limit starting in 1991.

sumed. Given that about 33 times more walleye fingerling than pike were stocked, we initially discounted the importance of pike.

Our current projections of piscivore biomass show northern pike continuing to increase with a peak in 1993, while walleye biomass declines from a peak in 1989 (Figure 16.13). These simulations assume 1989 fishing mortality rates, 457- and 813-mm minimum size limits for walleye and pike, respectively, and an end to stocking of pike in 1990 and of walleye in 1991. Continued stocking or a modest amount of natural recruitment would allow both populations to increase through 1997, but pike biomass (and the corresponding consumption) continues to outpace walleye biomass under current harvest regulations (Figure 16.13). Higher survival of stocked fingerlings, faster growth rate, and a higher minimum size limit keep pike biomass above that of walleyes. Walleyes are currently subjected to intense fishing pressure (Johnson and Staggs, Ch. 17)

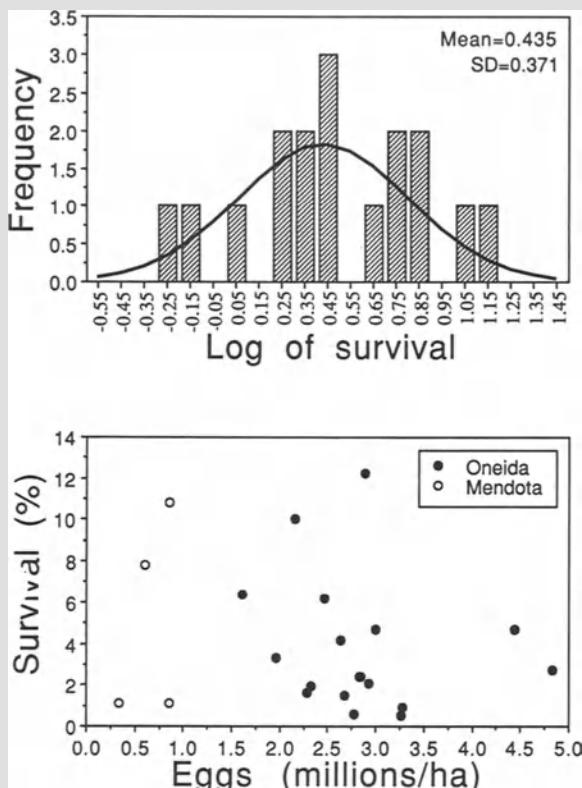
that severely limits predation inertia. A 711-mm “trophy” regulation would essentially eliminate fishing mortality on walleye, protecting fish beyond age 10, while pike exceed their 813-mm size limit at around age 7. Thus, a trophy regulation on walleyes would allow their biomass to overtake that of pike (protected by an 813-mm limit) by 1995.

### Effects on Prey Populations

We believe we can forecast piscivore biomass and consumption more confidently than we can predict the effects of piscivory on the prey populations (but see Johnson and Staggs, Ch. 17). Recruitment of piscivores arises primarily from stocking and not natural reproduction, and stocking quotas are known in advance. Recruitment of prey is less predictable. For example, year class strength of yellow perch is notoriously variable in Lake Mendota (this chapter) and in other systems (Forney 1971; Mills and Forney 1987), with a decided abiotic component (Clady 1976). At any given predicted level of piscivore consumption, a wide range of initial prey year class strengths is possible, depending on early survival. Thus, the importance of predation in controlling planktivore abundance depends on reproductive success of the planktivores.

Still, we can bound the problem by asking under what levels of adult prey biomass and prey recruitment will piscivory be an important force. This question is particularly interesting relative to the yellow perch population, because we have seen a decline in adult biomass and generally poor recruitment since 1985 (Luecke et al., Ch. 14). With burgeoning piscivore biomass concurrent with declining perch abundance, and the extreme popularity of yellow perch to anglers, we are interested in evaluating the importance of predation to future abundance of this species. More specifically, we wanted to know how many more years the perch population could sustain poor reproductive success before piscivores could consume all YOY perch produced from a high perch egg survival rate.

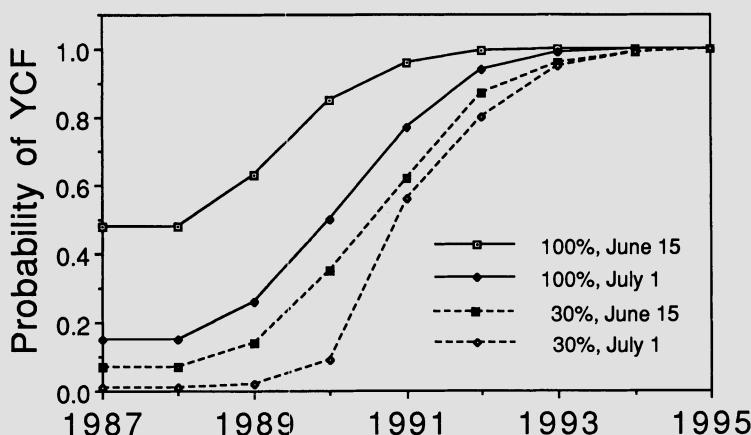
To address this question we proceeded as follows. First, we computed the number of eggs produced by the perch population each year from 1987 to 1995 using data from 1987–89 on adult perch abundance, a body size–fecundity relationship from Post and Rudstam (Ch. 19), an assumed total annual mortality rate of 50%, and the assumption that no recruitment occurred during this period. The probability of survival from egg to 18-mm larvae was derived from data on Oneida Lake, New York (Mills and Forney 1987). The log-transformed survival rates are reasonably well described by a normal probability density function (PDF) with a mean 0.435 and standard deviation of 0.371 (Figure 16.14). Egg survival rates in Lakes Oneida and Mendota do not appear to be density dependent, and



**Figure 16-14.** Upper panel: Frequency distribution of  $\log_{10}$  of egg survival (%) of yellow perch in Oneida Lake (date from Mills and Forney 1987), and a normal probability distribution fit to these observations. Lower panel: Egg production and survival from egg to 18-mm larvae in Oneida Lake (Mills and Forney 1987) and Lake Mendota.

Lake Mendota egg survival rates observed in 1987–90 fall within the range of values for Oneida Lake (Figure 16.14).

Next, bioenergetics model estimates of prey biomass consumed by walleye and pike populations from 15 June 1989 to 15 June 1990 under various piscivore diet scenarios were converted to numbers of perch consumed by dividing with the mean YOY perch weight at each time interval. We then computed the egg survival rate necessary to provide at least the number of YOY consumed from the estimated egg production by Lake Mendota perch. Finally, we used the PDF of egg survival rates to compute the probability of having less than the required survival rate. This then is the probability of having no YOY perch survive the year, which we define as a year class failure (YCF).



**Figure 16-15.** Probability of year class failure (YCF) in the yellow perch population using four walleye and northern pike diet scenarios. Percentages refer to the percentage of YOY yellow perch in piscivore diets. Dates refer to the date at which piscivores begin to feed on YOY yellow perch. See text for details on computations used to generate the curves.

In this analysis, adult perch biomass is at its peak in 1987 and 1988, and consequently the probability of a year class failure due to predation is lowest (Figure 16.15). As adult perch biomass declines, the probability that piscivores could consume all the YOY perch produced increases rapidly until 1993, when piscivore control is very likely (Figure 16.15).

Early in the simulation, when perch reproductive potential is relatively high (1987–90), assumptions about piscivore diet have pronounced effects on the importance of piscivory. Later, as adult biomass declines, year class failure becomes more likely, regardless of predation pressure. Effects of diet assumptions are illustrated by four piscivore diet scenarios: (1) pike and walleye consume only YOY perch, starting on 15 June when perch are 18 mm; (2) consumption of YOY perch begins on 1 July; (3) 30% of piscivore diet is YOY perch beginning on 15 June; (4) 30% of piscivore diet is YOY perch beginning on 1 July.

Simply deferring predation for 2 weeks (15 June to 1 July) substantially reduces the impact of predation on YOY perch abundance. This analysis demonstrates the well-established principle that early life history is critical to an understanding of recruitment dynamics, and it uncovers an important gap in our knowledge of food web interactions in Lake Mendota. More research on the fate of small perch after they are lost from the purse seine is needed to adequately assess the importance of piscivory for yellow perch recruitment.

Our probability approach provides a framework for dealing with uncertainty in prey recruitment. Remember that the probabilities in Figure

16.15 are conditional on no recruitment since 1987. With the highest piscivore impact scenario, the probability of actually getting no recruitment in all years 1987 to 1995 is about 0.15 (the product of the annual probabilities of year class failure). Further, any recruitment to the perch population will set back the time course of probabilities depicted in Figure 16.15, because recruits that are produced should be included in calculations of future reproductive potential. Also, walleye and pike are not dynamically coupled to their prey, and decreased growth and consumption or switching to alternative prey at low perch abundance are not included (see Post and Rudstam, Ch. 19, for an analysis of a dynamic walleye–perch model). Thus, we view the above analysis as a problem-bounding exercise rather than an explicit forecast of Lake Mendota perch recruitment in the 1990s.

### Concluding Remarks

We were surprised by the answers to some of the questions laid out at the start of this chapter. The summer distribution of piscivores, especially walleyes, in water less than 5 m deep underscores the importance of the littoral zone in Lake Mendota. Predation pressure exerted by piscivores and anglers is intensified here because of the small area of the littoral zone compared to the pelagic zone in Lake Mendota. Despite a 30-fold higher stocking rate of walleyes, northern pike biomass responded more strongly to management. Cannibalism, although difficult to observe, is probably an important constraint on walleye recruitment because of the small size of stocked fingerlings. In the face of intense fishing pressure, the greater protection afforded pike by an 813-mm minimum size limit also allowed stocked pike to flourish compared to walleyes. High fingerling survival and growth rate, combined with the ease with which restrictive harvest regulations were enacted, make northern pike the most effective piscivore for the Lake Mendota biomanipulation.

Piscivores face an imposing and possibly expanding exploitation pressure from Lake Mendota anglers who seek to enjoy returns from this showcase project. Our projections with fishery and bioenergetics models have identified fishing mortality as one of the major constraints on the effectiveness of this effort to dramatically increase piscivore predation pressure. High minimum size limits (trophy regulations) on piscivores would substantially improve predation inertia. However, translating these changes into forecasts of their effects on prey populations is challenging because of the importance of poorly understood early life history dynamics of the prey. This realization prompted us to accept variability in prey recruitment and use it as a measure of uncertainty in predicting the importance of piscivore–planktivore interactions.

The planktivore populations prior to 1987 probably would have been resistant to the effects of stocked walleye and pike because of the large biomass of planktivores and the small spatial overlap between cisco and piscivores. Because the summer kill in 1987 virtually eliminated cisco and because of the poor year class success of perch in 1987–89, there is presently (1990) the potential for piscivory by stocked game fish to be an important force regulating yellow perch recruitment. However, this conclusion depends heavily on assumptions about consumption rates of the piscivores on small (18–45 mm) yellow perch. Refining our predictive capability will require a better understanding of early life history of Lake Mendota fishes, suggesting critical data needs for our continuing study of piscivore–planktivore interactions in Lake Mendota.

*Acknowledgments.* Thanks to Kirsten Work, Denise Schael, Brady Phillips, Mike Miller, John McCarty, and Jim Yasko for processing piscivore guts; Chris Luecke, Tom Pellett, and The Yahara Fisherman's Club, for assisting with the sampling; Bill Jaeger and the WDNR Southern District Operations Crew for raising and stocking walleyes, maintaining the equipment, and helping to keep the sampling program running smoothly. Funding was provided by the Federal Aid in Sport Fish Restoration Act under F-95-P and the WDNR.

## References

- Becker GC (1983) Fishes of Wisconsin. University of Wisconsin Press, Madison
- Brock TD (1985) A eutrophic lake: Lake Mendota, Wisconsin. Springer-Verlag, New York
- Campbell EA (1989) Laboratory examination of size-selective predation by small walleye (*Stizostedion vitreum*) on yellow perch (*Perca flavescens*). M.Sc. Thesis, University of Wisconsin, Madison
- Carlander KD (1977) Handbook of freshwater fishery biology. Iowa State University Press, Ames
- Clady, MD (1976) Influence of temperature and wind on the survival of early stages of yellow perch, *Perca flavescens*. J. Fish. Res. Board Can. 33:1887–1893
- Fago DM (1990) Lake Mendota summer distribution of predatory fishes. Progress Report, Federal Aid in Fish Restoration Project F-83-R, Wisconsin Department of Natural Resources, Madison
- Forney JL (1967) Estimates of biomass and mortality rates in a walleye population. N.Y. Fish Game J. 14:176–192
- Forney JL (1971) Development of dominant year classes in a yellow perch population. Trans. Am. Fish. Soc. 100:739–749
- Gilbert SJ, Johnson BM (1992) An efficient, easy-to-use stomach pump for live fish. Administrative Report, Wisconsin Department of Natural Resources, Madison (in press)

- Hewett SW, Johnson BL (1987) A generalized bioenergetics model of fish growth for microcomputers. Technical Report WIS-SG-87-245, University of Wisconsin Sea Grant Institute, Madison
- Johnson BM, Stein RA, Carline RF (1988) Use of a quadrat rotenone technique and bioenergetics modeling to evaluate prey availability to stocked piscivores. *Trans. Am. Fish. Soc.* 117:127–141
- Johnson BM, Luecke C, Stewart RS, Staggs MD, Gilbert SJ, Kitchell JF (1992a) Forecasting effects of harvest regulations and stocking on prey fish communities in a eutrophic lake. *No. Am. J. Fish. Manag.* (in press)
- Johnson BM, Stewart RS, Gilbert SJ (1992b) Ecology of fishes in the Madison Lakes. Fisheries Management Report 148, Wisconsin Department of Natural Resources, Madison
- Kempinger JJ, Carline RF (1977) Dynamics of the walleye (*Stizostedion vitreum vitreum*) population in Escanaba Lake, Wisconsin, 1955–1972. *J. Fish. Res. Board Can.* 34:1800–1811
- Kempinger JJ, Carline RF (1978) Changes in population density, growth, and harvest of northern pike in Escanaba Lake. Technical Bulletin 104, Wisconsin Department of Natural Resources, Madison
- Klingbeil JH (1990a) Fish management reference book. Wisconsin Department of Natural Resources, Madison
- Klingbeil JH (1990b) Fish management handbook. Wisconsin Department of Natural Resources, Madison
- Knight RL, Margraf FJ, Carline RF (1984) Piscivory by walleyes and yellow perch in western Lake Erie. *Trans. Am. Fish. Soc.* 113:677–693
- Lathrop RC, Nehls SH, Brynildson CL, Plass KR (1992) The fishery of the Yahara lakes. Technical Bulletin, Wisconsin Department of Natural Resources, Madison (in press)
- Luecke C, Vanni MJ, Magnuson JJ, Kitchell JF, Jacobsen PJ (1990) Seasonal regulation of Daphnia populations by planktivorous fish: Implications for the clearwater phase. *Limnol. Oceanogr.* 35:1718–1733
- Lyons JJ (1989) Changes in the abundance of small littoral-zone fishes in Lake Mendota, Wisconsin. *Can. J. Zool.* 67:2910–2916
- McCarty, JP (1990) Diel periodicity of movement and feeding of yellow perch (*Perca flavescens*) in Lake Mendota, Wisconsin. *Trans. Wis. Acad. Sci. Arts Lett.* 76:65–76
- Mills EL, Forney JL (1987) Trophic dynamics and development of freshwater pelagic food webs. In Carpenter SR (ed) *Complex interactions in lake communities*, Springer-Verlag, New York, pp 11–30
- Novotny DW, Priegel GR (1974) Electrofishing boats: Improved designs and operational guidelines to increase the effectiveness of boomshockers. Technical Bulletin 73, Wisconsin Department of Natural Resources, Madison
- Pearse AS (1918) On the food of the shore fishes of certain Wisconsin lakes. *Bull. U.S. Bur. Fish.* 35:245–292
- Pearse AS, Achtenburg H (1920) Habits of yellow perch in Wisconsin lakes. *Bull. U.S. Bur. Fish.* 36:297–362
- Snow HE (1974) Effects of stocking northern pike in Murphy Flowage. Technical Bulletin 79, Wisconsin Department of Natural Resources, Madison
- Snow HE (1978) Responses of northern pike to exploitation in Murphy Flowage, Wisconsin. In Kendall R (ed) *Selected coolwater fishes of North America*.

- American Fisheries Society Special Publication 11, Washington, D.C., pp 320–327
- Stewart DJ, Kitchell JF, Crowder LB (1981) Forage fishes and their salmonid predators in Lake Michigan. *Trans. Am. Fish. Soc.* 110:751–763
- Taylor MW (1981) A generalized inland fishery simulator for management biologists. *No. Am. J. Fish. Manage.* 1:60–72
- Wahl DH (1982) Daily ration, feeding periodicity and prey selection of sauger (*Stizostedion canadense*) in the Ohio River. M.Sc. Thesis, Virginia Polytechnic Institute and State University, Blacksburg



**Plate 7.** Response of the angling public to the Lake Mendota fishery. This scene is typical of many days during the early part of each winter.

# 17

## The Fishery

**Brett M. Johnson and Michael D. Staggs**

### **Introduction**

Lake Mendota has been a popular fishing lake throughout the twentieth century (Plate 7). Historically, the fishery has been supported primarily by planktivorous fishes. Well known for its perch fishing since the turn of the century, Lake Mendota was even considered the perch capital of the Midwest in the 1950s (Lathrop et al., *in press*). Walleye were never very abundant, but northern pike sustained an excellent game fishery until recently. Over the past 30 years, habitat degradation, liberal harvest regulations, and sporadic stocking have made northern pike and walleye stocks unstable. By the late 1980s, perch fishing was still moderately good, but game fish stocks were low, with generally poor game fishing opportunities.

In addition to a thorough assessment of the management potential of biomanipulation, an equally important objective of the experiment was to dramatically improve sport fishing on Lake Mendota. In fact, this project was dubbed a “showcase management” project by the management agency (Wisconsin Department of Natural Resources, WDNR), aimed at showcasing the ability of fisheries management to make fishing better when efforts are focused on an important resource. In demonstrating this ability, considerable effort was devoted to making our constituents aware of our efforts, with the hope of gaining greater public support for future fisheries management programs.

To evaluate our efforts at improving the Lake Mendota fishery, a sophisticated creel survey was designed for this study. While monitoring

responses in the fishery, it became apparent that sport fishing was having a significant impact on the course of the biomanipulation experiment and on our expectations for improvements in piscivore biomass. This finding spurred a reevaluation of management objectives and approaches and stimulated investigations of the role of angling in aquatic food webs.

In this chapter we will discuss (1) how we have showcased the intensified management on Lake Mendota, (2) how the character of the fishery has changed, (3) the management implications of our findings for long-term success on Lake Mendota and for future showcase management efforts, and (4) the potential influences of angling in food web management.

### **Assessing the Fish Populations and the Fishery**

A broad range of assessment techniques was used to measure fish population parameters such as abundance, growth, size and age structure, diet, and distribution. These techniques are described in Johnson et al. (Ch. 16).

A year-round, 24-h/day access point creel survey was conducted on Lake Mendota from January 1987 through December 1989. Randomization of clerk schedules was done using the “bus-route” method of Robson and Jones (1989). The day was divided into three nonoverlapping 8-h strata and unequal waiting times were assigned to each access point based on expected use. The entire lake was covered once in each shift. During the prespecified waiting time at each site, the clerk recorded the number of boat or ice-angling parties that started or completed trips and made an instantaneous count of the number of anglers along the shore. Sampled days were stratified by month and weekday/weekend, with all weekends and three randomly selected weekdays sampled each week.

Methods of Robson and Jones (1989) were used to calculate boat and ice-angling efforts within each stratum except that initial estimates were of total fishing trips. Total hours of shore angling were calculated by multiplying the mean instantaneous count for each stratum by the stratum duration (Staggs 1989). Variance of both was based on the approximation given in Robson and Jones (1989).

Total harvests for boat and ice anglers were calculated separately for each stratum as the mean catch per party from the completed trip interviews multiplied by the estimated number of angling trips. Total harvest by shore anglers was calculated separately for each stratum as the mean catch per hour from both complete and incomplete interviews, times the estimated number of shore-angling hours (Staggs 1989). A standard formula for the variance of the product of two independent variables was used (Mood et al. 1974). Shore-angling catch rate was the total fish caught divided by the total hours fished by all anglers interviewed.

Catch rate variance was estimated using a second-order Taylor series approximation for the ratio of two random variables (Mood et al. 1974). Species-specific catch rates for all fishing methods were calculated using only interviews of parties specifically fishing for a particular species (Staggs 1989).

Total harvest estimates were obtained by summing individual stratum estimates and variances. Boat and ice-angling trip estimates were multiplied by the average trip length and number of anglers, and added to shore angling effort estimates to get total angling effort. Boat and ice-angling trips variance estimates also were expanded using the formula for the product of two independent variables (Mood et al. 1974), and summed with shore angling effort variances to get total variance. Pooled catch rates were made using a weighted average of individual stratum estimates with effort as the weighting factor.

Exploitation rates of walleye, largemouth bass, northern pike, and perch were computed from the total harvest (by age) generated by the creel survey divided by mark-recapture population estimates by age for each species. Estimates for smallmouth bass could not be computed because smallmouth were not vulnerable to sampling gear used in marking fish for population estimates.

### Tools for Managing the Fishery

We used two simulation models, the Generalized Inland Fishery Simulator (GIFSIM) and a bioenergetics model (Hewett and Johnson 1987), to forecast responses of the Lake Mendota fishery and fish community to various management initiatives. Although both techniques commonly are used independently, our work showed the utility of using the two models in tandem (Johnson et al., 1992a). Because of difficulties such as variable year class strengths of predators and prey, compensatory responses, and a lack of feedback from prey to predators, our modeling approach is probably most suited to evaluating management options on a short-term (~10 years) time frame. These tools are also probably inadequate to address the question of the actual impact of piscivory on planktivore population dynamics. A model more appropriate to larger-scale questions is presented by Post and Rudstam (Ch. 19).

The GIFSIM model is an age-structured computer model developed to provide freshwater fisheries managers with a flexible and easy-to-use analytical device for evaluating prospective management actions (Taylor 1981). The model is well suited to a variety of simulation problems, including effects of harvest regulations and supplemental stocking. Our simulations assumed constant recruitment from stocking, constant fishing and natural mortality rates, and growth rates independent of piscivore density. Rates were age-specific and they varied seasonally from January–

February (ice fishing season), to March–April (spawning, no fishing), May–October (open-water fishing season), and November–December (low fishing pressure).

Bioenergetics models estimate the biomass of food consumed by a fish population using physiological information about the predator, observed abundance and growth, and some information about the temperatures inhabited by the predators during the period in question. Diet information can be used to generate the biomass of particular species consumed by the predator population.

After gathering data on walleye demographics and fishing mortality in 1987, GIFSIM was used to forecast the effects of the proposed stocking and various harvest regulations on walleye population structure (Johnson et al., 1992a). These predictions were next input to the bioenergetics model to compute differences in projected consumption of planktivores by piscivores under various stocking and piscivore harvest regimes. These modeling tools allowed us to quickly assess the influence of unanticipated changes in the fishery or other input parameters on our expectations about piscivory, and also to reassess the adequacy of harvest regulations for protecting piscivore stocks.

### Initial Status of Piscivore Populations

Northern pike stocks were at an ebb when sampling began in spring 1987. Catch-per-effort in fyke nets in spring 1987 was the lowest for which comparable data were available (Johnson et al. 1992b), and indeed the lake did possess an exceptional northern pike population until relatively recently. Mark–recapture work estimated adult northern pike abundance at less than 1,314 fish of several year classes.

The walleye population was dominated by young fish arising from stocking in 1986 and a combination of stocking and natural reproduction in 1985. About 75% of the walleyes were under 380 mm; the remainder were mostly remnants of large year classes in the late 1970s (Johnson et al., Ch. 16). Despite being self-sustaining, smallmouth and largemouth bass were not abundant (Johnson et al., Ch. 16).

Historical records indicate that Lake Mendota never had an extensive walleye population and it is uncertain whether the walleye is native to Lake Mendota (Magnuson and Lathrop, Ch. 11). Large fingerling stockings during 1967–77, a large natural year class in 1978, and the concurrent decline of northern pike made walleye the most abundant game fish in the community in the 1980s. However, by the late 1980s the fishable stock of walleye had dwindled, and comparisons with past creel and fish population surveys indicate a general decline in game fish stocks (Lathrop et al., in press). In spring 1987, adult density of all piscivores combined was estimated at less than 2 fish/ha. Planktivores, on the other

hand, especially yellow perch, bluegill, and black crappie, were abundant and the size structure was desirable to anglers. Thus, at the time this project began, Lake Mendota was a panfish-dominated lake with poor game-fishing opportunities.

This condition probably was exacerbated during the last 20–30 years by at least three factors. Until relatively recently, many fisheries managers believed that a population could not be overfished by hook-and-line angling (Kempinger et al. 1975; Snow 1978). Thus, to avoid needlessly restricting angler expectations and potential opportunity, liberal harvest regulations (usually only a daily bag limit) were the norm for game fish species in Wisconsin, and Lake Mendota was no exception. Unfortunately, much of the research that supported liberal regulations was conducted in lakes with relatively undisturbed habitat and naturally reproducing game fish populations. In recent years there has been more concern that angling can exert a significant influence on fish populations, especially on population size structure (Snow 1981; Olson and Cunningham 1989). At least in systems with marginal recruitment or those sustained by stocking, sport fishing also limits total abundance.

A second factor contributing to the decline of piscivores, particularly of northern pike, has been degradation of spawning habitat. Wetlands are required for successful pike reproduction. By 1940 about 20% of the adjacent wetlands had been lost, and by 1980 this number increased to 42% (Magnuson and Lathrop, Ch. 11). Since the late 1970s, lake levels have been drawn down in winter to prevent high water in spring (Magnuson and Lathrop, Ch. 11). Low lake levels in spring cause reduced access to the remaining pike spawning habitat.

Finally, sporadic stocking in the face of rising fishing mortality and failing natural reproduction has not provided sufficient recruits to sustain populations. During 1974–86 walleye fingerlings were only stocked in three years (Johnson et al., Ch. 16). Northern pike fingerlings have been stocked every year since 1981, but in much lower numbers. When comparing northern pike and walleye fingerling stocking quotas, keep in mind that pike fingerlings are stocked at a much larger size (250 mm) than walleye fingerlings (50 mm). Consequently, survival of stocked pike fingerlings can be 10–20 times greater (Johnson et al., Ch. 16).

## Changes in Sport Fish Populations

In 1987 there was a substantial change in management intensity on the lake, brought about by the Lake Mendota project. Stocking occurred at rates that were double to fivefold higher than in the previous decade, and stocking was sustained (Johnson et al., Ch. 16). In 1988 Lake Mendota became one of the most strictly regulated sport fisheries in Wisconsin.

These management efforts resulted in changes in piscivore populations that could be measured as early as 1988.

Changes in piscivore populations are presented in detail in the previous chapter (Johnson et al., Ch. 16), so we will summarize these findings only briefly here. From 1987 to 1988, walleye biomass almost doubled, and the number of walleyes increased by a factor of 2.4 due to the recruitment of 1986 and 1987 year classes. Walleye biomass in 1989 was similar to 1988, but the number of walleyes was 1.9 times the 1987 abundance. Northern pike abundance doubled from 1987 to 1988, the result of recruitment of naturally produced fish in 1986 and stocked fish in 1987. By 1989, northern pike abundance was 10 times the number in 1987, as more of the 1987 year class was recruited. Pike biomass was similar to walleye biomass in 1989. Smallmouth and largemouth bass populations were constant during 1987–89.

Although not the result of management, changes occurred in the planktivore community as well. The yellow perch population was dominated by a single year class (1985), and these fish averaged about 240 mm in 1989. Perch recruitment was moderate to poor during 1987–89 (Johnson et al., Ch. 16; Post et al., Ch. 15), so there were few small fish in the population. The bluegill population appeared to expand during 1987–89, and crappies and white bass numbers appeared to be constant or declining.

### Showcasing the Project

Showcase management calls for intensive management on important, high-visibility waters. The objectives are to demonstrate the benefits of management efforts and win public support for and participation in management programs (Staggs, Ch. 27). During 1987–89, fisheries managers made a concerted effort to maximize public exposure to the food web experiment. In addition to distributing fact sheets and informational brochures, fisheries management personnel made appearances at numerous sport shows and made more than 50 public presentations on the project to diverse audiences such as civic clubs and service organizations, school and church groups, and of course fishing, boating, and conservation clubs.

Judging from the media reaction, public interest in the project was keen. Within days after the fisheries management field team was hired, they were interviewed by television news crews for stories on the project. A total of 21 television news stories on the Lake Mendota study were broadcast during 1987–89, including a story aired internationally on the Cable News Network (CNN). More than 10 radio interviews were conducted, most concerning the effects of the project on the fishery. We know of over 30 printed articles covering the project, in at least six

Wisconsin newspapers, several well-known sporting magazines, and club newsletters.

In addition to public presentations and media coverage, this project was highly visible to the public because of Lake Mendota's location within the city limits of the state's capital. Further, our ambitious sampling schedule maintained a high-profile presence on Lake Mendota. The full-time creel survey contacted thousands of anglers annually, and fish sampling from ice-out to ice-up was apparent to a multitude of lake users.

Word-of-mouth within the angling community is also an effective means of increasing awareness of a fishery, and this truth underlies the fact that it is hard to keep a hot spot secret. This mode of information transfer seems particularly effective in an urban area such as Madison, which forms one corner of the so-called magic triangle of major Wisconsin population centers (Milwaukee and the Fox River Valley complete the triangle). Enterprising bait shop owners are well aware of this fact, and fishing information networks are maintained with Milwaukee and even Chicago. Thus, Lake Mendota's proximity to several metropolitan areas undoubtedly contributed to the showcasing of the Lake Mendota Project.

### Changes in the Fishery

Anglers fished a total of almost 300,000 h (72.7 h/ha) on Lake Mendota in 1987 (Table 17.1), which is quite similar to fishing effort measured in a 1981 creel survey (Lathrop et al., in press). Ninety-nine percent of the harvest by number was planktivores and was composed of yellow perch, white bass, bluegill, and crappie (*Pomoxis* spp.) (Table 17.2). Catch rate

**Table 17-1.** Fishing effort (angler-h/ha) on Lake Mendota during 1987 through 1989, estimated by a creel survey. Winter period is January–February, summer is May–October. Total hours are all hours regardless of species sought, and specific hours are hours spent fishing for a particular species.

Year	Period	Total hours	Total hours/ha	Specific hours/ha seeking		
				Walleye	Pike	Perch
1987	Winter	108,834	27.3	5.0	3.3	14.3
	Summer	180,902	45.4	2.6	1.8	11.6
	All year	289,736	72.7	7.6	5.1	25.9
1988	Winter	73,317	18.4	7.1	4.8	9.4
	Summer	199,952	50.2	5.0	0.7	9.4
	All year	273,269	68.6	12.1	5.5	18.8
1989	Winter	92,418	23.2	6.3	3.8	15.0
	Summer	460,271	115.6	16.0	5.2	39.2
	All year	552,689	138.8	22.3	9.0	54.2

(computed from all fish caught whether kept or released) of planktivores was 1.46 fish/h, or about 24 times higher than the catch rate for piscivores (Table 17.1).

Total harvest and species composition of the piscivore catch in 1987 were also similar to that found in 1981 (Table 17.2). That the game fishery was found to be unchanged from 1981 to 1987 is not entirely surprising, given that the lake received infrequent stocking prior to each survey and liberal harvest regulations were maintained throughout the period. Catch rates were highest for walleye (0.02 fish/h) and smallmouth bass (0.02 fish/h), and northern pike catch rate was a mere 0.004 fish/h. Catch rate of all piscivores combined was only 0.06 fish/h (Table 17.1). Northern Wisconsin walleye lakes (over 200 ha) provide average walleye catch rates of 0.07 walleye/h (Staggs 1989).

When the study began, plans were underway to institute a 381-mm (15-inch) minimum size limit and daily bag limit of three for walleyes, and an 813-mm (32-inch) minimum size limit and daily bag limit of one for northern pike on Lake Mendota. In 1987 the creel survey showed that fishing mortality rates were high, particularly for northern pike (Table

**Table 17-2.** Annual harvest (number of fish removed by anglers) and catch rates (fish caught/angler-hour; derived from creel survey estimates of total catch, whether kept or released, and total hours of fishing effort) on Lake Mendota during 1981 and 1987–89.

Piscivores	1981 <sup>a</sup>		1987		1988		1989	
	Harvest	Catch rate	Harvest	Catch rate	Harvest	Catch rate	Harvest	
Walleye	1,494	0.025	1,422	0.071	1,471	0.088	3,989	
Northern pike	423	0.004	616	0.025	95	0.034	203	
Smallmouth bass	305	0.020	677	0.066	2,041	0.035	594	
Largemouth bass	163	0.006	323	0.019	624	0.022	628	
All piscivores	2,385	0.055	3,038	0.181	4,231	0.179	5,414	

Planktivores	1981 <sup>a</sup>		1987		1988		1989	
	Harvest	Catch rate	Harvest	Catch rate	Harvest	Catch rate	Harvest	
Yellow perch	121,153	0.943	214,457	0.418	95,692	0.714	342,042	
Bluegill	1,996	0.147	42,688	0.144	27,203	0.514	152,422	
White bass	521	0.233	67,487	0.164	27,850	0.089	33,282	
Crappie spp.	199,616	0.135	39,197	0.055	11,276	0.065	17,022	
All planktivores	323,286	1.458	363,829	0.781	162,021	1.382	544,768	

<sup>a</sup>Catch rate data not available.

17.3), and restrictive harvest regulations were in fact needed to protect stocked piscivores. These new rules went into effect on 1 January 1988, making Lake Mendota one of the state's most restricted fisheries.

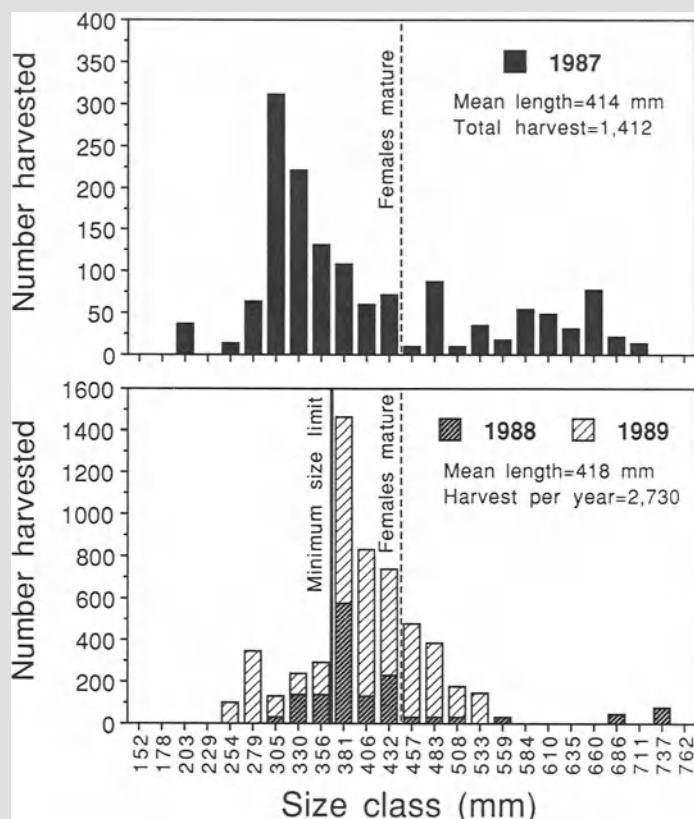
Catch rate of walleyes almost tripled in 1988, probably due to recruitment of 1986 and 1987 year classes to the fishery. Judging from the 1987 harvest, many of these small fish would have been harvested without a size limit in place. A similar number of walleyes was harvested compared to 1987, but unlike 1987, most of the harvest in 1988 was of fish over 381 mm (Figure 17.1). Compliance with the size limit was incomplete, and compliance was actually poorer in the second year (1989) of the regulation (Figure 17.1). There was a sixfold increase in northern pike catch rate (Table 17.2), again probably due to 1986 and 1987 year classes entering the fishery; however, only 95 pike were harvested. Most of the northern pike population was protected by the 813-mm (32-inch) size limit, but there was some illegal harvest in 1988 (Figure 17.2).

Planktivore catch rates declined by 50–75% during 1988, perhaps due to the cisco die-off in 1987 that allowed large zooplankton to remain abundant throughout the growing season. Bluegill catch rate stayed nearly constant, perhaps because rapidly increasing abundance offset a lower individual catch rate.

Promotion of the project continued through 1989, and angling effort directed at walleyes almost doubled again in 1989 to 22.3 h/ha (Table 17.1). In 1989 total angling effort also increased substantially. This increase took place primarily during summer, when total fishing effort was about double that for summer 1987 or 1988. Much of the increase in total fishing effort can be explained by the increase in perch fishing to 54.2 h/ha in 1989 (Table 17.1). This increase in fishing effort probably also contributed to the increased exploitation rate of walleye, as some walleye are caught incidentally by anglers who are not fishing for

**Table 17-3.** Exploitation rates (derived from mark—recapture population estimates of abundance by age and harvest by age) of piscivores in Lake Mendota during 1987 through 1989. Estimates were not obtainable for smallmouth bass in all years, nor for largemouth bass or northern pike in 1988.

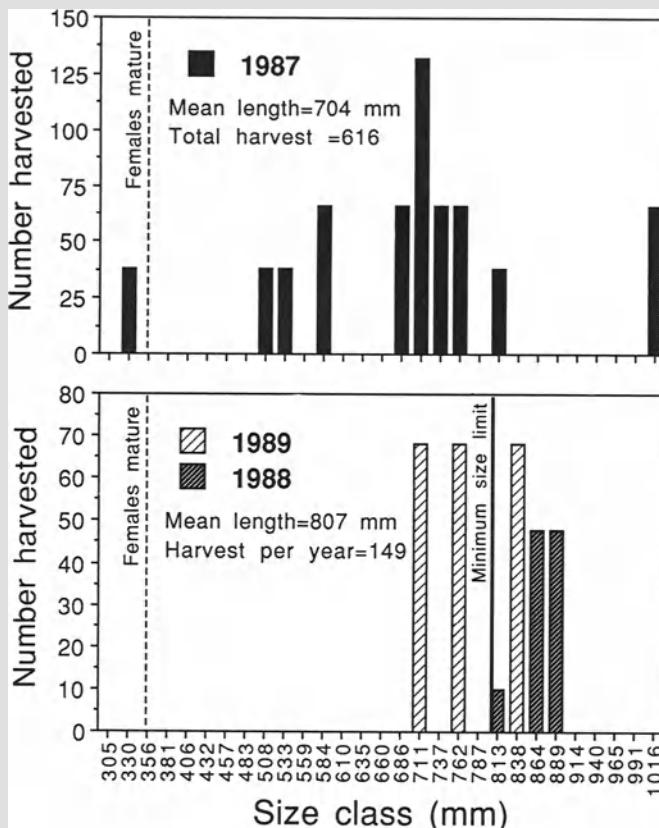
Species	Year	Exploitation rate (%)						
		I	II	III	IV	V	VI	VII+
Walleye	1987	0.6	10.2	22.0	27.5	20.0	23.5	22.5
Northern pike		0.0	12.3	19.8	23.9	41.6	52.0	54.4
Largemouth bass		—	0.0	12.6	16.5	27.6	12.2	0.0
Walleye	1988	0.0	0.7	6.3	31.7	36.0	49.7	14.6
Walleye	1989	0.0	6.2	13.4	50.9	57.2	69.7	41.3
Northern pike		0.0	0.0	0.0	0.0	3.8	16.7	22.1
Largemouth bass		—	17.8	8.5	44.8	49.1	35.0	53.1



**Figure 17-1.** Length-frequency of walleyes harvested by anglers in Lake Mendota before (1987) and after a 381-mm (15-inch) minimum size limit was enacted. The dashed line is the approximate size at which female walleyes become sexually mature in Lake Mendota.

walleyes. Average annual catch rate of perch was actually higher in 1987 than 1989, but the mean length of harvested perch in 1989 was a very desirable 230 mm, which was about 30 mm greater than in previous years. Also, an exceptionally high perch catch rate by a few knowledgeable anglers, as was observed in 1989, probably attracts many casual anglers who dilute overall catch rate and inflate total effort.

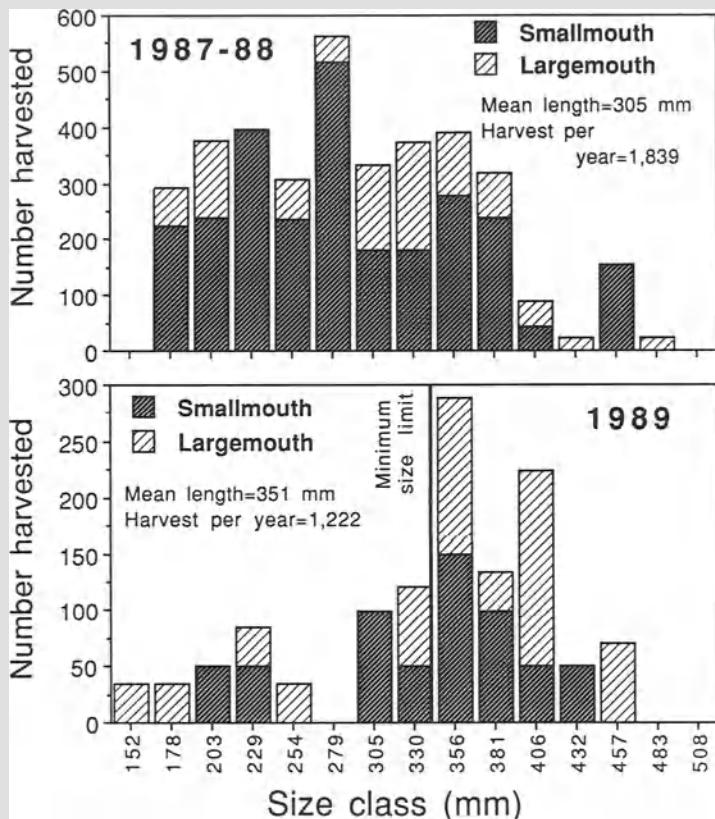
Bluegill catch rate rivaled that of perch in 1989, suggesting the increasing importance of the bluegill in the fishery and in the food web, as abundance and catch rate are presumably related. White bass catch rate continued a 3-year decline, and crappie catch rate stabilized at about half the 1987 rate (Table 17.2). Thus, assuming catch per unit effort



**Figure 17-2.** Length–frequency of northern pike harvested by anglers in Lake Mendota before (1987) and after an 813-mm (32-inch) minimum size limit was enacted. The dashed line is the approximate size at which female northern pike become sexually mature in Lake Mendota.

(CPUE) is proportional to abundance, the planktivore community in 1989 appeared to be dominated by similar numbers of yellow perch and bluegill. Total harvest of planktivores in 1989 was at least 50% higher than in 1981, 1987, or 1988.

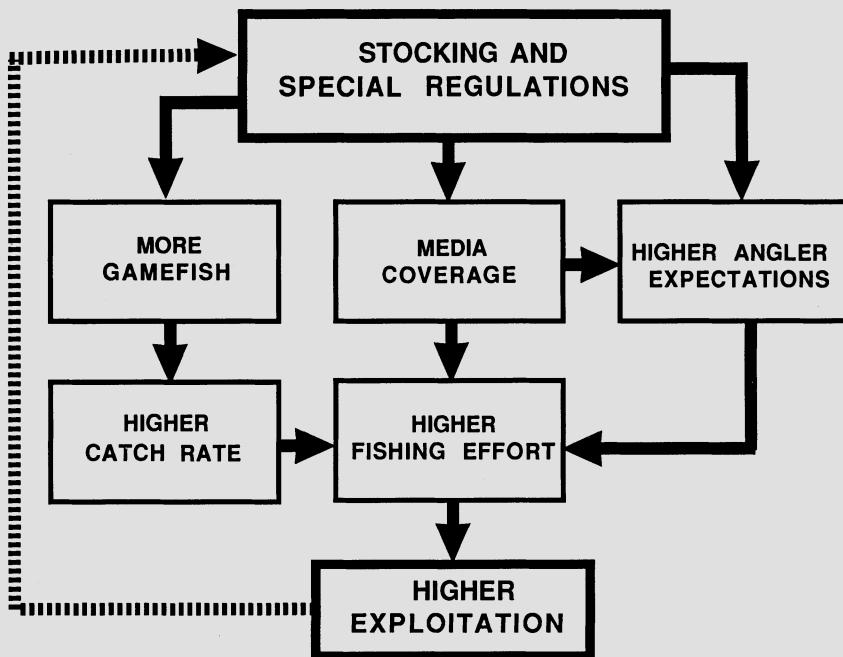
A statewide 356-mm (14-inch) minimum size limit on largemouth and smallmouth bass was established on 1 January 1989, and this limit also applied on Lake Mendota. However, despite this new rule, the largemouth bass exploitation rate on legal-sized age groups was higher than in 1987 (Table 17.3), probably a result of rising overall fishing effort on the lake. Compliance with the bass size limit (both largemouth and smallmouth bass) was poorer than for northern pike or walleye (Figure 17.3).



**Figure 17-3.** Length–frequency of smallmouth and largemouth bass harvested by anglers in Lake Mendota before (1987–1988) and after a 356-mm (14-inch) minimum size limit was enacted.

### Angler Numerical Response

Fishing effort, particularly angler-hours directed at walleyes, has steadily increased during 1987–89, and harvest has outpaced recruitment of game fish (walleye, pike, and largemouth bass). This led to a concomitant increase in exploitation of game fish stocks. Despite new restrictions on walleye harvest enacted in January 1988, average exploitation rate on vulnerable walleye age classes increased from 21% in 1987 to 33% during 1988 (Table 17.3). Even though total fishing effort declined slightly in 1988 (Table 17.1), angler-hours spent fishing specifically for walleye almost doubled. The hours anglers spent fishing for walleye doubled again in 1989, and the exploitation rate on legal age classes increased to 55% (Table 17.3). Apparently, with a minimum size limit in place,



**Figure 17-4.** Components of the anglers' numerical response. Their response includes a positive feedback, in that management efforts to reduce exploitation (more stocking and higher size limits) may attract more anglers.

harvest was redirected to older, less abundant age classes, which resulted in increased exploitation rates on those age classes.

Increased fishing for walleye and higher exploitation probably arose from a combination of factors (Figure 17.4). Intensive stocking, special regulations, and promotion of the project resulted in media coverage that probably raised angler expectations. Higher angler expectations and increased catch rates then attracted more anglers. Because relatively few fish grew into the >381-mm size class, intense harvest pressure was again applied to legal-sized age classes, resulting in unacceptably high exploitation rates (Table 17.3). Wisconsin fishery biologists consider 20–25% exploitation rates to be optimum, and only highly productive, naturally reproducing populations can withstand 35% exploitation rates (Staggs 1989). The Lake Mendota walleye population clearly cannot sustain 1989 exploitation rates, and new harvest regulations are required to protect the stock.

The rapid response of anglers observed in 1987–89 could also have occurred previously in Lake Mendota following large stockings or a large natural year class of walleye. Such a response would have rapidly depleted the occasional large year class that might have been produced.

The “slaughter of 1981” that followed natural reproduction of walleyes in 1978 is well known in the lore of the Lake Mendota fishing community.

### **Managing the Fishery**

Before the walleye size limit was enacted, we evaluated proposed fishing regulations using walleye demographics measured in the field and fishery statistics estimated by the creel survey in 1987. In projecting the effects of the regulation with GIFSIM and bioenergetics, we assumed fishing effort and exploitation rate were static. In fact, dramatic increases in effort and exploitation rate during 1988–89 showed these parameters to be dynamic, at least in this newly enhanced fishery.

The dynamic nature of fishing effort points out one challenge of managing inland sport fisheries. Inland fishery managers can control age at recruitment through size limits, but they cannot necessarily control fishing mortality on recruits. We can lower per capita angler harvest, but not total harvest. Even with a reduced bag limit (3 fish/day), harvest on Lake Mendota was excessive in 1988 and 1989, and 92% of successful walleye anglers harvested just one fish per day (Johnson et al. 1992b). Because we do not limit entry to the fishery, reduced bag limits may not work if more anglers are attracted to the fishery and the density of gamefish is low, as in Lake Mendota. Many anglers catching 1–2 fish/day can be excessive, and minimum size limits can result in anglers redirecting harvest at older, less abundant age classes. Of course, this is not necessarily a problem if the size limit protects an adequate spawning stock and anglers are satisfied with harvesting most fish just over the minimum size limit.

The limited spawning success of Lake Mendota walleyes to date suggests that stocking will be required to sustain the fishery. A stocking plan was developed to continue to build stock biomass within the constraints of a limited hatchery supply of walleye fingerlings. During 1990–92, about 250,000 walleye fingerlings are to be stocked each year. After 1992, the stocking rate will probably return to the statewide guideline for maintenance stocking (currently 100,000 fingerlings stocked every other year). If 1987 fingerling survival rates occur each year, this stocking plan will maintain a biomass of spawning age females about three times higher than spawner biomass expected in 1990, for a period of 6 years. During this period the lake will be monitored for evidence of natural reproduction. However, it appears that first-year survival of fingerlings is declining (Johnson et al., Ch. 16), so these projections of reproductive potential may be overly optimistic.

Because stocking is often not a cost-effective means of sustaining a fishery in the long term, an important consideration in regulating the fishery is preventing harvest from endangering the potential for natural reproduction. If a stock–recruit relationship holds, then fish should be

protected beyond the onset of sexual maturity. Perhaps the best that can be expected from minimum size regulations is an acceptable biomass of sublegal spawners that provides catch-and-release opportunities and contributes to recruitment. Fish that exceed the minimum size limit are subject to intense harvest pressure, and few individuals survive to a size well above the size limit.

Few female walleyes in Lake Mendota become sexually mature until they reach a length of about 430 mm. We have proposed a 457-mm (18-inch) minimum size limit to protect a minimum biomass of spawning females. This rule will take effect in May 1991. Few fish of the 1987–89 year classes will be vulnerable before this time, and thus most of these fish will be conserved. The GIFSIM model predicted a 31% increase in walleye reproductive potential (biomass of age-4 and older females) over that with the 381-mm (15-inch) size limit (Johnson et al. 1992b). Aside from increasing the biomass of the spawning stock, the new walleye size limit will also increase the total number of fish caught and released, providing better catch opportunities to anglers.

A concern with the proposed 457-mm (18-inch) rule is that it may be considered a “trophy” regulation, and the aura of trophy regulations on this lake may further increase fishing effort. However, it is unlikely that the majority of the anglers would accept much more restrictive regulations. Further, if spawning conditions are found to be unsatisfactory, then higher size limits on walleye to foster reproduction would be futile, at the expense of some anglers’ opportunity to harvest walleyes.

## Implications for Long-Range Success

A three-pronged management approach will be needed to overcome heavy fishing pressure and recruitment problems to protect the long-term viability of game fish populations: better stocking practices that build stock biomass, fishing regulations that protect spawners, and habitat manipulations that improve spawning conditions.

To build up spawner biomass or to maintain a fishery for walleye in the absence of natural reproduction, we must make provisions for a regular source of stocked walleye fingerlings. During 1986–87, the Lake Mendota Fishing Association (a local group of walleye enthusiasts) cooperated with the WDNR to raise and stock a total of 130,000 walleye fingerlings for Lake Mendota, above state stocking quotas. Because fish manager requests for walleye fingerlings routinely exceed state hatchery production, and because Lake Mendota received a sizable proportion of statewide hatchery production in 1987–89 (Staggs, Ch. 27), WDNR walleye fingerlings will not be available for Lake Mendota in many years. More cooperative agreements between the WDNR and local fishing clubs

must be pursued if walleye biomass is to be sustained above the typically low levels.

To improve the return from the limited supply of stocked fingerlings, new stocking techniques are needed to enhance post-stocking survival over the rather low levels observed in 1987–89 (Johnson et al., Ch. 16). Computer modeling of young-of-year (YOY) walleyes in Lake Mendota suggests that recruitment could be improved from achievable modifications in culture practices that improve prey availability and growth of stocked fingerlings (Madenjian et al., Ch. 25).

The more intensive nature of northern pike fingerling propagation and the growing demand among fish managers are putting northern pike fingerlings in even shorter supply than walleye (Staggs, Ch. 27). And yet, northern pike fingerling stocking has shown considerable promise during 1987–89 (Johnson et al., Ch. 16). Cooperative propagation agreements could provide a more reliable, local source of northern pike fingerlings. Also, WDNR development projects such as the controlled pike rearing marsh at Sixmile Creek near Lake Mendota can be used to offset the loss of spawning habitat.

More realistic expectations about the capacity of walleye fingerling stocking to bolster walleye biomass (Johnson et al., Ch. 16) suggest that steps must be taken to foster natural reproduction whenever possible. The 457-mm (18-inch) minimum size limit will protect female walleyes until they can spawn at least once, ensuring a minimum spawning stock. But efforts are needed to improve angler compliance with regulations. Stocking genetic strains different from the northern Wisconsin lake stocks typically propagated may result in a population better suited to surviving and reproducing in southern Wisconsin waters. The WDNR is currently expanding its capacity at southern Wisconsin fish hatcheries to accomplish this.

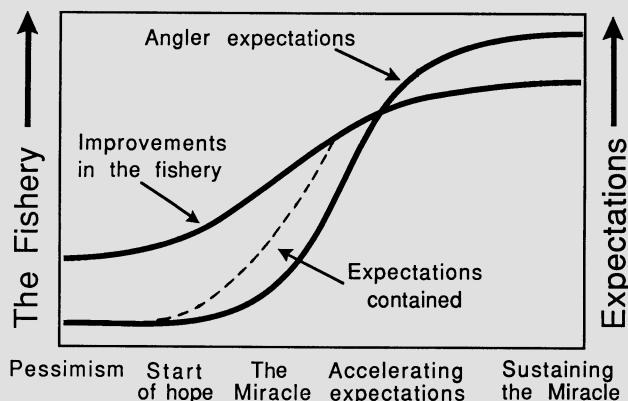
Stocking and a trophy size regulation have already begun to rehabilitate the northern pike population (Johnson et al., Ch. 16). The current 813-mm (32-inch) size limit on northern pike will protect the reproductive potential of stocked fingerlings, some of which become sexually mature at 350 mm.

However, spawning habitat must also be improved if increases in the spawning stock of northern pike are to be meaningful. We believe degenerating spawning habitat caused the near collapse of the native pike population, which was evidence by the extremely low pike abundance observed in 1987. Access to spawning areas once isolated from the lake has been improved by installing culverts. More importantly, protection of wetlands and higher spring lake levels will foster natural reproduction of northern pike in Lake Mendota. However, these changes may be objectionable to some segments of the community, particularly developers and some shoreline property owners.

## The Paradox of Enhancement

In principle, showcase management is an effective strategy for garnering public support for fisheries management programs. However, the Lake Mendota experience has demonstrated some potential pitfalls of showcase management that we call The Paradox of Enhancement. We now know managers must be able to anticipate intensified pressure on a rehabilitated or enhanced resource, and more restrictive harvest regulations may be required to keep pace with user response. Without these restrictions, efforts to improve the resource could be short-lived or even result in its degradation. Another solution to the paradox would be to increase the number of enhancement projects and special regulations to broaden the resource base and spread out angling pressure on more waters.

The Lake Mendota experience also serves as an interesting case history of the transformation of a resource and of the human factors that mediate that transformation. Gale (1987) discusses the challenges and opportunities presented to resource managers when a previously degraded resource is improved. The phenomenon of rapidly rising public expectations that exceed the capacity of the resource is common to resource enhancement programs. When expectations do not match actual improvements, public support ultimately can be harmed. Distilling Gale's theory into a figure (Figure 17.5), we see that angler expectations must be contained at a more realistic level that matches the trajectory of response in the resource. To do this, managers must act early in the process to inform and educate their constituents about realistic possibilities of the



**Figure 17-5.** Stages in the enhancement of a fishery, developed from Gale (1987). Early in the process, managers should educate anglers about realistic possibilities for the fishery so that expectations are aligned with what the resource can provide.

project. Only then can managers expect a reasoned response by the public.

Showcase management also presents important opportunities to the resource manager. New constituencies can be built when the public eye is focused on the resource and the general public, not just the direct resource users, is informed about the resource (Gale 1987). Public education during the rehabilitation process is needed to instill a respect for the natural resource and thereby ensure adequate protection. Support for restrictive harvest regulations that require the angler to give up something today for the long-term good, and a bolstered environmental ethic, must be achieved during the education process. Anglers who realize the improvements they are enjoying may be fleeting will maintain a greater respect for "their" fishery and assist the manager in spreading the word about compliance with rules, proper handling of undersized fishes, and increasing voluntary catch-and-release of harvestable game fish.

Showcasing the Lake Mendota project did increase opportunities to educate the public about the resource problems the project sought to correct, and built public support. We believe the informed public was more supportive of efforts to eliminate overharvest on game fishes and of our efforts to improve spawning habitat. We were surprised at the enthusiastic support for special Lake Mendota regulations, especially the "trophy" regulation for northern pike. In fact, anglers asked for these special regulations on adjacent waters as well. With the help of political pressure from anglers, spring lake levels were adjusted to improve spawning conditions for northern pike. Since 1987, local fishing groups have contributed hundreds of hours of labor and over \$23,000 to assist in management efforts on the Madison lakes.

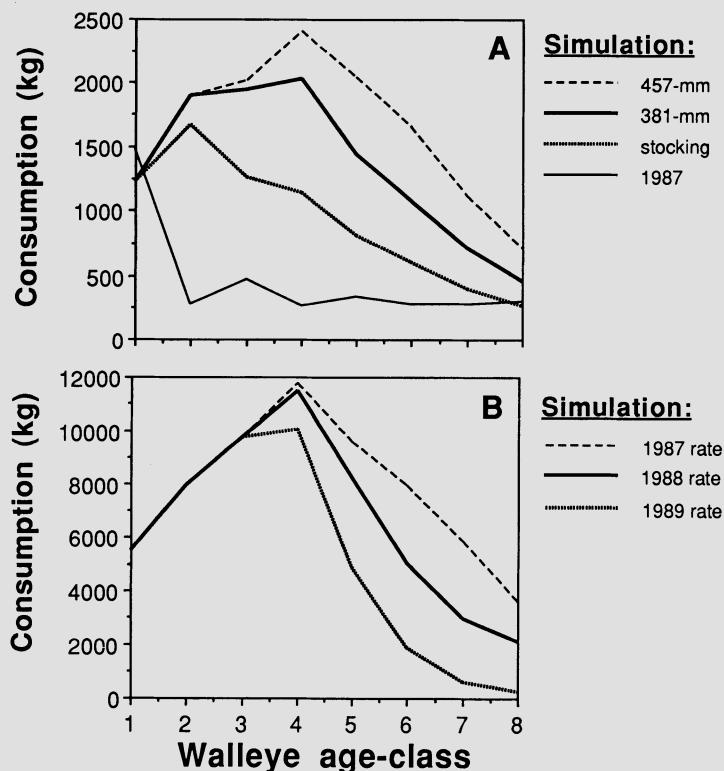
### The Angler as Top Predator

The response of anglers to actual and anticipated improvements in game fish biomass, concurrent with our comprehensive study of the entire aquatic food web, allowed us to examine the potential influence of angling on food web structure. Modeling has quantified the importance of the top trophic level, anglers, in mediating the effects of the biomanipulation. However, our creel survey also showed significant influence of pan-fishing on planktivore populations. The interplay between harvest of planktivorous and piscivorous fishes presents an interesting question as to the ultimate effects of angling on lake food web dynamics.

Because effective fishing regulations produce changes in piscivore populations, changes in prey consumption would also be expected. The GIFSIM and bioenergetics models used in tandem provided the means to track these changes and thereby predict how regulating anglers affects food web dynamics (Johnson et al., Ch. 16). To evaluate proposed fishing

regulations when the study began, we computed the relative predation pressure by walleyes under various alternative regulations using this technique.

In 1987 we projected substantial increases in total prey consumed by the walleye population in 1996 as a result of the project's stocking plan and special harvest regulations (Figure 17.6A). These projections assumed that walleye population and fishery parameters measured in 1987 were constant, and that annual stockings produced 8,000 yearling walleyes per year. The stocking program alone was predicted to more than double the estimated consumption of the walleye population existing in 1987 (Figure 17.6A). A 381-mm (15-inch) minimum size limit increased projected walleye consumption by an additional 47% (Figure 17.6A). A



**Figure 17-6.** Consumption by age-1 to age-8 walleyes of: (A) yellow perch in 1987, and at a stable age distribution under various management scenarios of stocking plus a 457-mm (18-inch) or 381-mm (15-inch) minimum size limit, or stocking and no size limit; and (B) all prey species at a stable age distribution, assuming various fishing mortality rates and a 381-mm (15-inch) minimum size limit.

457-mm (18-inch) minimum size limit (adopted in 1991) would protect recently stocked walleyes for approximately an additional 1.5 years. The protection of walleyes by a 457-mm (18-inch) size limit translated into a 79% increase in piscivory by walleye compared to piscivory with stocking but no size limit (Figure 17.6A).

The above simulations assumed constant fishing effort and exploitation rate. Unexpectedly large increases in the hours anglers spent fishing for piscivores and in piscivore exploitation rates even after harvest restrictions were enacted showed that fishery parameters can change annually. These changes have implications for the biomass consumed by the walleye population. Comparing projected walleye consumption using observed 1987, 1988, and 1989 exploitation rates shows how changes in the fishery affected our forecasts of walleye consumption arising from a stocking program and a 381-mm (15-inch) size limit (Figure 17.6B). If 1989 exploitation rates continued and the 381-mm size limit was retained, prey consumption by legal-sized (age 5+) walleyes would be almost negligible (Figure 17.6B). However, it is unlikely that 1989 effort and exploitation rates will continue indefinitely. As they did in 1987–89, these fishery parameters are more likely to vary with walleye catch rate, size structure, and perceptions about the fishery.

Modeling the angler dynamically in food webs is challenging because socioeconomic factors must be added to an already complex ecological system. As fishery managers, we have some control over angler impacts, primarily via harvest regulations; however, many components of the fishery are beyond the manager's control. Because catch rate is not always proportional to abundance, the angler's functional response is variable. Other than encouraging proper handling techniques, we have little control over the mortality rate of the large number of released fishes necessitated by high minimum size limits. Probably the greatest difficulty in modeling anglers is understanding their numerical response to changes in the prey resource (fish populations). Although the phenomenon of angler effort responding to changes in fishery resources is known (Walters 1986; Gale 1987), studies that have examined angler numerical response in detail are rare (Walters 1986).

Surprisingly, fishing can also affect adult planktivore biomass in Lake Mendota. Because Lake Mendota serves a large urban population base, there is a large pool of potential anglers that can choose to fish on the lake when fishing is good, as was the case when walleye catch rates improved. Despite the much greater abundance of planktivores, Lake Mendota anglers can at times have an impact on these fishes as well. Good catch rates of desirable-sized yellow perch in January and June–July 1989 attracted a multitude of perch anglers who harvested almost 350,000 perch during the year (Table 17.2). Given our mark–recapture population estimate of adult perch in 1988 and low perch recruitment from 1988 to 1989 (Johnson et al., Ch. 16), this bonanza represented

as much as 40% of the adult stock, which would be considered a high exploitation rate for a panfish species. Currently, panfish (all are planktivores) are subject to a daily bag limit of 50 fish in aggregate, but unlike walleye anglers, it is not uncommon for panfishers to attain the daily bag limit. It appears then that there is at least some potential for manipulating planktivore biomass by liberalizing panfishing regulations.

Because panfish anglers and piscivores share a common resource in Lake Mendota, there is the potential for exploitative competition. In 1989 anglers harvested approximately 75,000 kg of planktivores. Estimated biomass of all prey species consumed by walleye and pike in 1989 was about 67,700 kg (Johnson et al., Ch. 16). Obviously, piscivores select for smaller and younger prey than do anglers. Selectivity for smaller planktivores could allow piscivorous fishes to outcompete anglers for the resource in the long term because they reduce the number of planktivores that grow to become vulnerable to the anglers. If piscivorous fishes reduce recruitment of planktivores to the fishery, socioeconomic considerations may override ecological ones.

The ultimate impacts of angling on food web interactions and the efficacy of biomanipulation are not apparent. We have seen how anglers can either strengthen or inhibit top-down control of the food web, depending on the intensity of exploitation on planktivores versus piscivores. However, it is clear that fishery concerns cannot be divorced from food web management as a water quality tool. First, sport fishing is ubiquitous and it is likely to be popular in any lake where improving water quality is seen as a management objective. Second, anglers probably pay for a large share of the cost of fisheries management through license sales and federal excise taxes (Dingel-Johnson or Wallop-Breaux Sport Fish Restoration fund). Third, anglers have proven to be an extremely efficient and rapidly responding piscivore, and attempts at top-down control of food webs will present an enticing prey resource (enhanced piscivore abundance) to anglers. Finally, the angling public can provide substantial financial and labor contributions to management efforts, and they can be a powerful ally for protecting habitat.

In addition to their direct alteration of food web structure by harvesting piscivores, anglers can have other potential interactions with food web managers. Anglers could be reluctant to make the sacrifices necessary for biomanipulation to work, in the form of lower harvests of both planktivores and piscivores. Reduced planktivore (panfish) populations are an objective of food web management that may be unacceptable to some anglers. These anglers could be unwilling to trade panfish harvest for better water quality. Restrictive harvest regulations, even catch-and-release-only regulations, may be necessary to maintain sufficient piscivore biomass (Post and Rudstam, Ch. 19). However, Lake Mendota anglers have been quite willing to accept more restrictive regulations and forego game fish harvest to increase game fish stocks.

We now accept a broader view of aquatic food webs where anglers are an integral component. Interaction between fishery and water quality interests broadens the scope of food web management further. There are more constituencies involved than just anglers—namely, those interested in better water quality for other recreational pursuits or simply for esthetics. Thus, the development of food web management policy must involve an analysis of socioeconomic concerns. From a fishery management perspective, an attraction of food web management is that constituencies can be allied in a common interest. For example, nonanglers may be inclined to support the enhancement and protection of piscivore stocks when water quality improvements are the potential payoff.

### Concluding Remarks

Two basic messages derive from our experience studying the Lake Mendota fishery. First, success in showcasing the enhancement of the Lake Mendota fishery has resulted in increased pressure on the resource. This has presented managers with the potential paradox inherent in showcase management projects, in that enhancement efforts can result in eventual resource degradation. Fishery managers involved in major enhancement programs should anticipate increased pressure and adopt a management strategy to adequately protect piscivore stocks. Second, researchers and managers considering a food web management project that uses a desirable game fish as the predator of choice will find that efforts to enhance piscivore biomass may be undermined by the real top piscivore—the angler. Food web managers should recognize the angler as an integral component of the system.

*Acknowledgments.* Special thanks to the folks who helped squeeze the fish: Steve Gilbert, Ron Schwerdtfeger, Scot Stewart, Pat Cramer, Jeff Reed, and a host of talented hourly helpers and volunteers. Thanks also to the creel clerks who endured the schedule, the weather, and a few irate anglers. The help and support of all the Madison area fishing and conservation clubs and the Madison Fishing Expo is gratefully acknowledged. This study was funded in part by the Federal Aid in Sport Fish Restoration Act under Project F-95-P and the WDNR.

### References

- Gale RP (1987) Resource miracles and rising expectations: A challenge to resource managers. *Fisheries* 12:8–13
- Hewett SW, Johnson BL (1987) A generalized bioenergetics model of fish growth for microcomputers. Technical Report WIS-SG-87-245, University of Wisconsin Sea Grant Institute, Madison

- Johnson BM, Luecke C, Stewart RS, Staggs MD, Gilbert SJ, Kitchell JF (1992a) Forecasting effects of harvest regulations and stocking on prey fish communities in a eutrophic lake. *No. Am. J. Fish. Manag.* (in press)
- Johnson BM, Stewart RS, Gilbert SJ (1992b) Ecology of fishes in the Madison lakes. *Fisheries Management Report 148*, Wisconsin Department of Natural Resources, Madison
- Kempinger JJ, Churchill WS, Priegel GR, Christenson LM (1975) Estimate of abundance, and exploitation of the fish population of Escanaba Lake, Wisconsin, 1946–1969. *Technical Bulletin 84*, Wisconsin Department of Natural Resources, Madison
- Lathrop RC, Nehls SH, Brynildson CL, Plass KR (1992) The fishery of the Yahara lakes. *Technical Bulletin Wisconsin Department of Natural Resources*, Madison (in press)
- Mood AM, Graybill FA, Boes DC (1974) *Introduction to the theory of statistics*. 3rd edn. McGraw-Hill, New York
- Olson DE, Cunningham PK (1989) Sport-fisheries trends shown by an annual Minnesota fishing contest over a 58-year period. *No. Am. J. Fish. Manag.* 9:287–297
- Robson D, Jones CM (1989) The theoretical basis of an access site angler survey design. *Biometrics* 45:83–98
- Snow HE (1978) Hypothetical effects of fishing regulations in Murphy Flowage, Wisconsin. *Technical Bulletin 131*, Wisconsin Department of Natural Resources, Madison
- Snow HE (1981) A 15-year study of the harvest, exploitation, and mortality of fishes in Murphy Flowage, Wisconsin. *Technical Bulletin 103*, Wisconsin Department of Natural Resources, Madison
- Staggs MD (1989) Walleye angling in the ceded territory, Wisconsin, 1980–87. *Fish Management Report 144*, Wisconsin Department of Natural Resources, Madison
- Taylor MW (1981) A generalized inland fishery simulator for management biologists. *No. Am. J. Fish. Manag.* 1:60–72
- Walters C (1986) *Adaptive management of renewable resources*. Macmillan, New York

# 18

## Modeling in the Lake Mendota Program: An Overview

**Stephen R. Carpenter**

Integration of modeling and field research has been a keystone of the Lake Mendota Program. The numerous contributions of fish bioenergetics modeling in previous chapters are one example. Johnson and Staggs (Ch. 17) have combined bioenergetics models with conventional fisheries population models (Generalized Inland Fishery Simulator, GIFSIM) to forecast effects of stocking, harvest policy, and angling pressure on piscivory. Bioenergetics modeling and GIFSIM are already widely accepted tools in fisheries research and management. The models described in the next seven chapters are more speculative and exploratory. They represent our attempts to understand and predict ecosystem dynamics in Lake Mendota, from phosphorus to fish.

Our ecosystem models for Lake Mendota originated in a graduate seminar which I organized during a sabbatical at the University of Wisconsin (UW) Center for Limnology in spring 1988. One goal of the seminar was to develop models of the Lake Mendota ecosystem to examine several scientific and management issues. These included the interaction of nutrient flux and grazing in regulating water quality, the compensatory responses of trophically similar predators, and the joint effects of stock and harvest policy on structure of the ecosystem. We hoped to elaborate the conceptual framework of the research program in a way that stimulated interactions and collaborations among project participants. In this regard, we were motivated by the success of adaptive environmental assessment workshops in providing a common focus for managers and scientists with different backgrounds and goals (Holling 1978; Walters 1986).

Training graduate students, postdocs, and Wisconsin Department of Natural Resources (WDNR) staff in simulation modeling was a very important goal of the seminar. The insights, experimental questions, and collaborations that derive from the process of modeling are often more valuable than the resulting models (Walters 1986). Experimentalists and managers experience those benefits only through participation in the modeling process. Providing field scientists with firsthand experience in modeling helps build sorely needed bridges between theory and experimentation in ecology (Carpenter 1988; Roughgarden et al. 1989).

In the graduate seminar, the modeling problem was tackled in three parts: piscivory, planktivory, and herbivory–nutrient interactions. This approach made the problem more tractable and made best use of the talents of the students involved. These three modules correspond to the first three chapters of this section. Post and Rudstam (Ch. 19) address the dynamics of piscivory over decadal time scales. Luecke et al. (Ch. 20) examine complex interactions of vertebrate and invertebrate planktivores in the middle of the food web. Vanni et al. (Ch. 21) modeled the strong feedbacks that link herbivores (and the nutrients they excrete) with the phytoplankton and nutrient inputs to the ecosystem.

The models reported here represent stages of development, not final products. The original models written in the graduate seminar have largely been replaced with more effective model structures and up-to-date parameter estimates. In fact, two of the original modules (piscivory and herbivory–nutrients) were completely scrapped, and new model structures were programmed and analyzed for this book. In the fourth chapter of the section (Ch. 22), Carpenter et al. combine the piscivory, planktivory, and herbivory modules to test management scenarios for Lake Mendota, evaluate modeling progress to date, and suggest priorities for the next generation of models for Lake Mendota.

Two new modeling thrusts branched from our original line of thought and are reported in the last three chapters of this section. The variability and unpredictability of blue-green algal blooms remain a major challenge in Lake Mendota and other lakes. Carpenter (Ch. 23) shows that interannual variability in blooms may be represented as shifts in the stability of a relatively simple nonlinear model. In a similar vein, Leavitt (Ch. 24) presents a simple analogy for blue-green algal blooms that has been useful in presenting the phenomenon to nonspecialists. Since our earliest attempts to model the Lake Mendota ecosystem, we have been concerned that fish components were too aggregated to capture adequately the vagaries of trophic ontogeny and recruitment. In the last chapter of this section, Madenjian et al. (Ch. 25) address these issues using individual-based models of juvenile fish dynamics.

To what extent has the modeling program met our goals? In several cases, modeling has guided field work. The purse-seining effort and

research on larval fishes reported in previous chapters were prompted by modeling results. Models have also influenced our experimental work on dynamics of blue-green algae and are the keystone of our interpretation of *Leptodora*'s role in the ecosystem.

Lathrop and Carpenter (Ch. 7, Ch. 8) provide a good example of the feedback between modeling and field work. Carpenter's model of blue-green algal dynamics (Ch. 23) prompted a collaborative analysis of Lathrop's 14-year dataset using time series techniques as a statistical bridge between observation and simulation. The outcome of the analysis led to a new interpretation of the century-long Secchi transparency record for Lake Mendota (Lathrop, Ch. 6). Lathrop and Carpenter are now designing a plan for future monitoring of the ecosystem, guided by the simulation and time series models. The goals are improved forecasting of blue-green algal blooms and reliable capacity to detect change in the ecosystem. Some relevant lessons from the models are the following: winter sampling of algae is much more important than previously thought; water column phosphorus concentrations have more limited usefulness in forecasting than previously thought; temperature profiles (for calculating water column stability) should be measured as frequently as possible during ice-free seasons; rather crude, yet inexpensive and readily repeatable, vertical hauls of zooplankton are useful and adequate for forecasting purposes; and an inexpensive surrogate measure of phosphorus loading (e.g., rainfall or runoff) is likely to improve forecasts. Some of these conclusions surprised us. The resulting monitoring program will be quite different from what we would have done without the models.

Models are guiding management in Lake Mendota. The model of Post and Rudstam (Ch. 19) concurs with the conclusion of Johnson and Staggs (Ch. 17) that restrictive limits are essential to establish and sustain high piscivory by walleyes in Lake Mendota. The model of Madenjian et al. (Ch. 25) shows that modest changes in stocking practices could cause large changes in walleye growth and survivorship in the lake. Direct test of their hypothesis by managers would provide an independent test of the model and could yield a significant payoff for the fishery.

We have succeeded in training experimentalists and empiricists from both the UW and the WDNR in modeling. In fact, the modeling reported in this book was conducted by scientists whose principal skills are field experimentation. Different individuals have acquired varying abilities in modeling, and most have benefited from the broader view that develops through the modeling process.

We have partially met our goal of developing models with broad applications to management issues. Several of the models reported here are suitable for "gaming" to explore consequences of management scenarios. The individual-based models of fish recruitment are likely to

reach the level of reliability and utility for managers already achieved by fish bioenergetics models. Carpenter et al. (Ch. 22) point out some of the needs for future models of southern Wisconsin lake ecosystems.

Our experience supports the argument of Holling (1978) and Walters (1986) that the main beneficiaries of the modeling process are the participants. Consequently, there is no point in building a model to be distributed to managers as if it were word-processing software. Participation of the managers in the process is essential. Their perspective helps keep the scientists on track, and they benefit directly from the insights that develop as the model is conceived, implemented, and applied to management scenarios. Teams can develop useful models fairly efficiently, without extensive time commitments from those whose primary duties are field research or management. A more appropriate goal for our program is “modeling with managers” rather than “models for managers.” The future of lake management modeling in Wisconsin involves teams composed of a few seasoned modelers, researchers with scientific knowledge of the target system, and managers cognizant of the pragmatisms imposed by the institutional and political framework.

*Acknowledgment.* I thank Jim Kitchell for his enthusiastic support of the modeling component of the Lake Mendota Program and his comments on a draft of this manuscript.

## References

- Carpenter SR (ed) (1988) Complex interactions in lake communities. Springer-Verlag, New York
- Holling CS (ed) (1978) Adaptive environmental assessment and management. Wiley, New York
- Roughgarden J, May RM, Levin SA (1989) Perspectives in ecological theory. Princeton University Press, Princeton, New Jersey
- Walters CW (1986) Adaptive management of renewable resources. Macmillan, New York

# 19

## **Fisheries Management and the Interactive Dynamics of Walleye and Perch Populations**

**John R. Post and Lars G. Rudstam**

### **Introduction**

A major goal of fisheries management is to predict effects of management strategies on future population sizes. Natural populations are inherently variable through time. Analytical one-population models have revealed an impressive array of population behavior ranging from equilibrium to chaos (Ricker 1954; May and Oster 1976; Levin and Goodyear 1980), but these models are difficult to apply to the real world and it is unclear whether more complex biological systems behave similarly (Bledsoe and Megrey, in press). Empirical models are based on the observed relationships among variables and do allow description of average conditions from biological data. But these models often explain only a small portion of the variability in the data (see Walters 1986). This poor explanatory power is often assumed to be the result of environmental variability. It is therefore not surprising that application of empirical models to new situations has been largely unsuccessful (Sissenwine 1984; Getz and Haight 1989).

In an effort to overcome the limitations of analytical and empirical approaches, we develop a mechanistic model of the trophic interactions between populations of walleye, yellow perch, and zooplankton. In this mechanistic approach, we explicitly include the biological interactions of predator and prey, bioenergetics, reproductive biology, and fisheries exploitation. The goal of this chapter is to use our model to examine the impacts of fisheries management practices on the population dynamics of walleye and yellow perch. Walleye and yellow perch are a common

predator–prey combination in central North America and of substantial interest to both sport and commercial fisheries. These species are also of theoretical interest because of the diversity of their ecological interactions. While generally viewed as a simple predator–prey system, the two species undergo a trophic ontogeny and are at various stages of their life cycle competitors, predators, and prey. We hypothesize that the interactions between these two species occur both through competition for a common prey (zooplankton and small fish) and through predation. These interactions and the two species' growth and mortality rates change dynamically on a daily basis and are functions of body size, age, and trophic structure. Including these features explicitly in the model allows us to overcome the main limitation of the commonly used Leslie matrix models in that growth and mortality rates of each age class are static (Gurney and Nisbet 1983; Caswell 1989). Combining a matrix modeling approach with a bioenergetics model can simulate the relationships between growth, body size, and mortality rates for a single species (Johnson et al., 1992; Johnson and Staggs, Ch. 17) but is not possible for models of 2 or more interacting populations. A simplifying assumption that we do use is that each age group is characterized by a mean fish size. Models with individual fish of different sizes within an age class (Adams and DeAngelis 1987; Madenjian et al., Ch. 25) have not been developed for two interacting populations.

Our approach, to develop a simulation model based on biological mechanisms, allows us to examine (1) the importance of our hypothesized mechanisms, (2) the effect of interacting biological mechanisms, and (3) the effects of management policy on population dynamics and the interactions between populations.

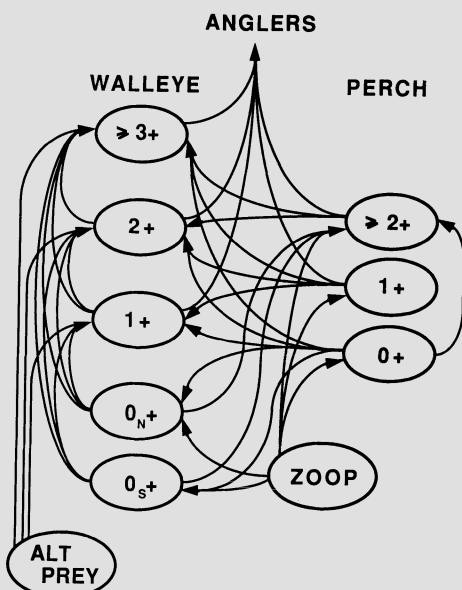
### **Model Description**

The model is a two-species, age-structured, coupled ordinary differential equation model. Functions occurring at a daily time step are consumption, growth, mortality, and zooplankton production. Annual time step functions are reproduction and graduation to subsequent age classes. The model was written using TIME0 (Kirchner 1989) and QuickBASIC 4.5 (Microsoft Corporation).

### **Lake Mendota, Wisconsin**

The physical setting for the model and initial conditions represents Lake Mendota, Wisconsin. The trophic interactions represented in Figure 19.1 are potential interactions that have been observed in at least some yellow perch and walleye lakes. The biological functions are driven by an annual temperature cycle modeled as a truncated sine function which reasonably

**Figure 19-1.** Structure of the simulation model designed to explore the interactive dynamics of exploited walleye and yellow perch populations in Lake Mendota. Age classes of both species and their potential trophic interactions are indicated. Naturally spawned ( $0_{N+}$ ) and stocked walleye ( $0_{S+}$ ) YOY walleye are modeled independently.



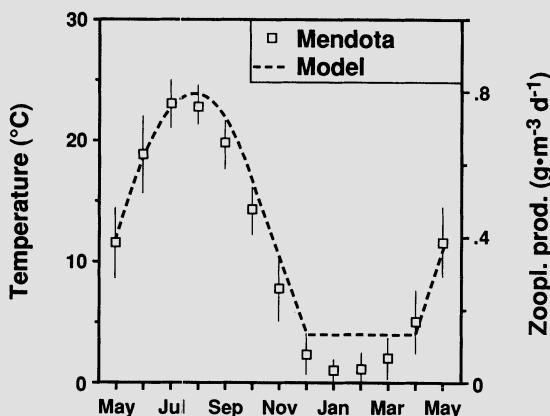
represents the mean epilimnetic temperature of Lake Mendota (Figure 19.2). Biomass, consumption, and production are modeled on a volumetric basis (in g wet weight  $m^{-3}$  for biomass and g wet weight  $m^{-3} d^{-1}$  for rates) within the epilimnion of Lake Mendota.

### Life History

The walleye population is represented by three preadult age classes (ages  $0_{n+}$ ,  $1+$ , and  $2+$ ) and adults (ages  $\geq 3+$ ) (Figure 19.1). Stocked walleye fingerlings (age  $0_{s+}$ ) are modeled separately from naturally spawned walleye (age  $0_{n+}$ ). The yellow perch population is represented by two juvenile age classes (ages  $0+$  and  $1+$ ) and adults (ages  $\geq 2+$ ). Each age class of each species is represented by an ordinary differential equation:

$$\frac{dB_i}{dt} = B_i + \sum_{j=1}^n \alpha_{ij} \text{CON}_{ij} B_i - \sum_{k=1}^n \text{CON}_{ki} B_k - R_i B_i - M_i B_i$$

where  $B_i$  is biomass of age class  $i$ ,  $\alpha_{ij}$  is the assimilation efficiency of age class  $i$  feeding on prey  $j$ ,  $\text{CON}_{ij}$  is the specific daily consumption rate of age class  $i$  feeding on prey  $j$ ,  $\text{CON}_{ki}$  is the specific daily consumption of predator  $k$  feeding on age class  $i$ ,  $B_k$  is the biomass of predator  $k$ ,  $R_i$  is specific daily metabolism of age class  $i$ , and  $M_i$  is daily nonpredatory mortality rate of age class  $i$ . In addition to biomass, numbers, weight, and length are calculated at each daily time step for each age class.



**Figure 19-2.** Average monthly epilimnetic temperatures  $\pm 2$  SD based on 50 years of observation (Robertson 1989), modeled temperature cycle, and daily zooplankton production used in the model.

All juvenile cohorts graduate to the next age class on the last day of the simulated year, 30 April. Spawning occurs on the first day of the year, 1 May, at which time 10% of the adult walleye and 12% of the adult yellow perch biomass is transferred to the age 0+ age classes. It is assumed that egg viability is high and that 90% of the biomass of eggs laid will hatch into first feeding larvae. The initial density of first feeding larvae is calculated by dividing the initial larval biomass by the individual larval weight of 0.0037 g for yellow perch and 0.01 g for walleye. This difference in initial body weight represents the effect of an earlier spawn and hatch time which is typical for walleye.

### Trophic Relationships

The trophic relationships in the model represent all potential predator-prey relationships (Figure 19.1). Juvenile yellow perch (ages 0+ and 1+) are obligate planktivores. Adult yellow perch (ages  $\geq 2+$ ) are facultative planktivores that can also feed on young-of-year (YOY) of both species. YOY walleye (age 0<sub>N</sub>+ and 0<sub>S</sub>+ ) are also facultative planktivores and can feed on age 0+ yellow perch. Age 1+ and older walleye are obligate piscivores and feed on younger age classes of walleye and equal age or younger age classes of yellow perch. An alternative prey is available for all obligate piscivorous walleye age classes when their metabolic costs exceed consumption rates. These alternative prey are benthic invertebrates and small littoral zone fishes that can be important in walleye diets when perch are rare (Forney 1966; Swenson 1977; Lyons and Magnuson 1987; Johnson et al., Ch. 16).

### Mortality Rates

The sole source of mortality for all age 0+ fish is predation by older age classes. The model does not include larval starvation mortality, since percid larvae hatch at relatively large body size and therefore are not very susceptible to starvation (Miller et al. 1988). Juvenile percids are susceptible to overwinter starvation mortality, but the duration of ice cover on Lake Mendota is sufficiently short that starvation mortality should be small (Post and Evans 1989; Shuter and Post 1990). Mortality rates of age 1+ and older fish are determined from the sum of (1) predation by older cohorts, (2) nonpredatory natural mortality, and (3) fishing mortality. Nonpredatory mortality for all cohorts older than YOY is modeled as 30% annually. Fishing mortality is varied from 0% to 76% annually (see Table 19.1 for the design of the exploitation rate simulations).

### Consumption and Growth Rates

Growth rates are a function of consumption rates, assimilation efficiencies, metabolic rates, and the relative energy density of the prey and predator. Assimilation efficiency, allometric and temperature-dependent metabolic rates, and relative energy densities were determined from published energetics models for YOY and adult walleye and yellow perch (Kitchell et al. 1977; Post 1990). The allometric functions for metabolism and maximum consumption have not been determined for YOY walleye, so it was assumed that the differences in allometry between YOY and adults for yellow perch (Post 1990) also apply to walleye.

Consumption rates were modeled as a type 2 functional response using the Holling Disk Equation for multiple prey (Holling 1965):

$$\text{CON}_{ij} = \frac{\text{FMAX}_i * \text{VUL}_{ij} * \text{AVB}_j}{\text{KS}_{ij} + \sum_{j=1}^n \text{VUL}_{ij} * \text{AVB}_j}$$

where

$\text{AVB}_j = 0$  for  $B_j \leq \text{REF}_j$  and

$\text{AVB}_j = B_j - \text{REF}_j$  for  $B_j > \text{REF}_j$

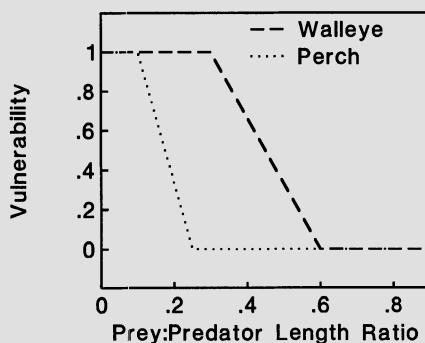
and where  $\text{CON}_{ij}$  is the specific daily consumption rate of age class  $i$  on prey  $j$ ;  $\text{FMAX}_i$  is the maximum specific daily consumption rate of age class  $i$ ;  $\text{VUL}_{ij}$  is the vulnerability of prey  $j$  to predation by age class  $i$ ;  $\text{AVB}_j$  is the available biomass of prey  $j$ , which becomes zero when its biomass is equal to or less than  $\text{REF}_j$ , which is the refuge biomass; and  $\text{KS}_{ij}$  is the prey biomass at which the specific daily consumption rate of age class  $i$  feeding on prey  $j$  is one-half of  $\text{FMAX}_i$ .

The maximum feeding rate for each age class  $i$ ,  $\text{FMAX}_i$ , is the maximum potential consumption rate determined from allometric and temperature-dependence relationships (Kitchell et al. 1977; Post 1990).

The half-saturation feeding rate for age class  $i$  feeding on prey  $j$ ,  $KS_{ij}$ , for planktivorous age classes (0.3736) was determined from in situ enclosure experiments with YOY yellow perch feeding on zooplankton (Post 1990).  $KS_{ij}$  for piscivorous age classes (0.1331) was determined from field data on piscivorous walleye presented by Swenson (1977). A similar value can be derived from the Poisson encounter rate model used in an individual-based model for Oneida Lake walleye (Madenjian and Carpenter, 1991). The functional response curves for fish as prey are constructed to give zero consumption at a low but nonzero prey abundance. This represents a refuge ( $REF_j$ ) from predation provided by structure in the littoral zone where YOY percids are commonly found (Lyons and Magnuson 1987; Post and McQueen 1988). The value of this refuge was set rather arbitrarily at  $0.05 \text{ g m}^{-3}$ .

Assimilation efficiency ( $\alpha_{ij}$ ) is 0.55 when predator and prey energy density are equal and 0.28 when predator energy density is double the prey energy density. The energy density of zooplankton and YOY fish is approximately  $600 \text{ cal g}^{-1}$ , and that of adult fish is approximately  $1,200 \text{ cal g}^{-1}$  (Treasurer 1989; Post 1990).

Since piscivores are gape-limited predators, prey availability is a function not only of prey density but also of prey size structure. Therefore, the vulnerability,  $VUL_{ij}$ , of a particular cohort to predation by another is a function of their relative sizes. Prey are consumed according to their density as determined by the functional response curve up to a lower threshold of prey:predator length ratio. Above an upper prey:predator length ratio, prey are invulnerable to the predator. Vulnerability at length ratios between the lower and upper thresholds is assumed to be a decreasing linear function of prey:predator length ratio (Figure 19.3). The upper



**Figure 19.3.** Vulnerability to predation as a function of prey:predator length ratio. A vulnerability of 1.0 means that prey will be eaten simply as a function of their density. A vulnerability of 0 means that the prey is completely invulnerable to piscivory and will not be eaten. At intermediate vulnerabilities, prey will be taken as the product of their density and their vulnerability.

ratios were derived from a variety of laboratory experiments and field observations and were chosen to be 0.60 for walleye (Nielsen 1980; Knight et al. 1984; Campbell 1989) and 0.25 for yellow perch (Knight et al. 1984; Tonn et al. 1991). The lower ratios were not available from the literature, but we assumed that walleye are more efficient piscivores and assigned a value of 0.25 for walleye and 0.10 for yellow perch. Therefore, realized consumption by piscivores is a function of predator weight, temperature, prey:predator length ratios, and the combined biomass of the vulnerable proportion of all potential prey types.

### Zooplankton Dynamics

Zooplankton biomass is modeled as a function of temperature-dependent production and consumption by planktivores:

$$\frac{dz}{dt} = \text{PROD} - \sum_{k=1}^n \text{CON}_{kz} B_k$$

where  $z$  is zooplankton biomass, PROD is zooplankton production,  $\text{CON}_{kz}$  is specific daily consumption by age class  $k$  on zooplankton, and  $B_k$  is biomass of age class  $k$ . Zooplankton production ranges from  $1 \text{ g m}^{-3}$  at the maximum summer temperature to  $0.17 \text{ g m}^{-3}$  at winter temperature (Figure 19.2). The bounds for zooplankton biomass are  $0.5\text{--}5.0 \text{ g m}^{-3}$ , which capture typical maxima and minima of zooplankton biomass in Lake Mendota (Lathrop and Carpenter, Ch. 8).

This simplified representation of the dynamic aspects of zooplankton communities was deemed to be sufficient for the purposes of driving the fish populations in this model, for the following reason. Runs of the model at a wide range of YOY yellow perch densities (obligate planktivores in the model) produced seasonal growth trajectories covering the range of observations in five natural lakes at approximately the same latitude as Lake Mendota (Post 1987) and in enclosure experiments where YOY yellow perch densities were manipulated *in situ* (Post 1990).

## Results

### Sensitivity Analysis

The parameters included in the model can be organized into four groups: (1) initial conditions—biomass and mean weight of different age classes; (2) population parameters—mortality, fecundity, size at hatch, and invertebrate production; (3) functional response parameters—half-saturation constants, maximum consumption, upper and lower prey:

**Table 19-1.** Experimental design used to explore the influence of walleye exploitation on the population dynamics of walleye, yellow perch, and zooplankton. Results of the simulations are presented in the figures indicated. The simulation used for the sensitivity analysis (S) is also indicated. The total mortality rates correspond to instantaneous mortality rates of 0.001, 0.002, 0.003, 0.004, and 0.005.

Annual perch fishing mortality (%)	Annual walleye fishing mortality (%)				
	0	30	51	66	76
0	8				8
30					
51	4, 9, 10	9, 10	(S) 5, 9, 10	9, 10	6, 9, 10
66					
76	8				8

predator ratios, and refuge; (4) bioenergetics parameters—metabolic rates and assimilation efficiencies.

We tested the sensitivity of the model to parameters and initial conditions by perturbing them, one at a time, by  $\pm 5\%$  and comparing the resulting changes in four response variables: (1) biomass of YOY yellow perch, (2) biomass of yellow perch older than YOY, (3) biomass of YOY walleye, and (4) biomass of walleye older than YOY. The sensitivity analysis was conducted on the parameter set that represents the midpoint of the range of exploitation scenarios that will be explored (Table 19.1). Simulations with this parameter set resulted in a stable 2-year cycle by about year 30. Therefore, the value of the response variables was calculated as the mean of the values at the end of year 49 and 50. In Table 19.2 we present the parameters to which the model is sensitive, i.e., there was a change in the response variable  $>5\%$  when parameters were perturbed 5%.

Initial conditions have no effect on the response variables once the stable 2-year cycle has been reached. The model is most sensitive to the parameters associated with the bioenergetics and the functional response of the fish species, and less sensitive to the population parameters. Not surprisingly, response variables are most sensitive to parameters included directly in the equations for that variable. The refuge parameter is among the parameters to which the model is sensitive, indicating the importance of littoral zone refuges for the population dynamics of fish (Diehl 1988; Eklov and Hamrin 1989; Wright 1990). The half-saturation constants in the functional response curves and prey:predator length ratios were not important for any response variable.

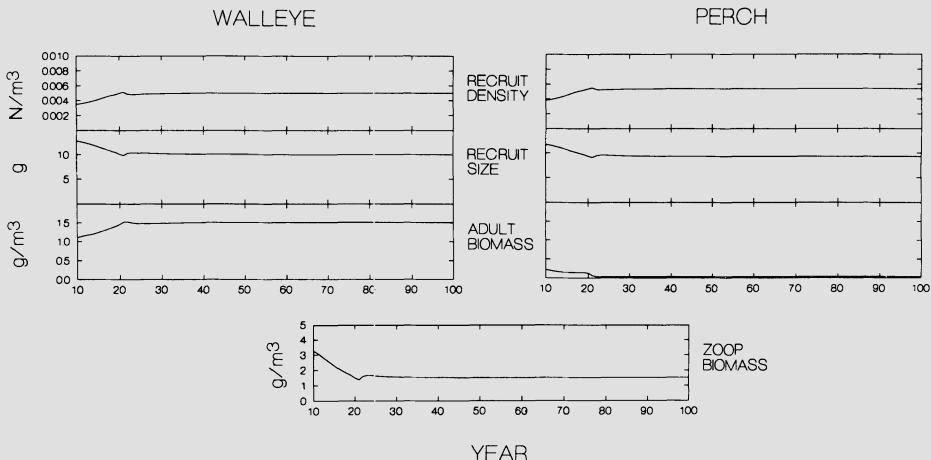
**Table 19-2.** Ranks of model sensitivity to individual parameter perturbation. The number indicates the rank of the sensitivity of a response variable to a change of  $\pm 5\%$  in a parameter value. Only parameters to which the model was sensitive (i.e., deviations of  $>5\%$  in response variable from the standard run) were ranked. The total number of parameters tested for each group is indicated in parentheses. The parameters ranked 1 (i.e., the parameters causing the greatest sensitivity) varied in deviation between 8% and 23%. P refers to yellow perch, W refers to walleye, INV refers to zooplankton.

Parameter	Response variables			
	YOY P	YOY W	Older P	Older W
Population parameters (12)				
Adult P mortality			4	
INV production		5		
Functional response parameters (13)				
Older P maximum consumption			1	
YOY P maximum consumption	3	4		7
YOY W maximum consumption	4	3		6
Refuge			5	
Bioenergetic parameters (8)				
Older P respiration			3	
YOY P respiration	2			5
YOY W respiration	6	2		4
Older P assimilation			2	
Older W assimilation				1
YOY P assimilation	1	6		3
YOY W assimilation	5	1		2

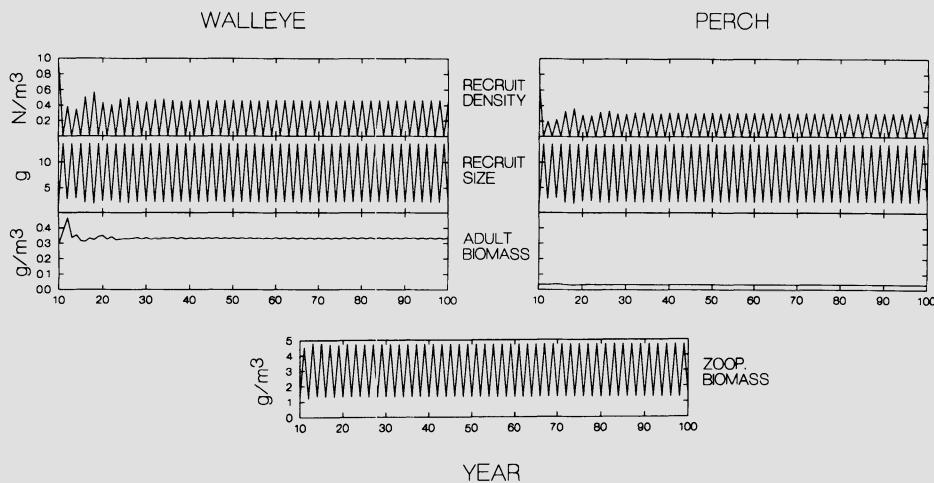
### Management of Exploitation Rates

The goal of this series of simulations is to examine the implications for walleye and yellow perch population dynamics and for zooplankton of strategies of exploitation management. Potential strategies range from managing a closed fishery on both species to the other extreme of high exploitation of both species. Here we explore a variety of potential management strategies spanning these extremes (Table 19.1).

The first series of simulations examines the effects of regulating the walleye fishery from a closed fishery to high exploitation rates (0–76% annual fishing mortality) with an intermediate yellow perch exploitation rate (51% annual fishing mortality). If walleye are unexploited, both the walleye and perch population reach an equilibrium within approximately 20 years (Figure 19.4). Under this scenario walleye are dominant in biomass. Moderate walleye exploitation (the parameter set used in the sensitivity analysis) produces 2-year cycles in both walleye and yellow perch populations (Figure 19.5). The 2-year cycle appears to be driven by



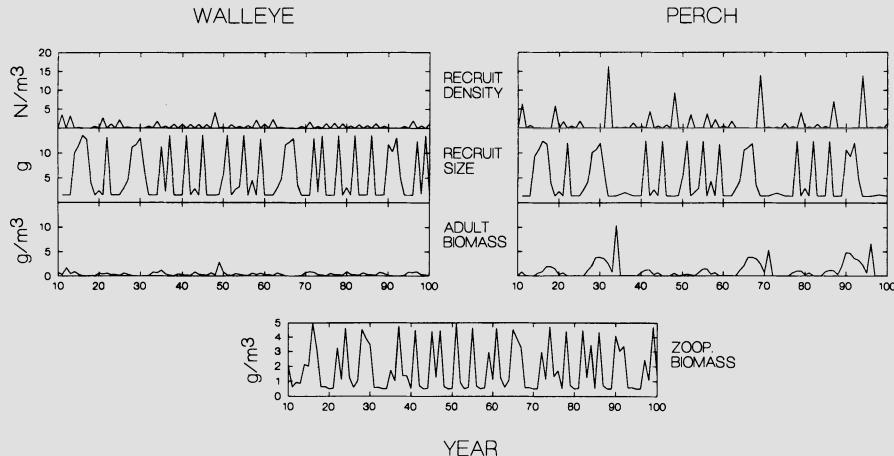
**Figure 19-4.** Time series of recruit density, recruit size, and adult biomass for walleye, yellow perch, and zooplankton biomass. This simulation was run with a walleye exploitation rate of 0% and a yellow perch exploitation rate of 51%.



**Figure 19-5.** Time series of recruit density, recruit size, and adult biomass for walleye, yellow perch, and zooplankton biomass. This simulation was run with walleye and perch exploitation rates of 51%.

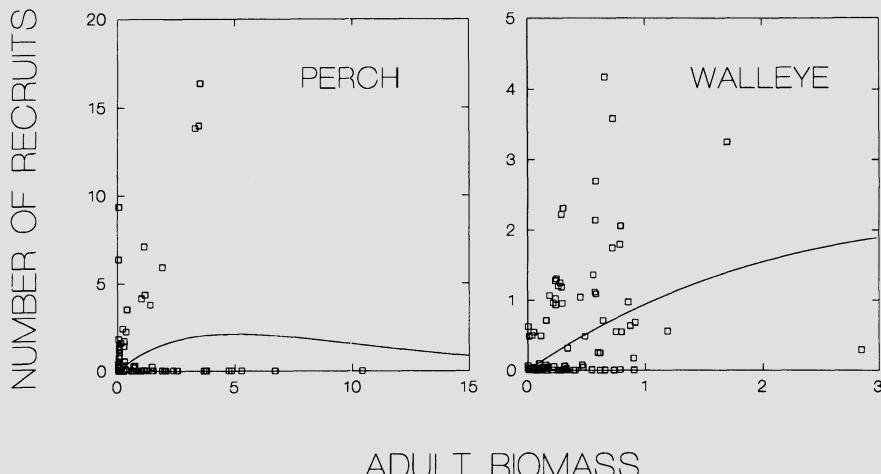
strong density-dependent growth and alternating strong and weak year classes of recruits (defined here as the fish that graduate to age 1+ on April 30). Since walleye and perch year class strengths are synchronous, the likely explanation for the cycle is strong competition between adjacent age classes of yellow perch.

At the highest walleye exploitation rates explored (76% annual fishing mortality), recruit density at 1 year of age, recruit body size and adult



**Figure 19-6.** Time series of recruit density, recruit size, and adult biomass for walleye, yellow perch, and zooplankton biomass. This simulation was run with a walleye exploitation rate of 76% and a yellow perch exploitation rate of 51%.

biomass of both walleye and perch, and mean summer zooplankton biomass are highly variable from year to year (Figure 19.6). There is still some evidence of 2-year cycles in year class strength for both species, in that a strong year class is typically followed by a weak one, but there are frequent sequential weak year classes. There is strong density-dependent growth for both species. Since the model is deterministic, the observed dynamics are caused by the underlying trophic relationships forced by a seasonal temperature cycle. There are no stochastic elements to the model. The mean and variability of recruit density and adult biomass are higher for perch than for walleye (Figure 19.4). These relationships are probably related to the shape of the stock-recruitment relationship produced by this simulation. The yellow perch population exhibits some evidence of a dome-shaped stock-recruitment curve (Figure 19.7). A wide range of year class strengths was observed at low stock densities, and year class strength is never high when stock biomass is high. The largest year classes and the largest variability in year class strength occurred at intermediate stock biomass. The walleye do not show much evidence of reduced recruitment at high stock size, but the data do suggest that recruitment is limited at low stock biomass. Cannibalism cannot explain the different shapes of the stock recruit curves, because both yellow perch and walleye are cannibalistic. An explanation may be that adult perch not only cannibalize their young, but also compete with their young for zooplankton prey. High adult perch biomass may reduce zooplankton biomass, which reduces growth rates of YOY fish and increases the length of time that they are vulnerable to cannibalism and predation by walleye. Adult walleye, as obligate piscivores, do cannibalize their young, but they also consume planktivores that compete with their offspring. Therefore

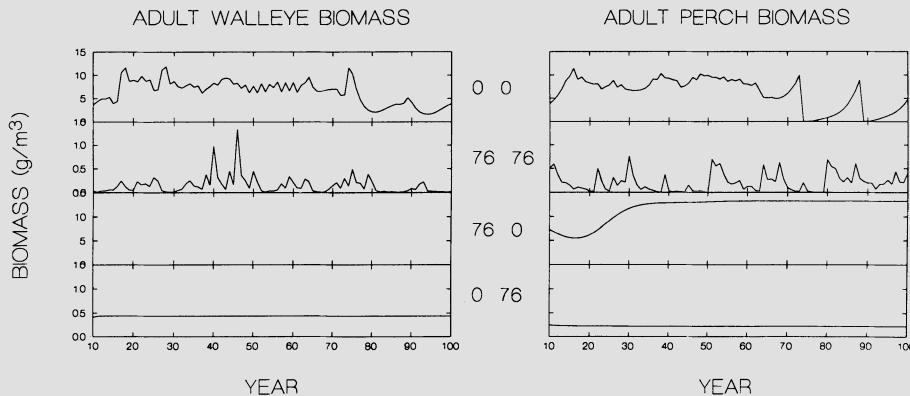


**Figure 19-7.** Relationship between adult biomass and number of recruits for yellow perch and walleye for the time series presented in Figure 19.4. The curves were fitted with a Ricker stock and recruit curve (Ricker 1975).

piscivory by walleye on YOY perch may partially release their offspring from competition, allowing higher growth rates and reducing the length of time that they are vulnerable to cannibalism by walleye and to predation by adult perch. In summary, varying walleye exploitation from unexploited to high rates of exploitation drives the population dynamics from equilibria through cycles to dynamics that appear chaotic.

Other combinations of managing exploitation in a two-species fishery are possible (Table 19.1, Figure 19.8). If neither population is exploited, population dynamics exhibit chaotic dynamics that have an upper bound, probably set by invertebrate production (Figure 19.8). In the last two to three decades of the simulation there is some evidence of long-term cycling (10–12 years). If both populations are highly exploited, both populations exhibit chaotic dynamics and the biomasses are an order of magnitude lower than in the unexploited state. In the situation of high walleye exploitation and no perch exploitation, the walleye population is driven to extinction within the first 10 years of the simulation, and yellow perch reach a high equilibrium biomass (Figure 19.8). Both the walleye and yellow perch populations attain equilibrium biomass when walleye is unexploited and yellow perch exploited heavily. This series of simulations demonstrates that yellow perch, which as an adult is both a competitor and a predator, can drive walleye to extinction, but walleye, which is an obligate piscivore as an adult, cannot drive perch to extinction.

The exploitation rates for walleye and yellow perch in Lake Mendota have increased from 35% and 10% annually in 1988 to 55% and 54% annually in 1989 (from Johnson and Staggs, Ch. 17, assuming 30% annual



**Figure 19-8.** Time series of biomass of adult walleye and yellow perch for combinations of exploitation rates. Exploitation rates are annual percent mortality for walleye and yellow perch, respectively.

natural mortality). Therefore the current 1989 situation in Lake Mendota is best represented by exploitation rates between those used in the simulations which produced the dynamics presented in Figure 19.5 and Figure 19.6. This suggests that the high exploitation rates currently observed in Lake Mendota may be sufficient to force the community to one in which eruptions and crashes are common and in which predictability is poor.

### Management by Stocking

In this section we examine the effects of the coordinated management of exploitation and stocking on the population dynamics of walleye and yellow perch. Walleye fisheries are managed by stocking hatchery- or pond-cultured fry and fingerlings in systems with and without natural spawning habitat. In Lake Mendota it is unclear how much walleye spawning habitat is available, and it has not been established what the contribution of naturally spawned YOY walleye is (Johnson et al., Ch. 16). Therefore we will contrast the impacts of walleye management in situations with and without natural recruitment. In these simulations total annual mortality of yellow perch was fixed at 66%. Fishing mortality for walleye was varied from 0% to 76%, yielding total mortalities of 30% to 83% annually. Stocking rates were 0, 0.05, 0.5, 5, and 50 million YOY annually. The current annual stocking rate for Lake Mendota is approximately 0.5 million walleye.

As expected, in systems with no natural walleye recruitment, walleye biomass is zero and biomass rises rapidly with increases in stocking (Figure 19.9). If the walleye population is unexploited, maximum biomass is attained at approximately the current stocking rate in Lake Mendota.

At the current high levels of walleye exploitation, maximum biomass is attained at stocking levels two orders of magnitude greater than current stocking rates. Interannual variability in walleye biomass is lowest at the lowest stocking and exploitation rates, and rises exponentially with increases in both stocking and exploitation. The density of recruits in the situation of no natural recruitment is maximum at maximum stocking and exploitation rates. In unexploited populations, stocking has minimal effects on recruit density, but when walleye exploitation is high, recruit density is strongly dependent on stocking rates (Figure 19.9). Interannual variability in recruit density is high at high stocking rates but largely unrelated to exploitation rates.

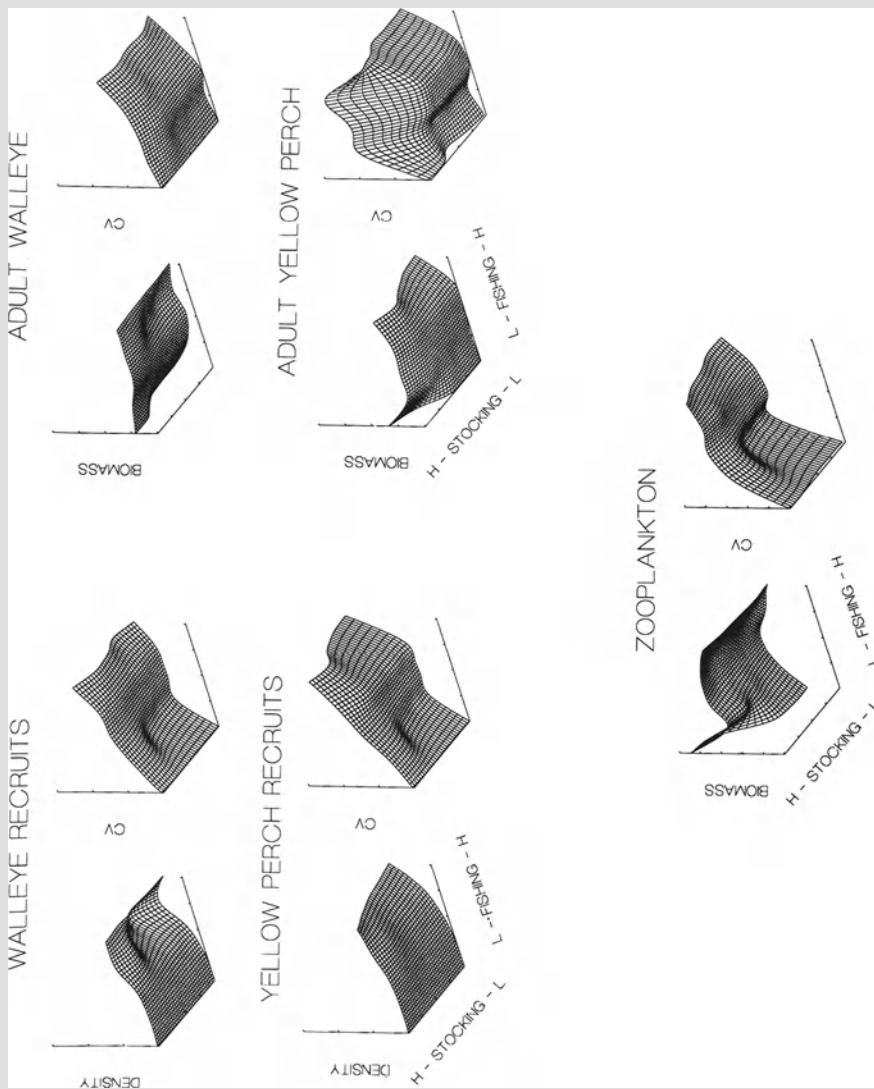
In walleye populations with successful natural reproduction, the impact of management of exploitation and stocking rates is substantially different. Means and variability in adult walleye biomass and in recruit density are largely unaffected by stocking rates ranging from zero through three orders of magnitude (Figure 19.10). Population dynamics are controlled primarily by walleye exploitation rates, as discussed in the previous section.

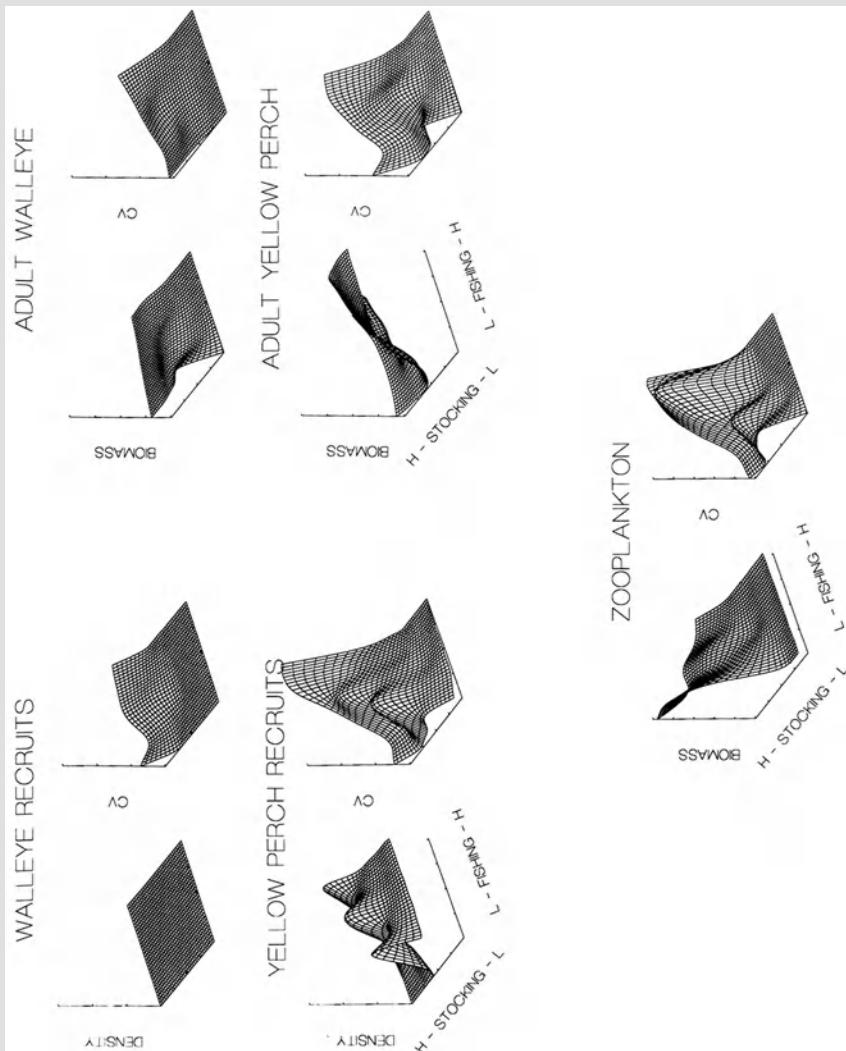
In systems with no natural walleye recruitment, mean yellow perch biomass is maximal in situations where stocking is low and walleye exploitation is moderate to high, and declines dramatically once past a threshold of increased stocking and decreased walleye exploitation (Figure 19.9). Interannual variability in yellow perch biomass is greatest at high stocking and high exploitation rates. Perch recruit density shows an interesting nonlinear ridge of maxima from low stocking–low exploitation to high stocking–high exploitation (Figure 19.9). Again, variability in recruit density is highest under a scenario of high stocking and high exploitation.

In systems with natural walleye recruitment, yellow perch dynamics are quite different. Mean adult perch biomass is maximal at the highest walleye stocking and exploitation rates (Figure 19.10). The probable explanation is that high stocking densities of slow-growing 0+ walleye are a high-density prey resource for large, fast-growing adult perch. As with the interannual variability in walleye biomass, perch biomass variability increases with increasing stocking and/or walleye exploitation. The mean density and interannual variability of perch recruits are essentially unaffected by stocking rates of 0+ walleye (Figure 19.10).

---

**Figure 19-9.** Response surfaces of mean and variability of walleye and yellow perch recruit density, adult biomass, and zooplankton biomass as a function of stocking and exploitation rates assuming that the system does not support natural walleye recruitment. The stocking axes have logarithmic units corresponding to 0, 0.05, 0.5, 5, and 50 million fry stocked annually. The fishing mortality axes are annual fishing mortality rates of 0%, 30%, 51%, 66%, and 76%.





Mean summer zooplankton biomass is directly proportional to stocking rate and inversely proportional to walleye exploitation when the system does not support natural walleye recruitment (Figure 19.9). Interannual variability in mean summer zooplankton biomass is highest at high stocking and exploitation rates. In systems with natural recruitment, only stocking rates one to two orders of magnitude greater than current Lake Mendota rates have a positive effect on zooplankton biomass, and only in unexploited walleye populations (Figure 19.10). In exploited walleye populations stocking has no impact on mean summer zooplankton biomass or on variability in mean summer zooplankton biomass.

Several general patterns emerge from this series of simulations designed to explore the consequences of management by stocking and exploitation. First, with no natural walleye recruitment, stocking enhances adult walleye biomass, density of walleye recruits, and mean summer zooplankton biomass but has the opposite effect on yellow perch. Second, mean annual variability when there is no natural recruitment increases with increased stocking and exploitation rates. Third, with natural walleye recruitment, stocking has minimal effects on walleye, yellow perch, and zooplankton biomass, and the dynamics are driven by walleye exploitation. Fourth, most of these relationships between stocking, exploitation, and biological dynamics are strongly nonlinear, suggesting that the dynamics are controlled by a combination of compensatory and decompensatory mechanisms within different domains of the state variables.

### Model Validation

A true model validation would require a time series over multiple generations for walleye and yellow perch. Such time series do not exist. However, even with such a time series, we do not expect our model, or any other, to be able to predict precise trajectories through time, and we should be satisfied with qualitatively similar population behaviors and similar aggregate measures of performance (see Bledsoe and Megrey, in press).

The literature does contain many short time series allowing comparisons of empirical means and coefficients of variation with those predicted by the model. Empirical measures of density of walleye and yellow perch age classes are most frequently reported as a catch per unit effort

---

← **Figure 19-10.** Response surfaces of mean and variability of walleye and yellow perch recruit density, adult biomass, and zooplankton biomass as a function of stocking and exploitation rates assuming that the system does support natural walleye recruitment. The stocking axes have logarithmic units corresponding to 0, 0.05, 0.5, 5, and 50 million fry stocked annually. The fishing mortality axes are annual fishing mortality rates of 0%, 30%, 51%, 66%, and 76%.

**Table 19-3.** Empirical estimates of annual variability in abundance and biomass of yellow perch, European perch, and walleye in the literature and in Lake Mendota.

Lake	Age	n	Mean	CV%	Units	Author
Yellow perch abundance						
Oneida	0+ (Aug)	12		74	CPUE	Nielsen 1980
Oneida	0+ (Oct)	12		98	CPUE	Nielsen 1980
Oneida	1+ (May)	11		138	CPUE	Nielsen 1980
Oneida	1+ (Sep)	12		193	CPUE	Nielsen 1980
Oneida	2+ (Sep)	12		103	CPUE	Nielsen 1980
Oneida	0+ (Aug)	9	0.20	45	$n \text{ m}^{-3}$	Mills et al. 1987
B. Quinte	Adults	17		34	CPUE	Hurley and Christie 1977
Michigan	0+	14		152	CPUE	Wells 1977
Michigan	1+	14		120	CPUE	Wells 1977
Michigan	Adults	14		195	CPUE	Wells 1977
Clear	0+	15		100	CPUE	Carlander and Payne 1977
Savanne	0+	12		110	CPUE	Ritchie and Colby 1988
Erie	0+	11		115	CPUE	Koone et al. 1977
Kabetogama	0+	5		88	CPUE	Kallemeyn 1987
Namakan	0+	5		44	CPUE	Kallemeyn 1987
Sand Point	0+	3		56	CPUE	Kallemeyn 1987
Rainy	0+	3		47	CPUE	Kallemeyn 1987
Mendota	>0+	9		126	CPUE	Rudstam et al. (Ch. 12)
Mendota	>0+	7	620	55	$n \text{ ha}^{-1}$	
European perch abundance						
Windermere-N	2+	35	247	126	$n \text{ ha}^{-1}$	Craig et al. 1979
Windermere-S	2+	35	831	114	$n \text{ ha}^{-1}$	Craig et al. 1979
Windermere-N	$\geq 3+$	36	741	86	$n \text{ ha}^{-1}$	Craig et al. 1979
Windermere-S	$\geq 3+$	36	2,448	51	$n \text{ ha}^{-1}$	Craig et al. 1979

Table 19-3. Continued

Lake	Age	n	Mean	CV%	Units	Author
IJssel	Larvae	9	106	CPUE	Willenssen 1977	
IJssel	0+	9	181	CPUE	Willenssen 1977	
IJssel	1+	9	158	CPUE	Willenssen 1977	
Walleye abundance						
B. Quinte	Adults	16	34	CPUE	Hurley and Christie 1977	
Clear	0+	15	106	CPUE	Carlander and Payne 1977	
Savanne	0+	12	170	CPUE	Ritchie and Colby 1988	
Erie	0+	11	116	CPUE	Koonee et al. 1977	
Kabetogama	0+	5	81	CPUE	Kallemyn 1987	
Namakan	0+	5	112	CPUE	Kallemyn 1987	
Sand Point	0+	3	136	CPUE	Kallemyn 1987	
Rainy	0+	3	110	CPUE	Kallemyn 1987	
Yellow perch biomass						
Mendota	>0+	7	96	kg ha <sup>-1</sup>	Rudstam et al. (Ch. 12)	
Red Lakes	≥4+	46	62	CPUE	Smith 1977	
European perch biomass						
Windermere-N	≥3+	36	43	kg ha <sup>-1</sup>	Craig et al. 1979	
Windermere-S	≥3+	36	118	kg ha <sup>-1</sup>	Craig et al. 1979	
Walleye biomass						
Oneida	Adult	12	24.3	kg ha <sup>-1</sup>	Nielsen 1980	
Escanaba	≥3+	16	12.3	kg ha <sup>-1</sup>	Kempinger and Carline 1977	
Clear	3+	27	5.6	kg ha <sup>-1</sup>	Carlander and Payne 1977	
Red Lakes	≥4+	46	48	CPUE	Smith 1977	
Hoover	≥2+	7	13.6	kg ha <sup>-1</sup>	Momot et al. 1977	

(CPUE), and annual variability can be calculated from such data (Table 19.3). A summary of the literature suggests that there are no major differences in annual variability in density of yellow perch, Eurasian perch (*Perca fluviatilis*), or walleye or between year classes of these species. The range in annual variability observed is 34–195% with a median of 108% (Table 19.3). Annual variability in biomass of adult yellow perch, Eurasian perch, and walleye is also high, ranging from 24% to 67% with a median of 50% (Table 19.3). In Lake Mendota the coefficients of variation in yellow perch density and biomass are 55–126% and 59%, respectively. Similar magnitudes of annual variability were also produced by our model under a range of management strategies (Figures 19.9 and 19.10). Although these comparisons do not confirm that the model structure is “correct,” they do suggest that the model can produce dynamics that resemble those of natural perch and walleye populations.

## Discussion

The goal of this chapter is to explore the interactive dynamics of walleye and yellow perch populations and the impact of fisheries management on their dynamics. To do this we have constructed and analyzed a two-species, age-structured model based on functions that mimic the biological mechanisms that we assume drive the two populations and their interactions throughout their life history. The two species are competitors and predators at different stages of their ontogeny. This “intraguild predation” is more common in nature than has previously been acknowledged (Polis et al. 1989).

Our mechanistic model reveals an impressive array of dynamic behavior much like that demonstrated by simpler one-species, nonoverlapping-generation models (May and Oster 1976; Levin and Goodyear 1980; May 1986; Kot et al. 1988; Olsen and Schaffer 1990). There are remarkable similarities in the dynamics of our and Levin and Goodyear’s (1980) model. Both models show development of population trajectories from equilibrium through period doubling to apparent chaos when adult mortality increases (30–83% in our model and 40–95% in Levin and Goodyear’s model). This similarity is particularly interesting because of the differences in structure of the two models. Levin and Goodyear’s model is a single-species model based on the assumption that recruitment is a density-dependent, Ricker-type, stock-recruit function. Our model was based on the biological mechanisms of prey production, predator–prey interactions, and bioenergetics with no explicit density-dependent function. Yet it yielded a Ricker-like relationship that is remarkably similar to empirical results with high variance in recruits at intermediate stock biomass (see review in Pitcher and Hart 1982).

The generally accepted explanation for this phenomenon is that density-dependent processes control the production of recruits at extremes of

adult stocks (Pitcher and Hart 1982) and that “density-vague” (*sensu* Strong 1983) processes such as environmental variability produce high variability in recruitment at intermediate stock densities. Our model results provide an example of instabilities caused by biotic interactions rather than by stochastic environmental forcing (i.e., the “biotic instability” of DeAngelis and Waterhouse 1987). Bledsoe and Megrey (in press) argue convincingly that variability is “simply an inherent property of the dynamics of biological properties imbedded in a biological food web.” If this is a common phenomenon, then: (1) an understanding of trophic interactions is necessary to understand population dynamics; (2) environmental and biotic variability may interact and environmental signals may either become damped or resonate and be difficult to extract from time series; (3) prediction of population trajectories through time will not be possible.

Analysis of simple, single-population analytical models suggested that rates had to be unrealistically high to generate chaotic dynamics (Hassell et al. 1976). The broad range of system dynamics observed here is consistent with the suggestion of Kot et al. (1988) that chaotic dynamics are more likely to be observed in more complex and biologically realistic systems than in simple, single-population analytical models.

Management initiatives such as exploitation and stocking can have substantial impact on population dynamics, because they alter the rates of growth, mortality, and fecundity. Increasing rates of exploitation of walleye, the obligate piscivore, with yellow perch mortality rate held constant, drove the dynamics from a simple equilibrium through cycles to chaotic dynamics. Empirical studies have identified population cycles in fish generally considered caused either by strong competition between year classes (Hamrin and Persson 1986; Townsend 1989; Townsend and Perrow 1989) or by annually discrete spawning stocks (Wyatt 1988; Northcote and Larkin 1989). Paleolimnological analysis has identified periodicities approximating the life span of piscivores (Carpenter and Leavitt 1991). Periodicities longer than the life span of predators may result from stochastic fluctuations at time scales longer than predator life cycles (Steele 1974; Carpenter and Kitchell 1987; Carpenter and Leavitt 1991) but may also occur deterministically in coupled prey–predator systems (May 1986). Our model produced the full range of period doubling dynamics, at exploitation rates intermediate to those presented in Figures 19.4–6, from 2-year cycles to multifrequency cycles at periodicities both less than and greater than the life cycles of the populations modeled. The addition of piscivorous fish to a pelagic food web model created 2-year cycles in planktivores, zooplankton, and phytoplankton (Bartell et al. 1988). It may be that population periodicity is a common phenomenon for species imbedded in food webs and can vary along a continuum from simple to complex periodicities to chaotic dynamics (Bledsoe and Megrey, in press).

Our simulations suggest that the walleye population is more likely than yellow perch to go extinct with high rates of exploitation because of its specialized trophic ontogeny. It is the interaction between competition and size-dependent piscivory that creates a recruitment bottleneck for the young walleye. YOY walleye compete with yellow perch of all age classes for zooplankton prey. Therefore, if there is a high biomass of perch of any age class, zooplankton biomass will be suppressed and growth of all planktivores will decline. Smaller, slower-growing 0+ walleye are more vulnerable and vulnerable for a longer period of time to gape-limited adult yellow perch and walleye. Piscivorous yellow perch can eliminate recruitment of YOY walleye long enough that highly exploited walleye populations will go extinct. Even at high rates of exploitation, yellow perch can coexist with walleye due to the strong compensatory processes of density-dependent growth and size-dependent vulnerability to predation.

A management tool frequently used in walleye fisheries is stocking to augment natural recruitment or to provide recruitment in situations where natural spawning habitat is not available (Laarman 1978). We used the model to address the question of whether we can augment an exploited walleye population by stocking and at the same time attain our water quality goals. The answer to this question is strongly dependent on whether the system allows natural walleye recruitment. In Lake Mendota it is unknown what proportion of the walleye population is the result of intermittent stocking by the Wisconsin Department of Natural Resources (WDNR) and local interest groups. Therefore we explored stocking scenarios for situations with and without natural recruitment. In systems with natural walleye recruitment, stocking rates ranging from zero to 100 times the current Lake Mendota stocking rate had minimal effects on population and community dynamics of the fish and zooplankton. The dynamics observed are driven by rates of exploitation, not stocking levels. On the other hand, in situations with no natural recruitment, walleye, yellow perch, and zooplankton dynamics are strongly related to stocking rates. Without natural walleye recruitment, there is a strong interaction between stocking rates and walleye exploitation rates in terms of walleye, yellow perch, and zooplankton biomass and also recruitment rates. When unexploited, current Lake Mendota stocking rates produce maximum adult walleye biomass. With current high exploitation, stocking rates 100 times current rates are insufficient to produce walleye biomass approaching unexploited conditions and insufficient to suppress yellow perch biomass and recruitment. Interannual variability in walleye and yellow perch recruitment and biomass increased exponentially with increasing stocking and exploitation, suggesting that both management techniques produce instability in the system.

The water quality management goal of high and stable zooplankton biomass (Carpenter and Kitchell 1987) was attained only in the situation

with stocking rates 100 times the current Lake Mendota rate and an unexploited walleye population. This suggests that stocking, even at high rates, is insufficient to overcome the impact of exploitation and that the best strategy would be to reduce exploitation rates.

We have demonstrated that deterministic coupled predator-prey systems can produce a variety of dynamics from equilibria to chaotic without invoking environmental variability. This full range of dynamics was observed by manipulating exploitation rates within biologically reasonable bounds. This has important implications for fisheries management, showing that high exploitation rates can have the effect of driving populations from stable states to states in which populations become highly variable and unpredictable.

*Acknowledgments.* We thank Steve Carpenter, Jim Kitchell, Chuck Madenjian, Brett Johnson, Barry Johnson, Don Ludwig, and Tony Ives for their constructive comments on earlier drafts. We also acknowledge the assistance of Rusty Wright, Xi He, Paul Jacobson, Brett Johnson, and Beth Campbell in the initial attempt to implement a piscivore model for Lake Mendota. John R. Post was supported by Postdoctoral Fellowships from the Natural Sciences and Engineering Research Council of Canada and the Department of Zoology, University of Wisconsin. Lars G. Rudstam was supported by a Postdoctoral Fellowship from the Swedish Council for Forestry and Agricultural Research, a Federal Aid in Sport Fish Restoration Act under Project F-95-P, and the WDNR.

## References

- Adams SM, DeAngelis DL (1987) Indirect effects of early bass-shad interactions on predator population structure and food web dynamics. In Kerfoot WC, Sih A (eds) *Predation: Direct and indirect effects on aquatic communities*, University Press of New England, Hanover, New Hampshire, pp 103–117
- Bartell SM, Brenkert AL, O'Neill RV, Gardner RH (1988) Temporal variation in regulation of production in a pelagic food web model. In Carpenter SR (ed) *Complex interactions in lake communities*, Springer-Verlag, New York, pp 101–117
- Bledsoe LJ, Megrey BA (1989) Chaos and pseudoperiodicity in the dynamics of a bioenergetics food web model. In Edwards EF and Megrey BA (eds) *Mathematical analysis of fish stock dynamics*. Am. Fish. Soc. Symp. 6:121–137
- Campbell EA (1989) Laboratory examination of size-selective predation by small walleye (*Stizostedion vitreum*) on yellow perch (*Perca flavescens*). M.Sc. Thesis, University of Wisconsin, Madison
- Carlander KD, Payne PM (1977) Year class abundance, population, and production of walleye (*Stizostedion vitreum vitreum*) in Clear Lake, Iowa, 1948–74, with varied fry stocking rates. J. Fish. Res. Board Can. 34:1792–1799
- Carpenter SR, Kitchell JF (1987) The temporal scale of variance in limnetic primary production. Am. Nat. 129:417–433

- Carpenter SR, Leavitt PR (1991) Temporal variation in a paleolimnological record arising from a trophic cascade. *Ecology* 72:277–285
- Caswell H (1989) Matrix population models. Sinauer, Sunderland, Massachusetts
- Craig JF, Kipling C, LeCren ED, McCormack JC (1979) Estimates of the numbers, biomass and year-class strengths of perch (*Perca fluviatilis* L.) in Windermere from 1967–1977 and some comparisons with earlier years. *J. Anim. Ecol.* 48:315–325
- DeAngelis DL, Waterhouse JC (1987) Equilibrium and nonequilibrium concepts in ecological models. *Ecol. Monogr.* 57:1–21
- Diehl S (1988) Foraging efficiency of three freshwater fishes: Effects of structural complexity and light. *Oikos* 53:207–214
- Eklov P, Hamrin SF (1989) Predator efficiency and prey selection: Interactions between pike *Esox lucius*, perch *Perca fluviatilis* and rudd *Scardinius erythrophthalmus*. *Oikos* 56:149–156
- Forney JL (1966) Factors affecting first-year growth of walleyes in Oneida Lake, New York. *N.Y. Fish Game J.* 13:146–167
- Getz WM, Haight RG (1989) Population harvesting. Princeton University Press, Princeton, New Jersey
- Gurney WCS, Nisbet RM (1983) The systematic formulation of delay-differential models of age or size structured populations. In Levin S (ed) *Lecture notes in biomathematics*, Vol. 52, Springer-Verlag, Berlin, pp 163–172
- Hamrin SF, Persson L (1986) Asymmetrical competition between age classes as a factor causing population oscillations in an obligate planktivorous fish species. *Oikos* 47:223–232
- Hassell MP, Lawton JH, May RM (1976) Patterns of dynamical behaviour in single species populations. *J. Anim. Ecol.* 45:471–486
- Holling CS (1965) The functional response of predators to prey density and its role in mimicry and population regulations. *Mem. Entomol. Soc. Can.* 45:1–60
- Hurley DA, Christie WJ (1977) Depreciation of the warmwater fish community in the Bay of Quinte, Lake Ontario. *J. Fish. Res. Board Can.* 34:1849–1860
- Johnson BM, Luecke C, Stewart RS, Staggs MD, Gilbert SJ, Kitchell JF (1992) Forecasting effects of harvest regulations and stocking on prey fish communities in a eutrophic lake. *No. Am. J. Fish. Manage.* (in press)
- Kallemeyn LW (1987) Correlations of regulated lake levels and climatic factors with abundance of young-of-the-year walleye and yellow perch in four lakes in Voyageurs National Park. *No. Am. J. Fish. Manage.* 7:513–521
- Kempinger JJ, Carline RF (1977) Dynamics of the walleye (*Stizostedion vitreum vitreum*) population in Escanaba Lake, Wisconsin, 1955–72. *J. Fish. Res. Board Can.* 34:1800–1811
- Kirchner TB (1989) TIME-ZERO: The integrated modelling environment. *Ecol. Modelling* 47:33–52
- Kitchell JF, Stewart DJ, Weininger D (1977) Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *J. Fish. Res. Board Can.* 34:1922–1935
- Knight RL, Margraf FJ, Carline RF (1984) Piscivory by walleyes and yellow perch in western Lake Erie. *Trans. Am. Fish. Soc.* 113:677–693
- Koonce JF, Baggenal TB, Carline RF, Hokanson KEF, Nagiec M (1977) Factors influencing year-class strengths of Percids: A summary and a model of temperature effects. *J. Fish. Res. Board Can.* 34:1900–1909

- Kot M, Schaffer WM, Truty GL, Graser DJ, Olsen LF (1988) Changing criteria for imposing order. *Ecol. Modelling* 43:75–110
- Laarman PW (1978) Case histories of stocking walleyes in inland lakes, impoundments and the great lakes—100 years with walleyes. *Am. Fish. Soc. Spec. Publ.* 11:254–260
- Levin SA, Goodyear CP (1980) Analysis of an age-structured fishery model. *J. Math. Biol.* 9:245–274
- Lyons J, Magnuson JJ (1987) Effects of walleye predation on the population dynamics of small littoral-zone fishes in a northern Wisconsin lake. *Trans. Am. Fish. Soc.* 116:29–39
- Madenjian CP, Carpenter SR (1991) Individual-based model for growth of young-of-the-year walleye: A piece of the recruitment puzzle. *Ecol. Applications* 1:268–279
- May RM (1986) The search for patterns in the balance of nature: Advances and retreats. *Ecology* 67:1115–1126
- May RM, Oster GF (1976) Bifurcations and dynamic complexity in simple ecological models. *Am. Nat.* 110:573–599
- Microsoft Corporation (1988) Microsoft QuickBASIC Programming in BASIC Version 4.5
- Miller TJ, Crowder LB, Rice JA, Marschall EA (1988) Larval size and recruitment mechanisms in fishes: Toward a conceptual framework. *Can. J. Fish. Aquat. Sci.* 45:1657–1670
- Mills EL, Forney JL, Wagner KJ (1987) Fish predation and its cascading effect on the Oneida Lake food chain. In Kerfoot WC, Sih A (eds) *Predation: Direct and indirect effects on aquatic communities*, University Press of New England, Hanover, New Hampshire, pp 118–131
- Momot WT, Erickson J, Stevenson F (1977) Maintenance of a walleye, *Stizostedion vitreum vitreum*, fishery in a eutrophic reservoir. *J. Fish. Res. Board Can.* 34:1725–1733
- Nielsen LA (1980) Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. *Can. J. Fish. Aquat. Sci.* 37:11–19
- Northcote TG, Larkin PA (1989) The Fraser River: A major salmonine production system. In Dodge DP (ed) *Proceedings of the International Large River Symposium (LARS)*. *Can. Spec. Publ. Fish. Aquat. Sci.* 106:172–204
- Olsen LF, Schaffer WM (1990) Chaos versus noisy periodicity: Alternative hypotheses for childhood epidemics. *Science* 249:499–504
- Pitcher TJ, Hart PJB (1982) *Fisheries ecology*. Croom Helm, London
- Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intraguild predation: Potential competitors that eat each other. *Annu. Rev. Ecol. Syst.* 20:297–330
- Post JR (1987) Size-dependent processes in yellow perch recruitment. Ph.D. Thesis, York University, Toronto
- Post JR (1990) Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): In situ estimates and bioenergetic models. *Can. J. Fish. Aquat. Sci.* 47:554–560
- Post JR, Evans DO (1989) Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): Laboratory, in situ enclosure, and field experiments. *Can. J. Fish. Aquat. Sci.* 46:1958–1968

- Post JR, McQueen DJ (1988) Ontogenetic changes in the distribution of larval and juvenile yellow perch (*Perca flavescens*): A response to prey or predators? *Can. J. Fish. Aquat. Sci.* 45:1820–1826
- Ricker WE (1954) Stock and recruitment. *J. Fish. Res. Board Can.* 11:151–225
- Ricker WE (1975) Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* 191
- Ritchie BJ, Colby PJ (1988) Even-odd year differences in walleye year-class strength related to mayfly production. *No. Am. J. Fish. Manage.* 8:210–215
- Robertson DM (1989) The use of lake water temperature and ice cover as climatic indicators. Ph.D. Thesis, University of Wisconsin-Madison
- Shuter BJ, Post JR (1990) Climate, population viability, and the zoogeography of temperate fishes. *Trans. Am. Fish. Soc.* 119:314–336
- Sissenwine MP (1984) Why do fish populations vary? In May RM (ed) *Exploitation of marine communities*, Springer-Verlag, Berlin, pp 59–94
- Smith LL, Jr (1977) Walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations and fisheries of the Red Lakes, Minnesota, 1930–1975. *J. Fish. Res. Board Can.* 34:1774–1783
- Steele JH (1974) The structure of marine ecosystems. Blackwell, Oxford
- Strong DR, Jr (1983) Natural variability and the manifold mechanisms of ecological communities. *Am. Nat.* 122:636–660
- Swenson WA (1977) Food consumption of walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) in relation to food availability and physical conditions in Lake of the Woods, Minnesota, Shagawa Lake, and western Lake Superior. *J. Fish. Res. Board Can.* 34:1643–1654
- Tonn WM, Paszkowski CA, Holopainen IJ (1991) Selective piscivory by perch: Effects of predator size, prey size, and prey species. *Verh. Internat. Verein. Limnol.* 24 (in press)
- Townsend CR (1989) Population cycles in freshwater fish. *J. Fish. Biol.* 35 (Supplement A):125–131
- Townsend CR, Perrow MR (1989) Eutrophication may produce population cycles in roach, *Rutilus rutilus* (L.) by two contrasting mechanisms. *J. Fish. Biol.* 34:161–164
- Treasurer JW (1989) The food and daily food consumption of lacustrine 0+ perch, *Perca fluviatilis* L.. *Freshwat. Biol.* 24:361–374
- Walters CJ (1986) Adaptive management of renewable resources. Macmillan, New York
- Wells L (1977) Changes in yellow perch (*Perca flavescens*) populations of Lake Michigan, 1954–75. *J. Fish. Res. Board Can.* 34:1821–1829
- Willemse J (1977) Population dynamics of percids in Lake Issel and some smaller lakes in the Netherlands. *J. Fish. Res. Board Can.* 34:1710–1719
- Wright RM (1990) The population biology of pike, *Esox lucius* L., in two gravel pit lakes, with special reference to early life history. *J. Fish. Biol.* 36:215–229
- Wyatt RJ (1988) The cause of extreme year class variation in a population of roach, *Rutilus rutilus* L., from a eutrophic lake in southern England. *J. Fish. Biol.* 32:409–421

# **20**

## **Impacts of Variation in Planktivorous Fish on Abundance of Daphnids: A Simulation Model of the Lake Mendota Food Web**

**Chris Luecke, Cynthia C. Lunte, Russell A. Wright,  
Dale Robertson, and Ann S. McLain**

Previous chapters in this volume have outlined the goals of the Lake Mendota food web manipulation study (Rudstam et al., Ch. 12) and have reported on variations in phytoplankton and zooplankton abundances during the past 15 years (Lathrop and Carpenter, Ch. 7 and 8). Because of the long time scales inherent in such a lake management manipulation, it became imperative to attempt to predict how the lake would respond to changes in planktivorous fish abundance over time scales of several decades. We know from the past 15 years of study (Lathrop and Carpenter, Ch. 7 and 8; Magnuson and Lathrop, Ch. 11) that substantial variation of planktivorous fish, zooplankton, and phytoplankton abundances can occur in the lake. Given the current stocking of piscivores, we have the potential to substantially modify the abundance of planktivorous fish and possibly shift the assemblages of phytoplankton and zooplankton beyond the ranges of those which occurred previously. In this chapter we describe the construction and use of a simulation model designed to examine how variation in planktivore abundance might impact zooplankton biomass and species composition.

This planktivory model was constructed to depict the middle portion of the Lake Mendota food web. This portion of the food web is represented by a series of state variables, the biomasses of trophic species (*sensu* Schoener 1989), which increase or decrease according to a series of differential equations describing growth, recruitment, and loss functions for each state variable. The model was constructed using a food web modeling program and is analogous to the herbivory model presented in the following chapter.

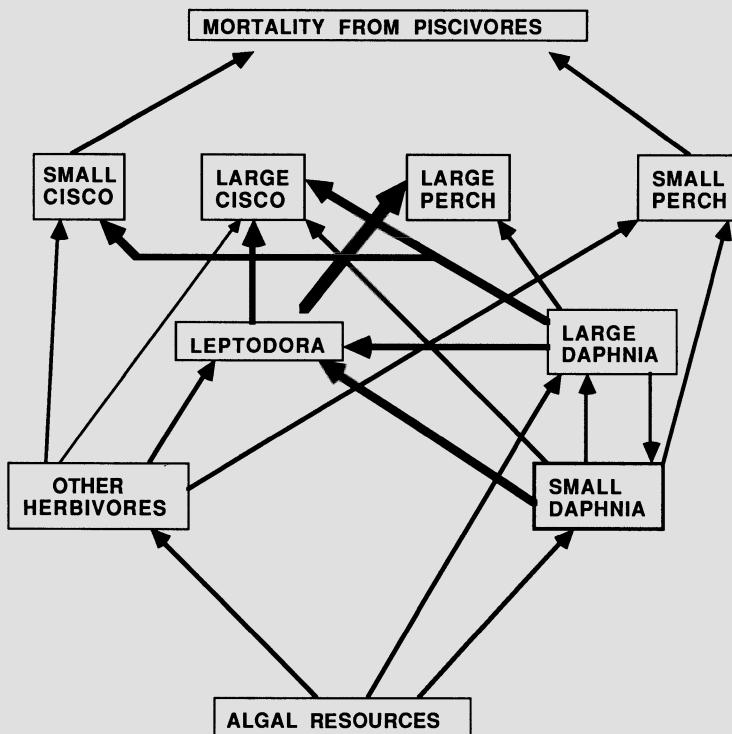
This modeling exercise had three goals: (1) to investigate the effects of varying the density of planktivorous fish on the seasonal and interannual densities of daphnids, (2) to examine the degree to which species-specific differences between yellow perch and cisco might impact the response of daphnids to variation in these planktivores, and (3) to examine the potential for *Leptodora* to buffer daphnid populations from variation in planktivorous fish abundance. Our approach was to define the likely limits of fish abundance from the historical records of Lake Mendota, other literature sources, and modeling results from Post and Rudstam (Ch. 19).

To accomplish these goals, we constructed a model to simulate the epilimnion of the lake during the stratified period of the year (1 May–1 September). The model was calibrated using field data from 1987 and then verified by comparing model predictions with field observations in 1988 and 1989. Twenty-five scenarios of varying perch and cisco abundance were simulated to examine the potential variation in daphnid abundance that might result from changes in planktivorous fish.

### Description of the Model

The model depicts the interactions of nine functional species groups as dynamic state variables (Figure 20.1). Three trophic species are herbivorous zooplankton (large daphnids, small daphnids, herbivorous copepods), one is an invertebrate predator (*Leptodora*), and four are planktivorous fishes (small and large cisco and perch). Algal resources are a state variable representing edible phytoplankton (all phytoplankton taxa except Cyanophyta and *Ceratium*). The biomass (g wet weight m<sup>-3</sup>) of each state variable can change through consumption of resources, by being fed upon by other consumers, or due to internal metabolic costs. Three forcing variables (temperature, algal production, and mortality from piscivores) control feeding and respiration rates of the fishes, resources available to herbivores, and predation pressure on planktivorous fishes.

The biomass of each state variable can increase by a feeding function based on a type II functional response (Hassell 1978) described as a Michaelis–Menten function with an asymptote for MAX and a half-saturation constant  $K$  (Table 20.1). The values for MAX and  $K$  for each species are derived from literature sources or best guesses based on the literature of similar species. A portion of consumed food is assimilated based on literature values (Table 20.1). The biomass of each state variable declines based on metabolic costs estimated from literature studies (Table 20.1) and by being fed upon by another consumer group. Total consumption and respiration for the fishes vary with temperature based on the temperature-dependence relationships reported in Hewett and



**Figure 20-1.** Structure of the planktivory model. Each box represents the state variables and the flow of biomass is indicated by arrows. The thickness of the arrows indicates the degree of predator preference for a given prey.

Johnson (1987) for perch and a generalized salmonid. Total temperature compensation was assumed to occur for the invertebrate groups (Walters et al. 1987). The temperature of the epilimnion varies from about 16°C in May to about 23°C in August, with most of that temperature change occurring in May. A low level of natural mortality was assigned to adult perch and adult cisco state variables (Table 20.1).

Selective feeding was modeled as a series of preference ratios based on calculation of a standardized forage ratio (SFR, Chesson 1983) from stomach contents of the fishes or from results of field experiments for *Leptodora* (Lunte and Luecke 1990). Total consumption was calculated based on a weighted availability of all prey, and then the forage ratios (Table 20.2) were used to proportion this total consumption to individual prey types. Prey availability was weighted by the preference ratios of each prey type. The SFR is relatively invariant over a broad range of available densities of prey (Chesson 1983).

From field data (Lathrop and Carpenter, Ch. 8; Pedros-Alio and Brock 1985; Lunte and Luecke 1990) we noticed that *Leptodora* appeared in the

**Table 20-1.** Parameters used in the simulation model. References refer to the footnoted numbers. Symbols refer to abbreviations used in the text.

Symbol	Description	Value	Ref.
AP	% useable energy for large perch	0.39 g/g	4
AL	% useable energy for <i>Leptodora</i>	0.76 g/g	5
AD	% useable energy for daphnids	0.8 g/g	12, 18
AH	% useable energy for other herbivores	0.77 g/g	6, 15
AC	% useable energy for large cisco	0.36 g/g	17
ASC	% useable energy for small cisco	0.72 g/g	17
ASP	% useable energy for small perch	0.67 g/g	13
MAXD	Maximum feeding rate of <i>Daphnia</i>	0.4 g/g/d	9, 10, 12
MAXC	Maximum feeding rate of other herbivores	0.32 g/g/d	1, 3, 9, 16
MAXL	Maximum feeding rate of <i>Leptodora</i>	0.5 g/g/d	5
MAXSP <sup>a</sup>	Maximum feeding rate of small perch	0.328 g/g/d	4, 13
MAXP <sup>a</sup>	Maximum feeding rate of large perch	0.072 g/g/d	4
MAXSC <sup>a</sup>	Maximum feeding rate of small cisco	0.348 g/g/d	17
MAXCI <sup>a</sup>	Maximum feeding rate of large cisco	0.051 g/g/d	17
KD	Half-saturation constant for <i>Daphnia</i>	15 g/m <sup>3</sup>	9, 10, 12
KC	Half-saturation constant for other herbivores	15 g/m <sup>3</sup>	6, 19
KL	Half-saturation constant for <i>Leptodora</i>	2.0 g/m <sup>3</sup>	8
KSP	Half-saturation constant for small perch	1.5 g/m <sup>3</sup>	11, 13
KP	Half-saturation constant for large perch	1.5 g/m <sup>3</sup>	13, 11
KSC	Half-saturation constant for small cisco	1.5 g/m <sup>3</sup>	13, 17
KCI	Half-saturation constant for large cisco	1.5 g/m <sup>3</sup>	13, 17
MSD	Respiration of small daphnids	0.13 g/g/d	9
MD	Respiration of large daphnids	0.13 g/g/d	9, 10, 12
MCR	Respiration of other herbivores	0.13 g/g/d	6, 15
ML	Respiration of <i>Leptodora</i>	0.13 g/g/d	5
MSP <sup>a</sup>	Maximum respiration of small perch	0.08 g/g/d	13
MP <sup>a</sup>	Maximum respiration of large perch	0.011 g/g/d	4
MSC <sup>a</sup>	Maximum respiration of small cisco	0.10 g/g/d	2, 17
MCI <sup>a</sup>	Maximum respiration of large cisco	0.009 g/g/d	2, 17
OMLP	Other mortality for large perch	0.001 g/g/d	7
OMLC	Other mortality for large cisco	0.001 g/g/d	7
RMAX	Maximum resource level	40 g/m <sup>3</sup>	1
EGG	% of large daphnid growth used for reproduction	85	9

References: <sup>1</sup> Brock 1985; <sup>2</sup> Dabrowski 1985; <sup>3</sup> Frost 1980; <sup>4</sup> Hewett and Johnson 1987; <sup>5</sup> Hillbricht-Ilkowska and Karabin 1970; <sup>6</sup> Kirby 1971; <sup>7</sup> Johnson et al., Ch. 16; <sup>8</sup> Lunte and Luecke 1990; <sup>9</sup> Lynch et al. 1986; <sup>10</sup> Paloheimo et al. 1982; <sup>11</sup> Perrson 1987; <sup>12</sup> Porter et al. 1982; <sup>13</sup> Post 1987; <sup>14</sup> Reed 1971; <sup>15</sup> Richman 1964; <sup>16</sup> Richman and Dodson 1983; <sup>17</sup> Rudstam 1983; <sup>18</sup> Schindler 1971; <sup>19</sup> Vanderploeg et al. 1984.

<sup>a</sup> Maximum feeding and respiration rates for fish varied as a function of temperature.

**Table 20-2.** Selectivity coefficients for the planktivores in the model. Consumption of prey by the predators is weighted by the preference ratio.

Predator	Prey	Preference ratio
Large perch	Large daphnids	1
	<i>Leptodora</i>	3.7
Large cisco	Copepods	1
	Small daphnids	13
	Large daphnids	57
	<i>Leptodora</i>	108
Small perch	Small daphnids	1
	Copepods	1
Small cisco	Small daphnids	1
	Copepods	1
<i>Leptodora</i>	Copepods	1
	Small daphnids	3
	Large daphnids	3

plankton as two distinct cohorts each year, one in late May and a second in early September. We modeled this occurrence by adding a small biomass of *Leptodora* ( $0.017$  and  $0.087 \text{ g m}^{-3}$ ) to the food web on 20 May and 1 September.

We felt that separation of daphnids into large and small groups was necessary given the differences in predator preferences exhibited by the fishes in 1987. We modeled the graduation of small daphnids into the larger size class as a sigmoid function of available algal resources. When algal resources were low ( $<5 \text{ g m}^{-3}$ ), only 4% of the small daphnid biomass recruited to the larger size class each day, but when resources were high ( $>30 \text{ g m}^{-3}$ ), 20% recruitment occurred daily. In turn, 85% of large daphnid growth was shunted to biomass of small daphnids each day to represent reproduction (McCauley et al. 1990).

The biomass of small daphnids was assumed to consist entirely of 1-mm animals and that of large daphnids to consist of 1.6-mm individuals. The herbivorous copepod was assumed to be a 1.0-mm calanoid, and *Leptodora* biomass was assumed to consist of 8-mm individuals. Small cisco and small perch represented young-of-year (YOY) fishes and were assumed to consist of 5-g individuals. The biomass of large cisco and large perch was represented by 400- and 100-g individuals, respectively.

The production of phytoplankton resources was modeled based on empirical relationships described by Brock (1985). Algal production (RR) was  $25\% \text{ d}^{-1}$  on 1 May, decreased linearly to  $5\% \text{ d}^{-1}$  on July 20, and remained at 5% for the rest of the simulation. Mortality losses of small fish to piscivores were modeled as a table function where losses were high early in the summer ( $3\% \text{ d}^{-1}$ ) and subsequently declined to low values

**Table 20-3.** Initial biomass ( $\text{g m}^{-3}$ ) of state variables for 1987–89

Variable	1987	1988	1989
Algal resources	27	2	3
Small daphnids	1.2	1.5	0.2
Large daphnids	2.6	4.2	0.5
Other herbivores	3.2	0.6	0.3
Small perch	0.05	0.05	0.05
Large perch	1.0	0.34	0.19
Small cisco	0.05	0.05	0.05
Large cisco	1.6	0.21	0.04

(0.6%  $\text{d}^{-1}$ ) by September. Rates of mortality for large fish (OMLP and OMLC) were low and constant throughout the simulation (Table 20.1). The initial biomasses used for the different simulations were estimated from field data (Table 20.3). Twenty-five scenarios consisting of a  $5 \times 5$  matrix of large perch and large cisco initial biomasses (0, 0.25, 0.75, 1.5, and 2.5 for each fish) were simulated to assess the impacts of varying abundance of perch and cisco on the zooplankton groups. Specific details and the equations used in the model are presented in the Appendix.

### Sensitivity Analysis

A sensitivity analysis was conducted on the 1987 model simulation in which each parameter was varied by  $\pm 10\%$  and the resultant change in large daphnid biomass was noted. Only change in the large daphnid variable was examined because this component appears to account for most of the cascading effects on phytoplankton assemblages in Lake Mendota (Vanni et al. 1990) and in other systems (Reinertsen and Langeland 1982; Benndorf et al. 1988; Carpenter, Ch. 23). A parameter was deemed sensitive if large daphnids changed by more than 10%. Large daphnid biomass could respond in two ways to the 10% change in a given parameter. A temporal shift in the timing of peak abundance could occur, or an overall change in the biomass of large *Daphnia* averaged throughout the summer could occur. To account for both of these responses, I examined the large daphnid biomass at day 50 and day 100 of each simulation and integrated large daphnid biomass through the simulation to calculate the average response.

Large daphnid biomass was sensitive to seven parameters (Table 20.4). The greatest responses occurred with the daphnid parameters themselves (A3 and MAXD) and with the parameters regulating algal production (RR and RMAX). Model simulations were also sensitive to perch and

**Table 20-4.** Sensitivity analysis of planktivory module. The following parameters caused a greater than 10% change in biomass of large *Daphnia* when the parameter was increased (+) or decreased (−) by 10%. Examination of large *Daphnia* biomass was made at day 50 and day 100 and summed over the 150-day simulation. The values refer to percent change; ns refers to changes of less than 10%.

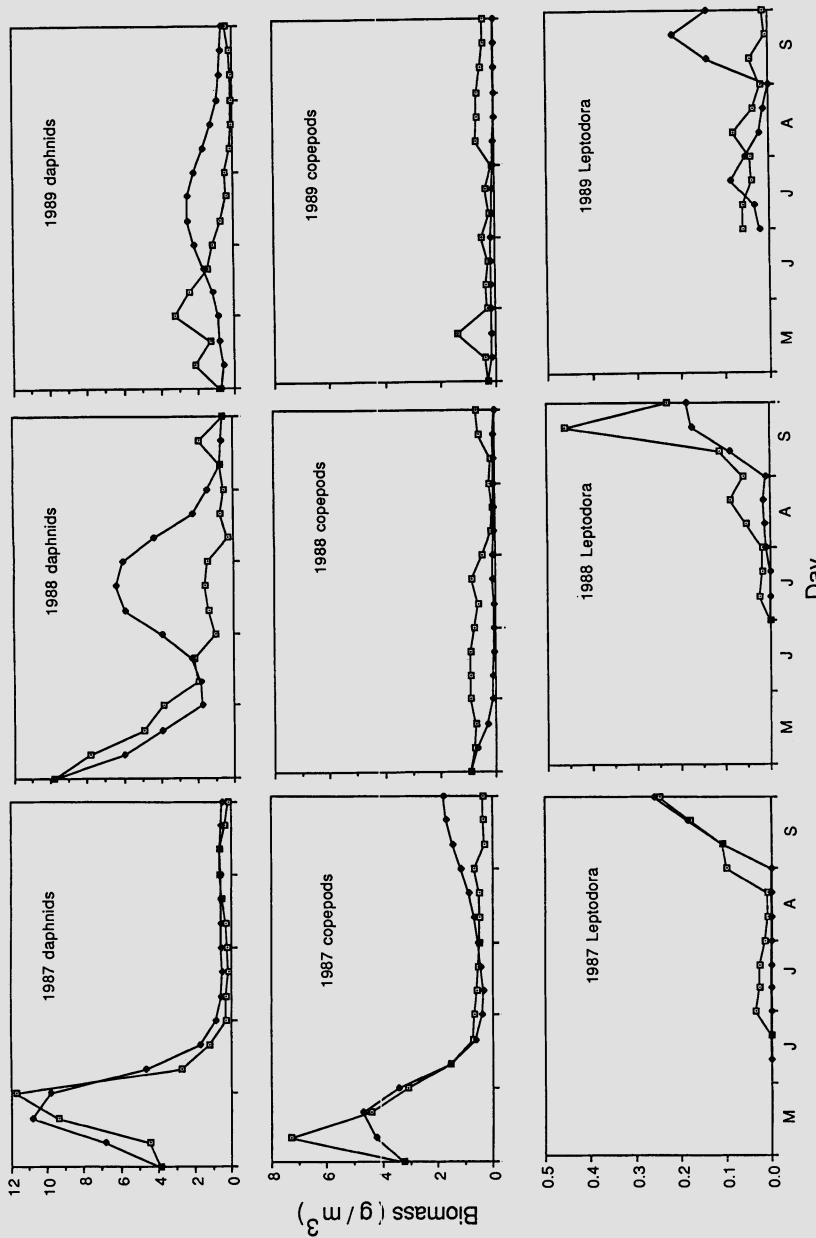
Parameter	Day 50	Day 100	Summed <i>Daphnia</i>
A1D – Perch assimilation	ns	+16	ns
A3+ <i>Daphnia</i> assimilation	-22	+39	+34
A3-	-69	-18	ns
ACL+ Cisco assimilation	-16	ns	ns
ACL-	+12	+15	ns
MAXD+ Max feeding <i>Daphnia</i>	-27	+61	+28
MAXD-	-65	-20	ns
MAXCI+ Max feeding cisco	-37	ns	ns
MAXCI-	+19	+32	ns
RR+ Intercept ResRenewal	+16	+111	+34
RR-	-20	ns	-12
RMAX – Max resource level	-25	+33	ns

cisco assimilation values (A1D and ACI) and to the maximum feeding rate of cisco (MAXCI). Six of the seven variables showed significant response on day 50, but only four of the parameters showed a response in integrated biomass of large daphnids. This differential response occurred because of the specific temporal response of large daphnids (see A3 in Table 20.4).

## Results of Simulations 1987–89

We calibrated the model by adjusting half-saturation constants and maximum feeding rates of the invertebrates such that they remained within the range reported from literature sources, and allowed the temporal dynamics of daphnids, herbivorous copepods, and *Leptodora* in the lake in 1987 to be sufficiently described by model interactions. Daphnid biomass rose to a maximum early in the simulations and then declined precipitously and remained low after day 50. Herbivorous copepods began the season at relatively high biomasses, increased slightly, and then declined to seasonal low values between days 50 and 100. After day 100 copepod biomass increased and reached almost  $2 \text{ g m}^{-3}$  by the end of the simulations. Copepod biomass in the lake increased slightly in September but then declined to lower values by the end of September (Figure 20.2).

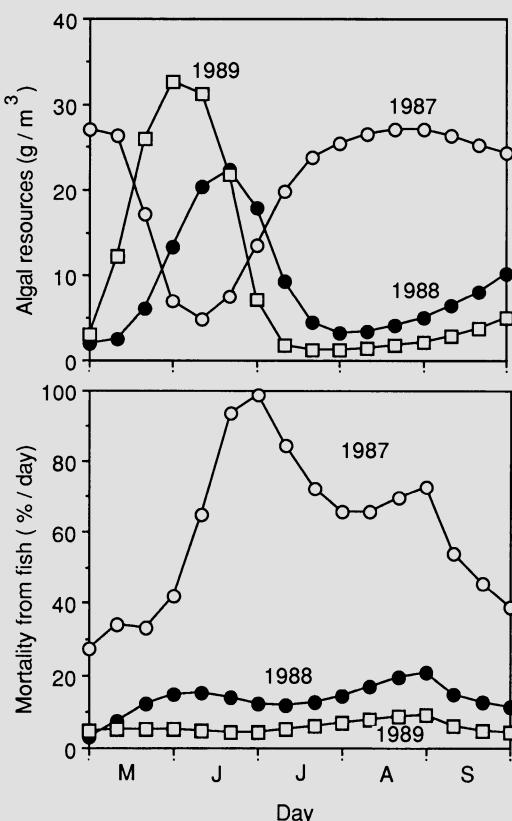
The decline of both daphnids and herbivorous copepods in early summer appeared to be related to food availability. Algal food resources



**Figure 20-2.** Time course depicting changes in biomass of daphnids, copepods, and *Leptodora* during 1987, 1988, and 1989 from model (◆) and field (□) data.

fell to below  $10 \text{ g m}^{-3}$  between day 30 and day 60 (Figure 20.3). During summer and autumn algal resources increased and remained at high levels, but daphnids were not able to utilize these high levels of food resources, as they did not increase in simulations during this period. Herbivorous copepods appeared to respond to this increase in available food, as evidenced by the slow accumulation of biomass (Figure 20.2).

In the model simulations, daphnids were not able to increase during the summer months because of an increase in predation pressure from planktivorous fish (Figure 20.3). The initial biomass of adult perch and cisco was high in 1987 and caused relatively high rates of mortality on the invertebrate prey species. Ninety-eight percent of the predation pressure on large daphnids resulted from adult fishes, with the remaining from *Leptodora* in the 1987 simulation. The per capita mortality rate for large daphnids indicates that predation pressure peaks in early July, remaining greater than 7% per day through late August (Figure 20.3). This seasonal pattern of predation pressure results from a combination of temperature effects, growth responses of adult and juvenile fishes, and changes in the density of large daphnids.



**Figure 20-3.** Temporal patterns of algal resources (top) and per capita mortality of large daphnids resulting from fish predation (bottom) in 1987, 1988, and 1989.

The biomass of *Leptodora* remained low throughout the summer. The September increase in *Leptodora* resulted from the pulse of biomass added at this time and from reductions in predation pressure from planktivorous fish.

After calibrating the simulation model with data from 1987, we ran the model using initial conditions present in 1988 and 1989 and compared the results of these simulations with the seasonal dynamics of plankton in the lake. The model provided reasonable fits with the field data for 1988 and 1989. The range of abundances predicted by the model closely approximated the range observed in the lake (Table 20.5); however, the temporal patterns of abundance of all three invertebrate groups frequently deviated from model predictions. The peak biomass of daphnids appeared to be consistently later in model simulations than that which occurred in the lake (Figure 20.2). The reason for this difference is not well understood but may be related to species-specific differences in the growth potential of daphnids early in the season. We calibrated our model to field data from 1987 when almost all of the daphnid biomass consisted of *Daphnia galeata*. In 1988 and 1989 *D. pulicaria* was the dominant daphnid in the lake. Lynch et al. (1986) and Luecke et al. (1990) indicated that *D. pulicaria* reproduced at a higher rate during cool, early spring conditions. This difference between the two daphnid species would result in the lake daphnid population increasing more rapidly than model populations in 1988 and 1989. The model did best at predicting overall differences in biomass of invertebrates between years.

The catastrophic mortality of cisco during the late summer and fall of 1987 (Vanni et al. 1990; Luecke et al., Ch. 20) caused large changes in the seasonal plankton dynamics in both field data and model simulations. Daphnid biomasses were greater in 1988, particularly in the summer months, and copepod biomass was low throughout the season. Biomass of *Leptodora* was greater during the summer in 1988 (Figure 20.2).

The decreased abundance of adult planktivorous fish in 1988 reduced predation pressure on daphnids and *Leptodora* compared to 1987, result-

**Table 20-5.** Mean biomass ( $\text{g m}^{-3}$ ) of daphnids (small + large), copepods, and *Leptodora* in Lake Mendota and in model simulations for 1987, 1988, and 1989.

Trophic species	1987	1988	1989
Lake daphnids	2.53	2.59	0.92
Model daphnids	2.74	2.71	1.30
Lake copepods	1.75	0.32	0.47
Model copepods	2.29	0.073	0.085
Lake <i>Leptodora</i>	0.034	0.048	0.026
Model <i>Leptodora</i>	0.033	0.028	0.055

ing in greater abundances in both model and field data (Figure 20.3). Herbivorous copepods responded in just the opposite manner, exhibiting reduced abundances in 1988. This reduction was likely due to the lower availability of food resources (Figure 20.3).

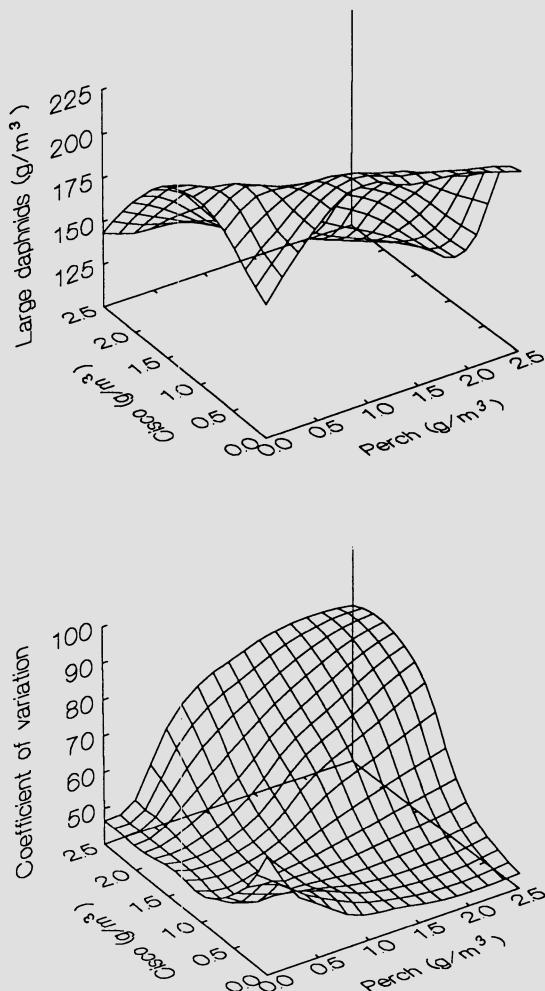
Reduced abundances of planktivorous fish persisted in 1989 but were coupled with low initial biomass of daphnids. The combination of these factors resulted in reduced biomass of daphnids during the spring period in both field data and model simulations. During summer the model predicted greater daphnid biomass than occurred in the lake (Figure 20.2). Biomass of herbivorous copepods was low in both model simulations and field data compared to 1987. The model consistently predicted lower biomass of copepods than actually occurred in the lake. Biomass of *Leptodora* was greater in 1989 in both model and field data compared to the other years. In the model simulations *Leptodora* responded positively to the low abundances of planktivorous fish and the greater abundances of daphnids that occurred during summer.

## Examining the Scenarios

Once the model was calibrated and tested, we investigated the impacts of varying planktivorous fish densities on the biomass of large daphnids present over the course of a season. Initial perch and cisco biomass was varied from 0 to  $2.5 \text{ g m}^{-3}$ , the range of biomasses observed between 1981 and 1989 (Rudstam et al., Ch. 12). Each combination of perch and cisco biomass was simulated and the large daphnid biomass integrated over the season was recorded. Two effects are evident from this analysis.

First, biomass of large daphnids exhibited a unimodal response to variation in abundance of perch and cisco, with maximum biomasses occurring at low to intermediate fish abundances (Figure 20.4). It was anticipated that daphnid biomass would be extremely low when perch and cisco were very abundant, but the decreased biomass of daphnids at very low abundances of perch and cisco was unexpected. The combination of low perch and low cisco biomass reduced predation pressure on *Leptodora* to the degree that predation by this invertebrate became extreme and limited the ability of daphnid populations to expand. At the lowest fish abundances, *Leptodora* reached peak biomass of  $1.5 \text{ g m}^{-3}$ . When perch and cisco biomass exceeded  $2 \text{ g m}^{-3}$  *Leptodora* was rare, remaining at biomasses of 0.001 for most of the season. These results are similar to those of Post and Rudstam (Ch. 19), who also conclude that maximum biomass of daphnids should occur at low to intermediate densities of planktivorous fish.

Second, variation of perch and cisco biomass has different effects on the zooplankton assemblages in the model simulations. Cisco appear to have a greater impact on the biomass of large daphnids than do perch, for



**Figure 20-4.** The biomass of large daphnids integrated over the course of a simulation (top) and coefficient of variation of daily biomass (bottom) as a function of initial biomass ( $\text{g m}^{-3}$ ) of perch and cisco.

two reasons. At high densities of planktivorous fish, cisco feed on both small and large daphnids, whereas perch feed only on large daphnids. When planktivorous fish are at low to intermediate levels, cisco have greater impact on daphnid abundance because they continue to feed extensively on daphnids, whereas perch begin feeding on *Leptodora* once this large invertebrate becomes more available. The presence of *Leptodora* appears to buffer daphnid populations from predation by perch to a greater extent than from predation by cisco.

In addition to affecting overall daphnid biomass, varying densities of planktivorous fish altered the variability of daphnid biomass (Figure 20.4, bottom). At low to intermediate fish biomass (combined perch and cisco biomass between 0.75 and 2.75 g m<sup>-3</sup>), the coefficient of variation for daily daphnid biomass remained below 50%. At very low (<0.75 g m<sup>-3</sup>) and very high (>3.0 g m<sup>-3</sup>) fish biomass, variation in the seasonal pattern of large daphnid biomass increased. This increased variation occurred for different reasons. At low fish biomass, large daphnids increased greatly in spring but were subsequently consumed by large populations of *Leptodora* and remained low throughout summer. Under simulations with high levels of planktivorous fish, the abundance of large daphnids declined throughout the spring and was reduced to near zero during the summer months.

## Discussion

Our modeling simulations indicate that strong consumer effects are possible in highly productive lake ecosystems. Changes in abundance of planktivorous fish have pronounced impacts on invertebrate planktivores and herbivores. In our model compensatory effects can and do occur. Predators consume more prey when prey are abundant, and the invertebrate planktivore *Leptodora* increased in abundance when planktivorous fish declined. The strength of compensation, however, is weak, having relatively modest impacts on the regulation of prey by predators. These results support the “cascading trophic interactions” theory of ecosystem productivity (Carpenter et al. 1985; Oksanen 1988), which states that the abundance of the top carnivore will have a pronounced impact on the biomass and production of organisms residing at lower trophic levels. Our results argue against the donor-controlled view of ecosystem production espoused by Vadas (1989), who suggests that compensatory mechanisms are usually strong enough to overcome temporal changes in consumer abundance. The synthesis of Lake Mendota food web models (Carpenter, Ch. 18) outlines the degree to which nutrient enhancement (donor control) is able to subvert the effects of strong piscivore manipulations. The results of this modeling exercise have implications for the management of water clarity in Lake Mendota. Maximum densities of daphnids occurred at low to intermediate densities of planktivorous fish. Planktivorous fish densities recorded for 1988 and 1989 were similar to the model fish densities that allowed maximum daphnid biomasses to occur. These results suggest that maintenance of present fish densities through piscivore stocking and angler harvest is a desirable lake management goal. The excellent water clarity associated with densities of *D. pulicaria* in 1988 supports this conclusion.

The 1989 field data indicated that biomass of perch and cisco was even less than in 1988. In both model and field data, daphnid biomass was reduced in 1989 compared to 1988. In the model this reduction was due to the increase in *Leptodora*, whereas in the field increased abundance of *Leptodora*, crappie, and bluegill and poor-quality algal food resources were likely responsible. In any event, the potential for other planktivores to increase in response to a reduction in perch and cisco biomass makes it unlikely that maximum daphnid abundance would occur under extremely low abundances of perch and cisco and argues for maintaining perch and cisco at 1988 levels.

The increase in invertebrate planktivores at very low fish abundances exhibited in our simulations has occurred in other lakes when abundance of planktivorous fish declined precipitously. The decrease in fish biomass associated with cultural acidification allowed *Chaoborus* populations to expand (Nyberg 1984; Yan et al. 1991). Also, the decrease in planktivorous fish following the stocking of piscivores in Bautzen Reservoir resulted in increased abundances of *Chaoborus* and *Leptodora* (Benndorf et al. 1988). Whether this increase in invertebrate planktivores reduced daphnid densities is unclear. Daphnid abundance, however, was greatest in the first year following a reduction in planktivorous fish but declined in subsequent years as populations of *Chaoborus* and *Leptodora* expanded, in spite of further reduction in planktivorous fish biomass (Benndorf et al. 1988). This report supports our modeling results that very low abundances of planktivorous fish may result in high levels of invertebrate planktivores and correspondingly low densities of herbivorous zooplankton.

*Leptodora* is the only invertebrate planktivore explicitly considered in our model. Its ability to reduce daphnid abundances in our simulations derives from its preference for daphnid over copepod prey. *Leptodora*'s preference for large cladocerans is rare among invertebrates (Lunte and Luecke 1990). In other systems with different assemblages of invertebrate planktivores, the absence of planktivorous fish could enhance daphnids in that the invertebrate planktivores may prey selectively on potential competitors of daphnids, such as copepods or smaller-bodied cladocerans. Large predacious copepods (Luecke and O'Brien 1983) and *Chaoborus* (Pastorok 1980; Luecke and Litt 1987) selectively consume small cladoceran and copepod prey. In fact, there is some indication that large-bodied daphnids may exclude *Chaoborus* from oligotrophic lakes by competitively reducing the smaller planktonic herbivores that served as prey for *Chaoborus* (Neill 1984).

Results from model simulations indicate that further reductions in perch biomass would have minimal impacts on daphnid abundance but that increased perch biomass would limit daphnid populations. Continued stocking of piscivores should be encouraged to limit the probability of

additional strong year classes of perch becoming established. These additional piscivores will likely reduce the ability of planktivorous fish to increase, although increased abundance of invertebrate planktivores may occur. Finally, the unpredictable nature of cisco recruitment will likely result in large interannual variation in cisco abundance that will continue to have dramatic impacts on the zooplankton assemblage of Lake Mendota (Luecke et al., Ch. 14). Once established, a strong year class of cisco would be difficult to reduce through food web manipulations. The continued enhancement of piscivore stocks, however, will likely reduce year class strength of cisco and dampen their effect on zooplankton populations.

*Acknowledgments.* We thank Steve Carpenter and Jim Kitchell for guidance with early versions of the simulation model, and Lars Rudstam and John Post for providing comments on previous drafts of the manuscript. We also thank John Magnuson and the Center for Limnology for providing the computers used to run preliminary simulations and the Ecology Center at Utah State University for providing additional monetary support.

## References

- Benndorf J, Schultz H, Benndorf A, Unger R, Penz E, Kneschke H, Kossatz K, Dumke R, Hornig U, Kruspe R, Reichel S (1988) Food-web manipulation by enhancement of piscivorous fish stocks: Long-term effects in the hypereutrophic Bautzen Reservoir. *Limnologica* 19:97–110
- Brock TD (1985) A eutrophic lake: Lake Mendota, Wisconsin. Springer-Verlag, New York
- Carpenter SR, Kitchell JF, Hodgson JR (1985) Cascading trophic interactions and lake productivity. *Bioscience* 35:634–639
- Chesson J (1983) The simulation and analysis of preference and its relationship to foraging models. *Ecology* 64:1297–1304
- Dabrowski KR (1985) Energy budget of coregonid (*Coregonus* spp.) fish growth, metabolism and reproduction. *Oikos* 45:358–364
- Frost BW (1980) Body size as a niche indicator. *Limnol. Oceanogr. Spec. Symp.* 3:742–753
- Hassell MP (1978) The dynamics of arthropod predation–prey systems. Princeton University Press, Princeton, New Jersey
- Hewett SW, Johnson BL (1987) A generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin Sea Grant Institute Technical Report. WIS-SG-87-245, Madison
- Hillbricht-Illkowska A, Karabin A (1970) An attempt to estimate consumption, respiration and production of *Leptodora kindtii* (Focke) in field and laboratory experiments. *Pol. Arch. Hydrobiol.* 17(30):81–86
- Kibby HV (1971) Energetics and population dynamics of *Diaptomus gracilis*. *Ecol. Monogr.* 44:311–328

- Luecke C, Litt AH (1987) Effects of predation by *Chaoborus flavicans* on crustacean zooplankton of Lake Lenore, Washington, Freshwat. Biol. 18:185–192
- Luecke C, O'Brien WJ (1983) The effect of *Heterocope* predation on zooplankton communities in arctic ponds. Limnol. Oceanogr. 28:367–377
- Luecke C, Vanni MJ, Magnuson JJ, Kitchell JF, Jacobson PJ (1990) Seasonal regulation of *Daphnia* populations by planktivorous fish: Implications for the clearwater phase. Limnol. Oceanogr. 35:1718–1733
- Lunte CC, Luecke C (1990) Trophic interactions of *Leptodora* in Lake Mendota. Limnol. Oceanogr. 35:1091–1100
- Lynch M, Weider LJ, Lampert W (1986) Measurement of the carbon balance in *Daphnia*. Limnol. Oceanogr. 31:17–33
- McCauley E, Murdoch WW, Nisbet RM, Gurney WSC (1990) The physiological ecology of *Daphnia*: Development of a model of growth and reproduction. Ecology 71:703–715
- Neill WE (1984) Regulation of rotifer densities by crustacean zooplankton in an oligotrophic lake in British Columbia. Oecologia 61:175–181
- Nyberg P (1984) Impact of *Chaoborus* on planktonic crustacean communities in some acidified and limed lakes in Sweden. Rep. Inst. Fresh. Res. Drottingholm 61:154–166
- Oksanen L (1988) Ecosystem organization: Mutualism and cybernetics or plain Darwinian struggle for coexistence? Am. Nat. 131:424–444
- Paloheimo JE, Crabtree SJ, Taylor WD (1982) Growth model of *Daphnia*. Can. J. Fish. Aquat. Sci. 39:598–606
- Pastorok RA (1980) Selection of prey by *Chaoborus* larvae: A review and new evidence for behavioral flexibility. Am. Soc. Limnol. Oceanogr. Spec. Symp. 3:538–555
- Pedros-Alio C, Brock TD (1985) Zooplankton dynamics in Lake Mendota: Short-term versus long-term changes. Freshwat. Biol. 15:89–94
- Perrson L (1987) The effects of resource availability and distribution on size class interactions in perch (*Perca fluviatilis*). Oikos 48:148–160
- Porter KG, Gerritsen J, Orcutt JD, Jr (1982) The effect of food concentration on swimming patterns, feeding behavior, ingestion, assimilation, and respiration by *Daphnia*. Limnol. Oceanogr. 27:935–949
- Post JR (1987) Size dependent processes in yellow perch recruitment. Ph.D. Thesis, York University, Toronto
- Reed RC (1971) An experimental study of prey selection and regulatory capacity of bluegill sunfish. M.S. Thesis, University of California, Santa Barbara
- Reinertsen H, Langeland A (1982) The effect of a lake fertilization on the stability and material utilization of a limnetic ecosystem. Holart. Ecol. 5:311–324
- Richman S (1964) Energy transformation studies on *Diaptomus oregonensi*. Verh. Internat. Verein. Limnol. 15:654–659
- Richman S, Dodson SI (1983) The effect of food quality on feeding and respiration by *Daphnia* and *Diaptomus*. Limnol. Oceanogr. 28:948–956
- Rudstam LG (1983) The cisco, *Coregonus artedii*, in Wisconsin lakes: Long term comparison of population structure and an analysis of their vertical distribution. M.S. Thesis, University of Wisconsin, Madison

- Schindler JE (1971) Food quality and zooplankton nutrition. *J. Anim. Ecol.* 40:589–595
- Schoener TW (1989) Food webs from the small to the large. *Ecology* 70:1559–1589
- Vadas RL, Jr (1989) Food web patterns in ecosystems: A reply to Fretwell and Oksanen. *Oikos* 56:339–343
- Vanderploeg HA, Scavia D, Liebig J (1984) Feeding rate of *Diaptomus sicilis* and its relation to selectivity and effective food concentration in algal mixtures and in Lake Michigan. *J. Plankton Res.* 6:919–941
- Vanni M, Luecke C, Kitchell JF, Magnuson JJ, Rentmeester Y, Temte J (1990) Cascading trophic interactions and phytoplankton abundance: Effects of massive fish mortality. *Nature* 344:333–335
- Walters CJ, Krause E, Neill WE, Northcote TG (1987) Equilibrium models for seasonal dynamics of plankton biomass in four oligotrophic lakes. *Can. J. Fish. Aquat. Sci.* 44:1002–1006
- Yan ND, Feller W, MacIsaac HJ, McEachern LJ (1991) Regulation of zooplankton community structure in an acidified lake by *Chaoborus*. *Ecol. Appl.* 1:52–65

## Appendix

The biomass ( $\text{g/m}^3$ ) of each of nine state variables in the simulation model varies as functions of the following differential equations. Most of the parameters used in this model are defined and referenced in Table 20.1. Calculation of rates of ingestion ( $\text{g/g/day}$ ) for each consumer, and functions describing algal renewal rates (RR), daphnid egg deposition (EGG), and graduation of small into large daphnids (GRAD) are defined in the text. The model was run for 150 days with an intergration step of 0.25 days.

### Algal Resources (AR)

$$d\text{AR}/dt = \text{RR} - \text{ILD} - \text{ISD} - \text{IOH}$$

where RR is the resource renewal rate and ILD, ISD, and IOH are ingestion of algal resources by large daphnids, small daphnids, and other herbivores, respectively.

### Other Herbivores (OH)

$$d\text{OH}/dt = \text{AH IOH} - \text{MCR} - \text{ILO} - \text{ISPO} - \text{ISCO} - \text{ILCO}$$

where AH is an assimilation rate, IOH is ingestion by other herbivores, MCR is the other herbivore metabolic rate ( $\text{g/g/day}$ ), and ILO, ISPO, ISCO, and ILCO are ingestion of other herbivores by *Leptodora*, small perch, small cisco, and large cisco, respectively.

### **Large Daphnids (LD)**

$$d\text{LD}/dt = \text{AD ILD} - \text{MD} - \text{ILPD} - \text{ILCD} - \text{ILD} + \text{GRAD} - \text{EGG}$$

where AD is an assimilation rate, ILD is ingestion by large daphnids, MD is daphnid metabolic rate, and ILPD, ILCD, and ILD are ingestion of large daphnids by large perch, large cisco, and *Leptodora*, respectively. GRAD is the rate at which small daphnids become large daphnids (g/g/day), and EGG is the rate at which large daphnids transform biomass into small daphnids (g/g/day).

### **Small Daphnids (SD)**

$$\begin{aligned} d\text{SD}/dt = & \text{AD ISD} - \text{MSD} - \text{ILSD} - \text{ISPSD} - \text{ISCSD} - \text{ILCSD} \\ & - \text{GRAD} + \text{EGG} \end{aligned}$$

where AD is an assimilation rate, ISD is ingestion by small daphnids, and MSD is daphnid metabolic rate. ILSD, ISPSD, ISCSD, and ILCSD are ingestion of small daphnids by *Leptodora*, small perch, small cisco, and large cisco, respectively.

### ***Leptodora* (L)**

$$d\text{L}/dt = \text{AL IL} - \text{ML} - \text{ILPL} - \text{ILCL}$$

where AL is an assimilation rate, IL is ingestion by *Leptodora*, and ILPL and ILCL are ingestion of *Leptodora* by large perch and large cisco, respectively.

### **Small Perch (SP)**

$$d\text{SP}/dt = \text{ASP ISP} - \text{MSP} - \text{PMSP}$$

where ASP is an assimilation rate, ISP is ingestion by small perch, MSP is small perch metabolic rate, and PMSP is mortality from piscivorous fish (g/g/day).

### **Large Perch (LP)**

$$d\text{LP}/dt = \text{AP ILP} - \text{MP} - \text{OMLP}$$

where AP is an assimilation rate, ILP is ingestion by large perch, MP is large perch metabolic rate, and OMLP is other mortality of large perch (g/g/day).

**Small Cisco (SC)**

$$dSC/dt = ASC \text{ ISC} - MSC - PMSC$$

where ASC is an assimilation rate, ISC is ingestion by small cisco, MSC is small cisco metabolic rate, and PMSC is mortality from piscivorous fish.

**Large Cisco (LC)**

$$dLC/dt = AC \text{ ILC} - MCI - OMLC$$

where AC is an assimilation rate, ILC is ingestion by large cisco, MCI is large cisco metabolic rate, and OMLC is other mortality of large cisco.

# 21

## A Simulation Model of the Interactions Among Nutrients, Phytoplankton, and Zooplankton in Lake Mendota

**Michael J. Vanni, Stephen R. Carpenter, and  
Chris Luecke**

Freshwater plankton communities are regulated by a variety of factors, among which nutrients and predators are two of the most important. Increases in limiting nutrients such as phosphorus and nitrogen can stimulate production and biomass of phytoplankton (Schindler 1978), which in turn can stimulate production and biomass of herbivorous zooplankton. Predators such as fish can influence plankton communities through selective predation on large zooplankton species (Zaret 1980; Northcote 1988). Because large zooplankton species have relatively high grazing rates (per individual) on phytoplankton and graze on a wider range of food particles (Burns 1969), size-selective predation on large zooplankton can also have a substantial influence on phytoplankton (Carpenter and Kitchell 1988; Vanni et al. 1990a).

In lacustrine ecosystems, predation and nutrients interact to influence phytoplankton community dynamics, and a major goal of aquatic ecology is to ascertain the relative importance of these two factors and their interactions. The influences and interaction of these factors can be investigated through manipulation experiments, comparative studies, and simulation modeling. Simulation modeling can be used to forecast community response to planned manipulations and to elucidate the mechanisms responsible for changes in community dynamics in response to altered predator and/or nutrient conditions. For example, Scavia et al. (1988) used simulation modeling to determine whether recent changes in phytoplankton dynamics arose from changes in phosphorus loading rate or reduced planktivory by alewife, and Carpenter and Kitchell (1984, 1987) used simulation modeling to investigate the influence of food

web interactions on the magnitude and scale of variability in primary production.

Here we use simulation modeling to investigate various scenarios of planktivory and phosphorus loading rate, and the response of the Lake Mendota phytoplankton community to these scenarios. Lake Mendota is currently the site of a whole-lake addition of piscivorous fish, which is expected to reduce the abundance of planktivorous fish (Kitchell, Ch. 1; Addis, Ch. 2). In addition, a summer kill of planktivorous fish in late summer 1987 resulted in reduced predation on zooplankton (Vanni et al. 1990a and Ch. 13), and nutrient loading rates declined greatly from the early 1970s to the 1980s (Lathrop, in press and Ch. 6). All of these factors can interact to influence phytoplankton community dynamics, and it is our goal here to explore some of the potential responses of Lake Mendota phytoplankton to changes in planktivory (and hence grazing by zooplankton) and phosphorus loading rates. These are similar to the questions addressed by the more general model of Carpenter et al. (Ch. 22). In this chapter, however, we analyze a more detailed model tailored specifically to key components of the Lake Mendota ecosystem.

## Methods

### Model Structure

The model consists of a simplified Lake Mendota food web and represents the pelagic community within the mixed layer based on 1987 data. The model includes three herbivore groups—*Daphnia*, copepods, and small cladocerans; two phytoplankton groups—nanoplankton and blue-green algae (cyanobacteria); and one potentially limiting nutrient—phosphorus (Figure 21.1).

The currency of this model was  $\mu\text{g C} \cdot \text{L}^{-1}$ . Dynamics of *Daphnia* ( $D$ ) and small cladocerans ( $S$ ) in  $\mu\text{g C} \cdot \text{L}^{-1}$  were modeled as:

$$dD/dt = (G_D - R_D - M_D)D \quad (1)$$

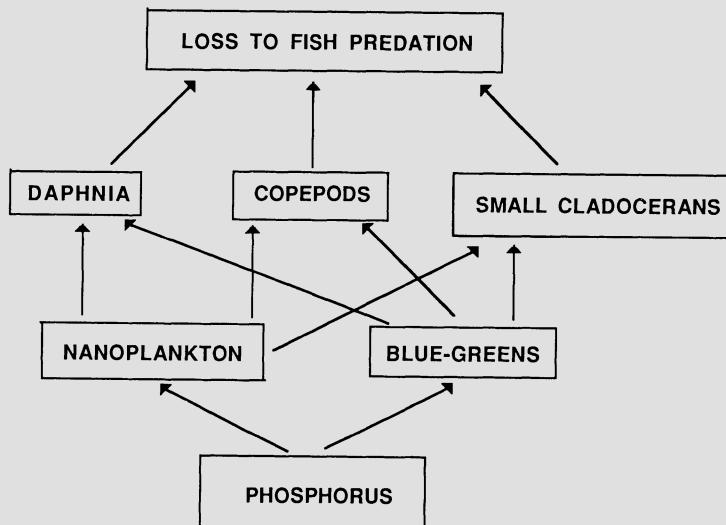
$$dS/dt = (G_S - R_S - M_S)S \quad (2)$$

where  $G$  and  $R$  are the gains and losses through grazing and respiration ( $\mu\text{g C} \cdot \mu\text{g C}^{-1} \cdot \text{d}^{-1}$ ) and  $M$  is the mortality rate attributable to fish predation ( $\text{d}^{-1}$ ).

Copepods ( $C$ ) were modeled similarly except that a loss rate due to diapause ( $\mu\text{g C} \cdot \text{L}^{-1}$ ) was added:

$$dC/dt = (G_C - R_C - M_C)C - L \quad (3)$$

where  $L$  is the loss of individuals to diapause.



**Figure 21-1.** Generalized food web of Lake Mendota used in these simulations.

Following Scavia et al. (1988), grazing rates for each zooplankton group  $j$  ( $G_j$ ) were described by saturation kinetics and the “effective food concentration” (Vanderploeg et al. 1984):

$$G_j = G_{\max,j} \cdot A_j \cdot \text{EFC}_j / (K_j + \text{EFC}_j) \quad (4)$$

where  $G_{\max,j}$  is the maximal mass-specific ingestion rate ( $\mu\text{g C} \cdot \mu\text{g C}^{-1} \cdot \text{d}^{-1}$ ),  $A_j$  is the assimilation efficiency (proportion of ingested food that is assimilated, dimensionless),  $\text{EFC}_j$  is the effective food concentration ( $\mu\text{g C} \cdot \text{L}^{-1}$ ) (Vanderploeg et al. 1984), and  $K_j$  is the half-saturation constant ( $\mu\text{g C} \cdot \text{L}^{-1}$ ). For each zooplankton species,  $\text{EFC}_j$  is defined as  $\sum W'_i X_i$ , where  $W'_i$  is the selectivity coefficient for food type (phytoplankton group)  $i$  at concentration  $X_i$  (Vanderploeg and Scavia 1979).

Maximal ingestion rate  $G_{\max}$  was set to 0.7 for *Daphnia* and 0.2 for copepods (Muck and Lampert 1984).  $G_{\max}$  was 0.6 for small cladocerans, based on the equations of Peters and Downing (1984), assuming a body mass of 10  $\mu\text{g}$  dry mass and a food concentration of 1  $\text{mg C} \cdot \text{L}^{-1}$ . Assimilation efficiency ( $A$ ) was 0.65 for *Daphnia*, 0.5 for small cladocerans, and 0.75 for copepods. Half-saturation constants ( $K$ ) for both *Daphnia* and small cladocerans were 50  $\mu\text{g C} \cdot \text{L}^{-1}$  (Porter et al. 1982), while  $K$  was 150  $\mu\text{g C} \cdot \text{L}^{-1}$  for copepods.

The selectivity coefficient  $W_i$  was assumed to be equal to 1.0 (highest possible selectivity) for all three zooplankton groups feeding on nanoplankton (Scavia et al. 1988). Estimating the selectivity of

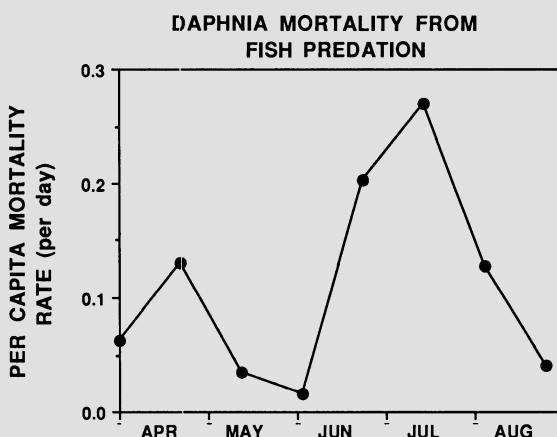
cyanobacteria is more problematic, as a variety of values exists in the literature. However, it can be assumed that cladocerans are less selective than copepods and that copepods select against cyanobacteria colonies. Thus we assigned  $W_i$  values of 0.25, 0.3, and 0.1 for *Daphnia*, small zooplankton, and copepods feeding on cyanobacteria.

Respiration rates were expressed as a function of food concentration, with well-fed animals exhibiting higher rates than starved animals, as in Scavia et al. (1988):

$$R = R_1 + R_2 \cdot \text{EFC}/(K + \text{EFC}) \quad (5)$$

$R_1$  and  $R_2$  were set to 0.1 and 0.15 ( $\mu\text{g C} \cdot \mu\text{g C}^{-1} \cdot \text{d}^{-1}$ ) for both *Daphnia* and small cladocerans. This yields a maximal respiration rate of  $\sim 0.25$  at high food concentration (Scavia et al. 1988). For copepods,  $R_1$  and  $R_2$  were set to 0.04 and 0.07, yielding a maximal respiration rate of  $\sim 0.11$  (Scavia et al. 1988).

*Daphnia* mortality attributable to fish predation ( $M_D$ ) was estimated from the bioenergetic analyses of Luecke et al. (in press) for *Daphnia galeata mendotae* in Lake Mendota. Per capita mortality rate ( $\text{d}^{-1}$ ) was estimated at 21-d intervals by dividing daily consumption of *D. galeata* by fish ( $\text{Daphnia} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$ ) by *D. galeata* density ( $\text{Daphnia} \cdot \text{L}^{-1}$ ), the values of which were obtained from Luecke et al. (in press). Consumption of *Daphnia* by fish varies with temperature and *Daphnia* density, resulting in seasonally variable per capita mortality of *Daphnia*. Values of  $M_D$  used in the model are given in Figure 21.2. Mortality of small cladocerans from fish predation ( $M_S$ ) was held constant at 0, while that of copepods ( $M_C$ ) was held constant at  $0.001 \text{ d}^{-1}$ ; these values were based on diet analyses of fish from Lake Mendota.



**Figure 21-2.** Schedule of *Daphnia* mortality rate from fish predation used in the baseline simulation (1987 dynamics). Data from Luecke et al. (in press).

Cyclopoid copepods in Lake Mendota enter diapause in late spring, at which time their populations decline precipitously (Luecke et al., Ch. 14). The proximate and ultimate causes of their diapause are unknown, and we have no direct quantitative estimates of the fraction of the population entering diapause at any given time interval. However, based on diet analyses, we are confident that mortality due to fish predation is negligible and the major cause of population decline is diapause. We therefore adjusted copepod diapause rate ( $L$ ,  $\mu\text{g C} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$ ) until the dynamics matched those in the lake. While this ad hoc approach yields no insight into copepod loss factors, it does allow us to predict the effects of particular zooplankton dynamics on phytoplankton abundance.

The dynamics of nanoplankton ( $N$ ) and cyanobacteria ( $B$ ) were described as:

$$dN/dt = (r_N Sh_N - Si_N - G_N)N + If_N \text{ and} \quad (6)$$

$$dB/dt = (r_B Sh_B - Si_B - G_B)B + If_B \quad (7)$$

where  $r$  is the per capita growth rate ( $\text{d}^{-1}$ ),  $Sh$  is a factor by which growth is reduced by shading (dimensionless),  $Si$  is the per capita sinking rate ( $\text{d}^{-1}$ ),  $G$  is the per capita mortality rate due to grazing ( $\text{d}^{-1}$ ), and  $If$  is the rate at which biomass enters from the inflow and the sediments ( $\mu\text{g C}^{-1} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$ ).

Phytoplankton growth rates ( $r_N$ ,  $r_B$ ) were assumed to follow Monod kinetics:

$$r = r_{\max} P / (K_P + P) \quad (8)$$

where  $r_{\max}$  is the maximal per capita growth rate,  $P$  is the concentration of the limiting nutrient phosphorus, and  $K_P$  is the half-saturation constant for growth, i.e., the concentration of  $P$  at which growth rate is half maximal growth rate. “Nanoplankton” here is meant to characterize small, rapidly growing cells of various taxonomic origins. In Lake Mendota this includes diatoms, cryptomonads, and *Chlamydomonas*. Given that disparate groups were pooled, it seemed that maximal nanoplankton growth rate should be estimated from patterns derived from a number of taxonomic groups. Therefore, following Carpenter et al. (Ch. 22), maximal nanoplankton per capita growth rate was estimated from the allometric relationship of growth and cell volume derived from a variety of taxa (Reynolds 1984):

$$r_{\max} = 1.855 - 0.266 \log v \quad (9)$$

where  $v$  is cell volume. Nanoplankton were assumed to be spherical cells 5  $\mu\text{m}$  in diameter, yielding a volume of  $65 \mu\text{m}^3$  and  $r_{\max} = 1.373 \text{ d}^{-1}$ . This value is intermediate between maximal growth rates for diatoms (1.1) and flagellates (1.5) used by Scavia et al. (1988). The  $r_{\max}$  of cyanobacteria was  $0.4 \text{ d}^{-1}$ , following Scavia et al. (1988). The  $K_P$  was 1.0

for nanoplankton [equivalent to the value used by Scavia et al. (1988) for flagellates] and 1.3 for cyanobacteria (Scavia et al. 1988).

The shading function limiting growth of both phytoplankton groups ( $Sh$ ) was obtained as:

$$Sh = 1 - (T/Y) \quad (10)$$

where  $T$  is total algal biomass ( $N + B$ ) and  $Y$  is maximum total algal biomass (Carpenter et al., Ch. 22). Algal biomass in Lake Mendota has rarely exceeded 20,000 kg of chlorophyll (Brock 1985). Assuming that all summer chlorophyll is located in the top 11 m, this translates into a maximum chlorophyll concentration of  $60 \mu\text{g} \cdot \text{L}^{-1}$ . This was converted to  $1,500 \mu\text{g C} \cdot \text{L}^{-1}$  by assuming that chlorophyll and carbon comprise 2% and 50% of dry mass, respectively (Reynolds 1984).

Sinking rate ( $Si$ ) of nanoplankton was calculated according to Stokes' law as applied by Reynolds (1984) and Carpenter et al. (Ch. 22, this volume):

$$Si = 0.0188(d'/2)^2/Z_E \quad (11)$$

where  $d'$  is cell diameter ( $5 \mu\text{m}$ ). Sinking rate of cyanobacteria is highly variable because of the ability to regulate buoyancy; in this model it was assumed that cyanobacteria sinking rate was  $0.005 \text{ d}^{-1}$ , roughly half that of nanoplankton.

Grazing losses of nanoplankton and cyanobacteria were a summation of losses to each of the three zooplankton groups:

$$G_N = G_{N,D} + G_{N,S} + G_{N,C} \quad (12)$$

$$G_B = G_{B,D} + G_{B,S} + G_{B,C} \quad (13)$$

The grazing loss to each zooplankton group is equal to the product of the ingestion rate of that zooplankton group (equation 4), the weighted diet portion attributable to phytoplankton group  $i$ ,  $W'_i X_i / \Sigma W'_i X_i$  (Scavia et al. 1988), and the biomass of that zooplankton group. For example, the grazing loss of nanoplankton to *Daphnia* ( $G_{N,D}$ ) is

$$G_{N,D} = G_D \cdot (W'_i X_i / \Sigma W'_i X_i) \cdot D \quad (14)$$

The inflow of nanoplankton ( $If_N$ ) was assumed to be very small ( $0.0001 \mu\text{g C} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$ ) and was employed to prevent extinction. The cyanobacteria influx to the water column from the sediments can be substantial at certain times of the year (Reynolds 1984). In Lake Mendota, recruitment from the sediments is thought to be substantial in late May–early June, i.e., at the end of the clear-water period, and negligible at other times. This is based on the observation that during the onset of cyanobacterial blooms, the observed increase in population density exceeds maximal growth rates reported from laboratory experiments under optimal conditions (Reynolds 1984). We estimated recruitment rate

from the sediments by assuming maximal growth (cell division) rates for in-lake cyanobacteria during the initial bloom in 1987, then calculating the difference between observed and “maximal” growth rates. Based on these calculations, the inflow of cyanobacteria ( $If_B$ ) was set to  $75 \mu\text{g C} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$  from day 73 to day 79 of the simulation and to zero for the rest of the year.

The dynamics of phosphorus (soluble reactive P,  $\mu\text{g L}^{-1} \cdot \text{d}^{-1}$ ) were:

$$dP/dt = E + H + X - U - O \quad (15)$$

where  $E$  represents the inflow from external (watershed) sources,  $H$  the net flux from the hypolimnion,  $X$  excretion by zooplankton,  $U$  uptake by phytoplankton, and  $O$  the outflow.

Direct measurement of external P loading rates to Lake Mendota are available only from the 1970s. However, the runoff of surface water to Lake Mendota has been measured annually since 1954 (Lathrop, in press), and here external loading is assumed to be proportional to runoff. Runoff in 1987 was  $\sim 72\%$  of the long-term (1954–89) mean annual runoff (Lathrop, in press and Ch. 6). Annual external P loading for this model was therefore estimated as the long-term mean annual P loading (from Lathrop, in press and Ch. 6) times 0.72. The temporal sequence of external P loading was assumed to follow the pattern reported in Brock (1985, his Fig. 3.3) for Lake Mendota in 1976, and is shown in Figure 21.3. Net flux of P from the hypolimnion to the epilimnion ( $H$ ) was estimated from the detailed measurements for Lake Mendota in Stauffer (1987).  $H$  was assumed to be zero in April and May (unstratified period) and to be constant during stratification (Figure 21.3). In late summer,  $H > E$ , in agreement with Stauffer (1987).

For each zooplankton group, excretion of P per unit zooplankton biomass ( $\mu\text{g P} \cdot \mu\text{g C}^{-1} \cdot \text{d}^{-1}$ ) was obtained as:

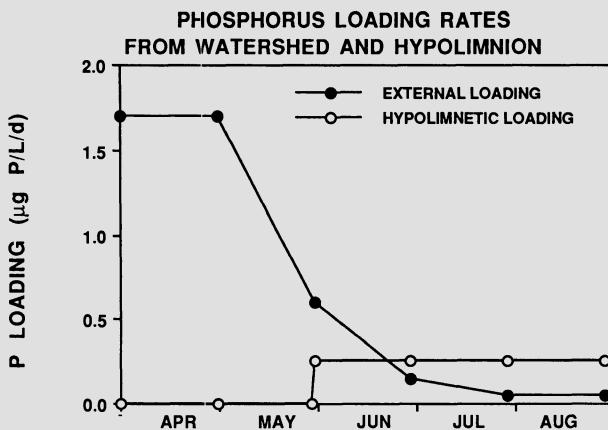
$$x = G_j \cdot Q \cdot F \quad (16)$$

where  $G_j$  is ingestion of algal biomass (from equation 4),  $Q$  is the P:C ratio of phytoplankton (assumed to be the Redfield P:C ratio, 0.024), and  $F$  is the fraction of ingested P excreted in a form available to phytoplankton [set to 0.5 in these simulations; Lehman (1980)]. Excretion by each zooplankton group was obtained as the product of  $x$  and the biomass of that zooplankton group ( $\mu\text{g C}^{-1} \cdot \text{L}^{-1}$ ), and total excretion ( $X$ ,  $\mu\text{g P} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$ ) was found by summing population excretion rates across the three zooplankton groups.

Uptake of P by phytoplankton ( $U$ ) and sedimentation ( $Se$ ) of P were described as

$$U = [(r_N \cdot N) + (r_B \cdot B)]Sh \cdot Q \text{ and} \quad (17)$$

$$Se = [(Si_N \cdot N) + (Si_B \cdot B)] \cdot Q \quad (18)$$



**Figure 21-3.** P loading rates from the watershed (external) and the hypolimnion used in the baseline simulation (1987 dynamics). External loading rate data derived from Brock (1985) and Lathrop (in press) as explained in text. Hypolimnetic loading data derived from Stauffer (1987).

Outflow of P was held constant at  $0.0005 \mu\text{g} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$ .

Although it is not explicitly modeled here, we were interested in assessing the model's ability to simulate total phosphorus (TP) as well as soluble reactive phosphorus (SRP). Total phosphorus was calculated as

$$\text{TP} = P + (N+B) \cdot Q + (D+C+S) \cdot 0.010$$

This assumes that the P:C ratio of zooplankton is 0.01.

### Model Calibration and Execution

The model was calibrated against the Lake Mendota plankton dynamics of 1987, a year typical of the previous decade (Vanni et al. 1990a; Lathrop and Carpenter, Ch. 7 and 8). During this time the planktivorous fish cisco (*Coregonus artedii*) was abundant, and zooplankton and phytoplankton seasonal succession was typical of eutrophic lakes (Vanni and Temte 1990; Vanni et al., Ch. 13).

As Scavia et al. (1988) point out, coupled nonlinear differential equations such as those employed in this model can yield similar state-variable simulations with quite different sets of coefficients. Thus it is possible to adequately simulate plankton dynamics using coefficients that may be inaccurate. However, requiring that the model adequately simulate both state variables and rate processes minimizes compensating rate process errors and increases the chance of producing a realistic model of plankton dynamics (Scavia et al. 1988). Therefore, to calibrate the model, coefficient values were varied within ranges expected for Lake Mendota

until the model adequately reproduced both observed state variables and process rates measured in 1987 and earlier years. Coefficient values are given in Table 21.1.

Equations of the model were solved numerically using the Adams–Bashforth integration method with a time step of 0.1 d. The model was run for 150 d, approximating the time between ice-out (usually early April) through summer (end of August).

### Sensitivity Analysis

To explore the sensitivity of plankton dynamics to small changes in coefficient values, each coefficient was varied individually and the effects on several response variables observed. Each coefficient value was increased 5%, except as noted (Table 21.2), and the model was considered to be sensitive to a coefficient if any response variable changed >5% in response to this increase in the coefficient value. Response variables were mean spring phytoplankton biomass (nanoplankton + cyanobacteria), mean summer phytoplankton biomass, length of the spring clear-water period (days with total phytoplankton biomass <100 µg C·L<sup>-1</sup>), maximum *Daphnia* biomass, mean spring *Daphnia* biomass, and mean summer *Daphnia* biomass (Table 21.2).

The parameters that had the greatest effects by far were those related to zooplankton feeding and respiration, such as maximal feeding rates, assimilation rates, and respiration rates (Table 21.2). Most response variables were sensitive to 5% increases in these parameters, sometimes changing by >40%. Increases in other influential parameters produced changes of >5% in magnitude in only one or a few response variables, and most of these changes were <10% in magnitude (Table 21.2).

### Planktivory × Nutrient Scenarios

The food web of Lake Mendota has recently undergone and is currently undergoing substantial changes (Rudstam et al., Ch. 12). In particular, planktivorous fish densities are being reduced through both unintentional and deliberate means. In late summer 1987, the biomass of planktivorous fish was reduced substantially by massive mortality of cisco (caused by warm temperatures and low hypolimnetic oxygen) (Vanni et al. 1990a; Luecke et al., Ch. 14). In addition, piscivorous fish (walleye and northern pike) were introduced as fry and fingerlings in the springs of 1987–89. When these young fish reach large size, they may reduce the abundance of planktivorous fish (Johnson and Staggs, Ch. 17). Nutrient loading rates have varied considerably in Lake Mendota since the early 1970s. External loading from the watershed and spring concentration of P have decreased since the 1970s (Lathrop, in press). Within the 1980s, loading rates were variable as well. For example, both 1987 and 1988 were low runoff years

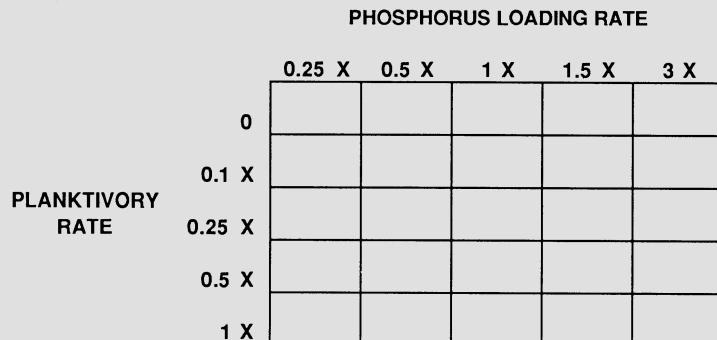
**Table 21-1.** Parameters and initial conditions used in simulations.

Parameter/ initial condition	Equation	Value and units	Ref.
$G_{\max}$	4	0.7 $\mu\text{g C} \cdot \mu\text{g C}^{-1} \cdot \text{d}^{-1}$ for <i>Daphnia</i> 0.6 $\mu\text{g C} \cdot \mu\text{g C}^{-1} \cdot \text{d}^{-1}$ for small cladocerans 0.2 $\mu\text{g C} \cdot \mu\text{g C}^{-1} \cdot \text{d}^{-1}$ for copepods	1 2 1,3
$A$	4	0.65 (dimensionless) for <i>Daphnia</i> 0.5 for small cladocerans 0.75 for copepods	
$K$	4	50 $\mu\text{g C} \cdot \text{L}^{-1}$ for <i>Daphnia</i> and small cladocerans 150 $\mu\text{g C} \cdot \text{L}^{-1}$ for copepods	4
$W'_i$	4	1.0 for all zooplankton groups feeding on nanoplankton 0.25 for <i>Daphnia</i> feeding on cyanobacteria 0.3 for small cladocerans feeding on cyanobacteria 0.1 for copepods feeding on cyanobacteria	5
$R_1$	5	0.1 $\mu\text{g C} \cdot \mu\text{g C}^{-1} \cdot \text{d}^{-1}$ for <i>Daphnia</i> and small cladocerans	5
$R_2$	5	0.04 $\mu\text{g C} \cdot \mu\text{g C}^{-1} \cdot \text{d}^{-1}$ for copepods 0.15 $\mu\text{g C} \cdot \mu\text{g C}^{-1} \cdot \text{d}^{-1}$ for <i>Daphnia</i> 0.11 $\mu\text{g C} \cdot \mu\text{g C}^{-1} \cdot \text{d}^{-1}$ for copepods	5 5 5
$M_D$	1	See Figure 21.2	6
$M_S$	2	0 $\text{d}^{-1}$	7
$M_C$	3	0.001 $\text{d}^{-1}$	7
$L$	3	0 $\mu\text{g C} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$ for days 0–29 and 40–150 100 $\mu\text{g C} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$ for days 30–39	7
$r_{\max}$	8, 9	1.373 $\text{d}^{-1}$ for nanoplankton 0.4 $\text{d}^{-1}$ for cyanobacteria	8,9 5
$K_P$	8	1.0 $\mu\text{g P} \cdot \text{L}^{-1}$ for nanoplankton 1.3 $\mu\text{g P} \cdot \text{L}^{-1}$ for cyanobacteria	5 5
$Y$	6, 7, 10	3,000 $\mu\text{g C} \cdot \text{L}^{-1}$	10
$Si$	6, 7, 11	0.012 $\text{d}^{-1}$ for nanoplankton 0.005 $\text{d}^{-1}$ for cyanobacteria	9 8
$If_N$	6	0.0001 $\mu\text{g C} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$	
$If_B$	7	0 $\mu\text{g C} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$ for days 0–72 and 80–150 75 $\mu\text{g C} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$ for days 73–79	7
$E$	15	See Figure 21.3	10,11
$H$	15	See Figure 21.3	12
$Q$	16	0.024 $\mu\text{g P} \cdot \mu\text{g C}^{-1}$	13
$F$	16	0.5 (dimensionless)	14
$O$	15	0.0005 $\mu\text{g P} \cdot \text{L}^{-1} \cdot \text{d}^{-1}$	

**Table 21-1.** *Continued*

Parameter/ initial condition	Equation	Value and units	Ref.
Initial conditions			
<i>Daphnia</i>	$1 \mu\text{g C} \cdot \text{L}^{-1}$		7
Copepods	$400 \mu\text{g C} \cdot \text{L}^{-1}$		7
Small cladocerans	$10 \mu\text{g C} \cdot \text{L}^{-1}$		7
Nanoplankton	$100 \mu\text{g C} \cdot \text{L}^{-1}$		7
Blue-greens	$1 \mu\text{g C} \cdot \text{L}^{-1}$		7
Phosphorus	$50 \mu\text{g P} \cdot \text{L}^{-1}$		7

References: <sup>1</sup>Muck and Lampert 1984; <sup>2</sup>Peters and Downing 1984; <sup>3</sup>Vanderploeg et al. 1984; <sup>4</sup>Porter et al. 1982; <sup>5</sup>Scavia et al. 1988; <sup>6</sup>Luecke et al. in press; <sup>7</sup>data from Lake Mendota project; <sup>8</sup>Reynolds 1984; <sup>9</sup>Carpenter et al., Ch. 22; <sup>10</sup>Brock 1985; <sup>11</sup>Lathrop in press; <sup>12</sup>Stauffer 1987; <sup>13</sup>Goldman et al. 1979; <sup>14</sup>Lehman 1980.



**Figure 21-4.** Factorial design of planktivory and nutrient loading rate scenarios. Rates are expressed as multiples of 1987 rates, i.e.,  $1\times = 1987$  rate. Phosphorus loading rate refers to external loading only.

(~72% and ~84% of the mean from 1954 to 1989, respectively), while 1989 was more typical of mean runoff for the 1980s (~10% above long-term mean; Lathrop, in press and Ch. 6).

Because of these changes and expected changes in fish and nutrients in Lake Mendota, and to assess fish  $\times$  nutrient interactions in general, model scenarios involving various levels of external nutrient loading rates and planktivory rates were created in a factorial design (Figure 21.4). The levels were chosen as multiples of 1987 values. Planktivory in 1987 was considered high, as cisco were quite abundant and summer *Daphnia* biomass was quite low (Vanni et al. 1990a; Luecke et al., in press). Furthermore, an objective of the Lake Mendota research project is to assess the feasibility of reducing planktivorous fish to reduce algal bloom frequency and severity. Therefore we explored several reductions in

**Table 21-2.** Change in magnitude (% increase or decrease) of response variables for all cases in which a 5% change in the value of a parameter or initial condition resulted in a >5% change in magnitude of any response variable.

Parameter/ initial condition	Response variable and change in magnitude of response variable (%)					
	Mean spring algal biomass	Mean summer algal biomass	Duration of clear-water period	Maximum spring <i>Daphnia</i> biomass	Mean spring <i>Daphnia</i> biomass	Mean summer <i>Daphnia</i> biomass
$G_{\max}$						
<i>Daphnia</i>	-10.7	+41.3	+40.0	+15.2	+62.9	-23.9
Small clad.		-27.2	+6.7	-18.3	-7.1	-27.2
Copepods	-11.6	+16.9	+20.0	-46.3	-25.7	-60.2
$A$						
<i>Daphnia</i>	-10.6	+40.9	+40.4	+14.6	+62.8	-23.9
Small clad.		-27.2	+6.7	-18.4	-7.1	-29.2
Copepods	-11.6	+17.0	+20.0	-46.3	-25.7	-60.2
$R_1$						
<i>Daphnia</i> , small clad.			-13.3		-20.7	+11.5
Copepods		-5.1	-6.7	+10.8		+20.3
$R_2$						
<i>Daphnia</i> , small clad.			-20.0			
Copepods		-8.2	-6.7	+20.5		+31.8
$M_D$			-6.7			
$L^a$					-8.9	-9.7
$L^b$			-6.7			+9.7
$Y$		+5.3		-9.2		-9.7
$Si$						
Nanoplankton				-5.1		
$If_B^a$			+6.7			
$E$		-5.1	-6.7		+14.2	
$Q^c$		-8.5	-6.7	+16.1		+25.7
$F$			-6.7	+15.8		+15.0
Initial conditions						
Phosphorus			-6.7		+8.0	
Copepods				-13.3		-15.0

<sup>a</sup> Delayed timing by 1 d.

<sup>b</sup> Increased by 5% on all dates.

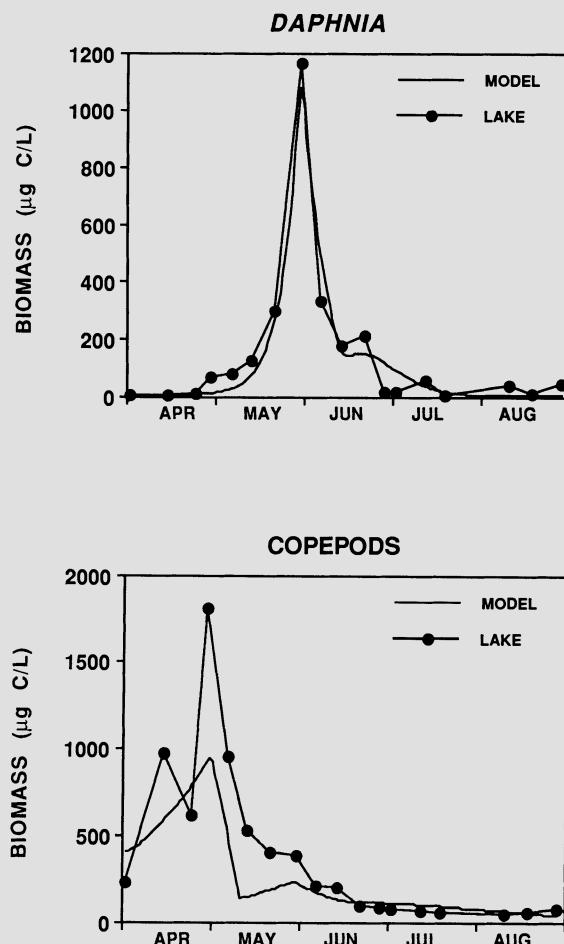
<sup>c</sup> Decreased  $Q$  (P:C ratio) by 5%.

planktivory in the simulations. Nutrient loading rates in 1987 were lower than in the 1970s (Lathrop, in press) but probably much higher than presettlement rates. Therefore we considered P loading scenarios both well above and below estimated 1987 rates.

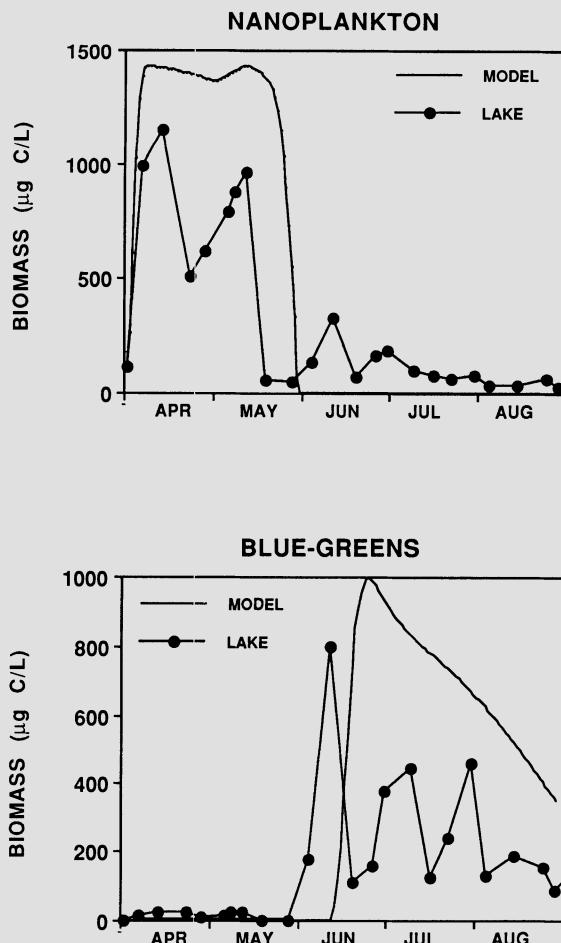
## Results

### Simulation of 1987 Plankton Dynamics

The model simulated 1987 dynamics reasonably well (Figures 21.5–7). The agreement between the model and actual 1987 dynamics was especially strong for *Daphnia* and copepod abundance (Figure 21.5) but was also adequate for nanoplankton, cyanobacteria TP, and SRP (Figures 21.6 and 21.7).



**Figure 21-5.** Comparison of model output with the observed dynamics of *Daphnia* and copepods in Lake Mendota in 1987.

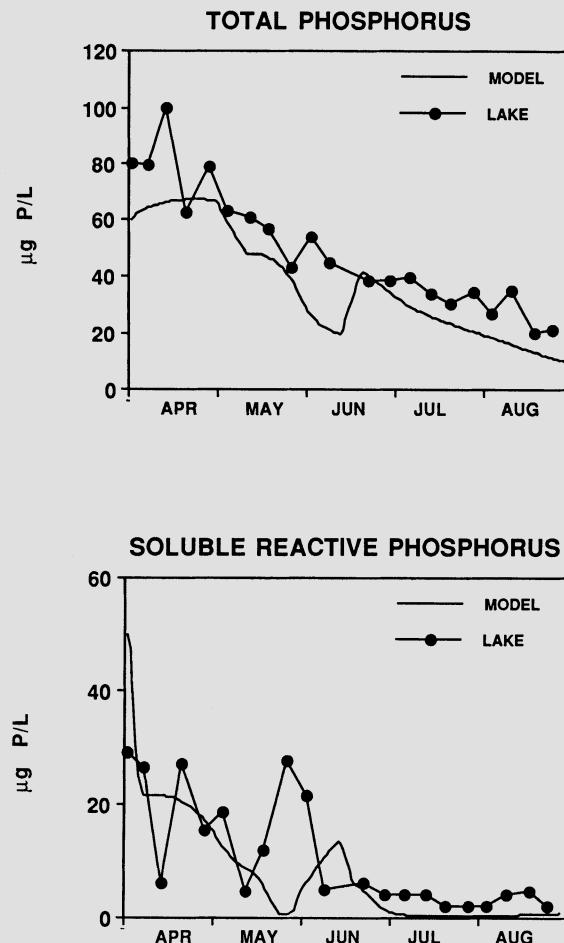


**Figure 21-6.** Comparison of model output with the observed dynamics of nanoplankton and blue-green algae (cyanobacteria) in Lake Mendota in 1987.

#### Planktivory × Nutrient Scenarios

Most response variables were quite sensitive to large changes in phosphorus loading and planktivory rates (Figures 21.8 and 21.9). In general, increased P loading resulted in increased phytoplankton abundance, and decreased planktivory resulted in decreased phytoplankton abundance. However, interactions of fish and nutrients resulted in many counterintuitive responses.

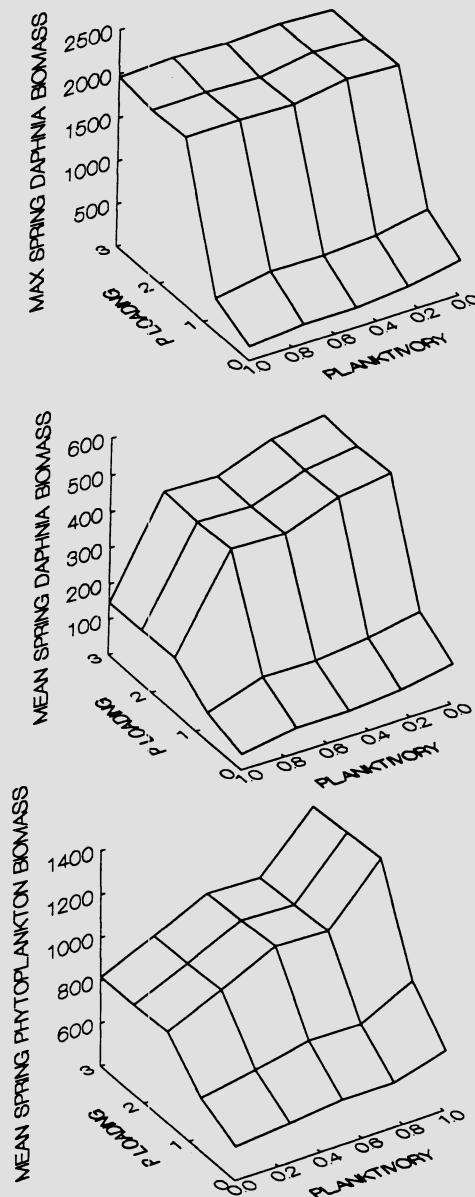
Maximum spring *Daphnia* biomass was relatively insensitive to changes in planktivory rates (Figure 21.8). This is not unexpected, since spring *Daphnia* dynamics in Lake Mendota seem to be relatively independent of planktivory rates (Luecke et al., in press). *Daphnia* began the ice-



**Figure 21-7.** Comparison of model output with the observed dynamics of SRP and TP in Lake Mendota in 1987.

free season at low biomass, increased to an annual maximum in late spring, and declined precipitously shortly thereafter, regardless of fish planktivory rate. In contrast, maximum spring *Daphnia* biomass was quite responsive to changes in P loading rate. *Daphnia* biomass increased with increasing P loading, except that *Daphnia* biomass was similar at relatively high P loading rates (Figure 21.8).

Mean spring *Daphnia* biomass responded to the scenarios in a manner similar to maximum spring *Daphnia* biomass, except that mean spring *Daphnia* biomass was reduced substantially at 1 $\times$  planktivory rates, compared to lower planktivory rates (Figure 21.8). The effect of planktivory was especially pronounced at high P loading rates ( $\geq 1\times$ ; Figure 21.8).



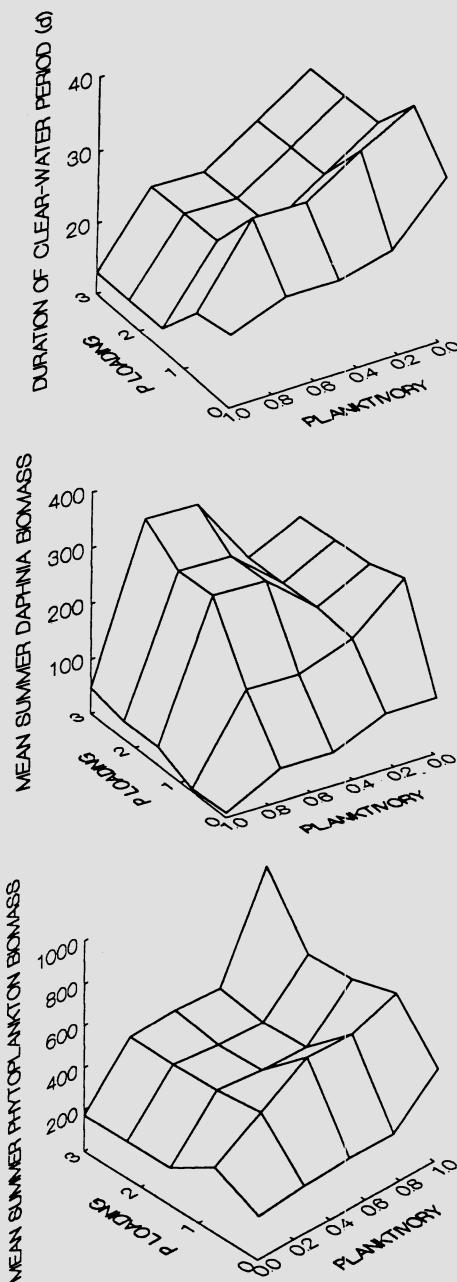
**Figure 21-8.** Response of maximum spring *Daphnia* biomass (top), mean spring *Daphnia* biomass (middle), and mean spring phytoplankton biomass (bottom) to changes in planktivory and P loading rates. Note that planktivory scale (x-axis) is reversed for spring phytoplankton biomass relative to the other graphs. All biomass values expressed as  $\mu\text{g C L}^{-1}$ . Mean spring biomass was defined as the simple arithmetic mean of all April and May dates of model output.

Mean spring phytoplankton biomass was responsive to both planktivory and P loading rate (Figure 21.8). Spring phytoplankton biomass increased with increasing P loading rate, especially at lower P loading. Reductions in planktivory resulted in decreased spring phytoplankton biomass, corresponding to changes in *Daphnia* biomass. The response of spring phytoplankton biomass to reduced planktivory was more pronounced at high P loading rates than at low P loading rates.

Duration of the spring clear-water period was responsive to both planktivory and P loading, but trends were more complex than for spring *Daphnia* and phytoplankton biomass (Figure 21.9). Duration of the clear-water period increased with decreasing planktivory. The biggest increase in clear-water period duration occurred when planktivory rate was reduced from 1 $\times$  to 0.5 $\times$ . Duration of the clear-water period was also sensitive to P loading, but the response to P loading varied with planktivory rate. At 1 $\times$  planktivory rate, duration of the clear-water period was a steadily decreasing function of P loading, but at lower planktivory rates, maximum duration occurred at 0.5 $\times$  P loading rather than 0.25 P loading. As P loading rate was reduced from 0.5 $\times$  to 0.25 $\times$ , spring *Daphnia* density was reduced such that grazing pressure was lower than at 0.5 $\times$  P loading, resulting in a shorter clear-water period. At P loadings above 0.5 $\times$ , increased algal growth reduced the efficiency of *Daphnia* grazing compared with 0.25 $\times$ . Thus, at all planktivory rates except 1 $\times$ , duration of the clear-water period was maximal at intermediate P loading rate.

Summer *Daphnia* biomass was much more sensitive to planktivory than spring *Daphnia* biomass, and planktivory and P loading rate influenced summer *Daphnia* biomass in an interactive manner (Figure 21.9). Initial reduction of planktivory below 1 $\times$  resulted in a great increase in summer *Daphnia* biomass, especially at high P loading rates. Further decreases in planktivory produced increases in summer *Daphnia* biomass only at lower (<1 $\times$ ) P loading rates. Summer *Daphnia* biomass was also sensitive to P loading rate, but the response to P loading was dependent on planktivory rate. While *Daphnia* increased in response to further increases in P loading at all planktivory rates, the magnitude of the response was highly dependent on planktivory rate.

In general, summer phytoplankton biomass was greatest at high planktivory and P loading rates (Figure 21.9). Decreased planktivory resulted in decreased summer phytoplankton biomass, at all P loading rates. Increased P loading caused consistently increased summer phytoplankton biomass only at relatively high planktivory rates. At low and intermediate planktivory rates, when *Daphnia* were relatively unconstrained by fish predation, increased P loading actually caused reduced or constant summer phytoplankton biomass, because increased P resulted in greatly increased *Daphnia* biomass and hence greater subsequent grazing pressure on phytoplankton.



**Figure 21-9.** Response of duration of the clear-water period (top), mean summer *Daphnia* biomass (middle), and mean summer phytoplankton biomass (bottom) to changes in planktivory and P loading rates. Note that planktivory scale ( $x$ -axis) is reversed for summer phytoplankton biomass relative to the other graphs. The clearwater period was defined as the number of days with total phytoplankton biomass  $<100 \mu\text{g C}\cdot\text{L}^{-1}$ . All biomass values expressed as  $\mu\text{g C}\cdot\text{L}^{-1}$ . Mean spring biomass was defined as the simple arithmetic mean of all June, July, and August dates of model output.

## Discussion

### Simulation of 1987 Plankton Dynamics

It is wise to examine process rates as well as state variable values in evaluating a simulation model (Scavia et al. 1988). Examination of rate processes suggests that the model is a reasonable analogue of the Lake Mendota food web. For example, the decline of nanoplankton in spring in the model can be accounted for by grazing loss to *Daphnia*. In the simulation, nanoplankton growth rate (excluding loss to zooplankton,  $r_N$ ) remained high throughout the nanoplankton decline. These model results are in agreement with observations and experiments from 1987 in Lake Mendota, which showed that the decline of nanoplankton and resultant clear-water period were caused by *Daphnia* grazing, and that nanoplankton were not nutrient limited during this time (Vanni and Temte 1990). In addition, model *Daphnia* dynamics agreed with those in the lake. The spring decline of *Daphnia* in the model occurred because of decreased production rather than an increase in fish predation rate, in agreement with fish bioenergetics and *Daphnia* demographic data (Luecke et al., in press) which showed that the spring *Daphnia* decline was caused by reduced birth rates and not predation. *Daphnia* remained scarce in summer in both the model and the lake because of high fish predation rates and not because of food limitation. The agreement between rates and state variables of the model and the lake suggests that the model adequately simulates the Lake Mendota plankton community.

### Planktivory $\times$ Nutrient Scenarios

This modeling exercise revealed that the Lake Mendota food web is sensitive to both predation and nutrients. Most response variables responded to changes in planktivory and P loading rates (Figures 21.6–11). Furthermore, many response variables responded in complex ways.

Some of the responses were fairly predictable from previous data on Lake Mendota. For example, maximum spring *Daphnia* biomass was largely unaffected by changes in planktivory rate in the simulations, and mean spring *Daphnia* biomass was also largely unaffected except at the highest planktivory rate (Figures 21.6 and 21.7). These patterns agree with the observations of Luecke et al. (in press) that the spring *Daphnia* dynamics were largely independent of fish planktivory.

Other responses require more explanation. For example, despite the loose dependence of spring *Daphnia* dynamics on planktivory, reducing planktivory led to an increase in duration of the clear-water period (Figure 21.9), which is determined largely by *Daphnia* grazing. These two trends appear to be contradictory; in fact Luecke et al. (in press) suggested that reducing planktivory in Lake Mendota would have little

effect on the spring clear-water period because of the apparent independence of *Daphnia* dynamics and planktivory. In the model, the increase in duration of the clear-water period upon reduction of planktivory was due in large part to an earlier onset of clear water (phytoplankton biomass  $<100 \mu\text{g C}\cdot\text{L}^{-1}$ ), because *Daphnia* increased sooner than at higher planktivory rates. These model dynamics agree generally with the dynamics in the lake during times when planktivory has been decreased. For example, in 1988, after massive mortality had removed  $\sim 90\%$  of the 1987 cisco biomass, and in 1976, when cisco were also rare, *Daphnia* began increasing earlier, and the clear-water period was longer, than in years when cisco were abundant (Brock 1985; Vanni et al. 1990b).

The response of summer phytoplankton (cyanobacteria) biomass to the various scenarios suggests that both nutrients and planktivory can have strong impacts on summer phytoplankton biomass (Figure 21.9). Furthermore, the results suggest that reduction of planktivory rates may be a useful management strategy in reducing summer cyanobacteria blooms. However, interactions of planktivory and P loading rates produced complex overall patterns in summer phytoplankton biomass (Figure 21.9). For example, increased P loading led to decreased phytoplankton biomass under certain conditions, because increased P also led to increased biomass of *Daphnia* and other zooplankton and subsequent increase in grazing rates. However, at higher planktivory rates, summer phytoplankton increased steadily with increasing P loading (Figure 21.9). Complex responses such as these may reduce predictability and thus could hinder management of cyanobacteria blooms through food web manipulation.

Despite the complexities in the response of summer phytoplankton biomass to the scenarios, it is clear based on the model output that large reductions in planktivory should result in reduced cyanobacteria biomass (Figure 21.9). This prediction agrees with the simulation model of Scavia et al. (1988) for Lake Michigan and with the response of the Lake Mendota food web to the cisco die-off of late 1987 (Vanni et al. 1990a). However, the model output appears to be at odds with large changes in the Lake Mendota food web in the 1970s (Lathrop and Carpenter, Ch. 7 and 8). Vanni et al. (1990b) analyzed data from 1976 to 1978 and showed that summer phytoplankton appeared to be insensitive to large fluctuations in cisco and *Daphnia* abundance. They suggested that the lack of response of phytoplankton to these changes in planktivory and apparent grazing pressure, compared to the response of 1987–88, was due to a higher P concentration in the 1970s. Higher P may reduce food web effects on phytoplankton (Benndorf et al. 1988). Thus, data from the late 1970s conflict with the model predictions that summer phytoplankton biomass should respond to reduced planktivory even at P loading rates 3× those of 1987 (Figure 21.9). It may be that at very high P loading rates, cyanobacterial colonies attain a density at which they interfere with

*Daphnia* energy acquisition (Gliwicz and Lampert 1990). This interference is not accounted for in our model.

Many of the responses to planktivory and P loading rate manipulations illustrate the importance of considering both predation and nutrient influences on phytoplankton. The response of most seasonal means to planktivory was dependent on P loading rate (Figures 21.8 and 21.9). Also, temporal dynamics were dependent on both processes. For example, extremely low P loading resulted in extremely low *Daphnia* biomass, which in turn resulted in low grazing rates and a relatively short clear-water period. As mentioned in the preceding paragraph, reduced P loading also resulted in lower summer grazing rates and relatively higher summer phytoplankton biomass. The model runs also emphasized the importance of temporal scale in considering phytoplankton dynamics (Carpenter and Kitchell 1987). Short time scales may permit enough time only for phytoplankton to increase in response to increasing nutrients, but not enough time for zooplankton to respond to increased food availability and subsequently reduce phytoplankton biomass.

### General Conclusions

All simulation models are subject to errors from the inherent simplicity and the lack of precise data for certain coefficients. Nevertheless, the model constructed here seems to adequately simulate the Lake Mendota plankton food web of the late 1980s and to accurately predict some consequences of observed food web changes. The scenarios created here suggest that food web manipulation represents a viable management strategy for reducing the severity of summer algal blooms; reductions in planktivory generally led to reduced summer phytoplankton biomass. Simulation models such as these can be useful tools in forecasting the consequences of such food web manipulations, in elucidating mechanisms responsible for responses of food webs to perturbations, and in identifying critical parameter estimates and mechanistic questions for experimental work.

### References

- Benndorf J, Schultz H, Benndorf A, Unger R, Penz E, Kneschke H, Kossatz K, Dumke R, Hornig U, Kruspe R, Reichel R (1988) Food-web manipulation by enhancement of piscivorous fish stocks: Long-term effects in the Bautzen reservoir. *Limnologica* 19:97–110
- Brock TD (1985) A Eutrophic lake: Lake Mendota, Wisconsin. Springer-Verlag, New York
- Burns CW (1969) The relationship between body size of filter-feeding Cladocera and the maximum size of particle ingested. *Limnol. Oceanogr.* 13:675–678

- Carpenter SR, Kitchell JF (1984) Plankton community structure and limnetic primary production. *Am. Nat.* 124:159–172
- Carpenter SR, Kitchell JF (1987) The temporal scale of variance in limnetic primary production. *Am. Nat.* 129:417–433
- Carpenter SR, Kitchell JF (1988) Consumer control of lake productivity. *BioScience* 35:634–639
- Gliwicz ZM, Lampert W (1990) Food thresholds in *Daphnia* species in the absence and presence of blue-green filaments. *Ecology* 71:691–702
- Goldman JC, McCarthy JJ, Peavey DG (1979) Growth rate influence on the chemical composition of phytoplankton in oceanic waters. *Nature* 279:210–215
- Lathrop RC (1990) Response of Lake Mendota (Wisconsin, USA) to decreased phosphorus loadings and the effect on downstream lakes. *Verh. Internal. Ver. Theoret. Angew. Limnol.* 24:457–463
- Lehman JT (1980) Nutrient recycling as an interface between algae and grazers in freshwater communities. In Kerfoot WC (ed) *Evolution and ecology of freshwater zooplankton communities*, University Press of New England, Hanover, New Hampshire, pp 251–263
- Luecke C, Vanni MJ, Magnuson JJ, Kitchell JF, Jacobson PT (1990) Seasonal regulation of *Daphnia* populations by planktivorous fish: Implications for the spring clear-water phase. *Limnol. Oceanogr.* 35:1718–1733
- Muck P, Lampert W (1984) An experimental study on the importance of food conditions for the relative abundance of calanoid copepods and cladocerans. *Arch. Hydrobiol. (Suppl.)* 66: 2:157–179
- Northcote TG (1988) Fish in the structure and function of freshwater ecosystems: A “top-down” view. *Can. J. Fish. Aquat. Sci.* 45:361–379
- Peters RH, Downing JA (1984) Empirical analysis of zooplankton filtering and feeding rates. *Limnol. Oceanogr.* 29:763–784
- Porter KG, Gerritsen J, Orcutt JD (1982) The effect of food concentration on swimming patterns, feeding behavior, ingestion, assimilation, and respiration by *Daphnia*. *Limnol. Oceanogr.* 27:935–949
- Reynolds CS (1984) *The ecology of freshwater phytoplankton*. Cambridge University Press, Cambridge
- Scavia D, Lang GA, Kitchell JF (1988) Dynamics of Lake Michigan plankton: A model evaluation of nutrient loading, competition, and predation. *Can. J. Fish. Aquat. Sci.* 45:165–177
- Schindler DW (1978) Factors regulating phytoplankton production and standing crop in the world’s lakes. *Limnol. Oceanogr.* 23:478–486
- Stauffer RE (1987) Vertical nutrient transport and its effects on epilimnetic phosphorus in four calcareous lakes. *Hydrobiologia* 154:87–102
- Vanderploeg HA, Scavia D (1979) Calculation and use of selectivity coefficients of zooplankton grazing. *Ecol. Model.* 7:135–149
- Vanderploeg HA, Scavia D, Liebig JR (1984) Feeding rate of *Diaptomus sicilis* and its relation to selectivity and effective food concentration in algal mixtures and in Lake Michigan. *J. Plankton Res.* 6:919–941
- Vanni MJ, Luecke C, Kitchell JF, Allen Y, Temte J, Magnuson JJ (1990a) Effects on lower trophic levels of massive fish mortality. *Nature* 344:333–335
- Vanni MJ, Luecke C, Kitchell JF, Magnuson JJ (1990b) Effects of planktivorous fish mass mortality on the plankton community of Lake Mendota, Wisconsin: Implications for biomanipulation. *Hydrobiologia* 200/201:329–336

- Vanni MJ, Temte J (1990) Seasonal patterns of grazing and nutrient limitation of phytoplankton in a eutrophic lake. *Limnol. Oceanogr.* 35:697–709
- Zaret TM (1980) Predation and freshwater communities. Yale University Press, New Haven, Connecticut.

# **22**

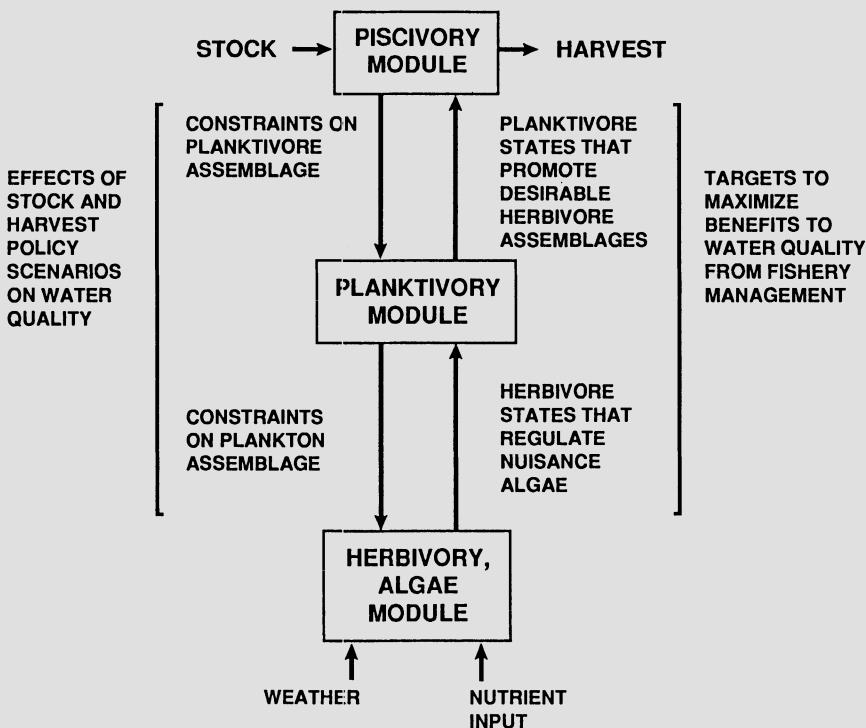
## **Modeling the Lake Mendota Ecosystem: Synthesis and Evaluation of Progress**

**Stephen R. Carpenter, Brett M. Johnson,  
Chris Luecke, Charles P. Madenjian, John R. Post,  
Lars G. Rudstam, Michael J. Vanni, Xi He,  
Yvonne Allen, Richard Dodds, Kathleen McTigue,  
and Denise M. Schael**

### **Introduction**

The models presented in the three preceding chapters were planned as elements of an integrated ecosystem approach from phosphorus to fishes. The modeling problem was broken into three parts in order to maximize our rate of progress and make best use of the people involved. The modules—piscivory, planktivory, and herbivory—algae—nutrients—have fundamentally different time scales yet strong vertical interactions (Figure 22.1). Within a given nutrient and weather regime, differences in return time cause the upper modules to act as constraints on lower ones (O'Neill et al. 1986). Piscivore dynamics have return times of years (Post and Rudstam, Ch. 19). Stock and harvest policies as well as resource levels must be considered in modeling piscivory. Planktivory by fishes has return times of years, while that by the zooplankter *Leptodora* has return times of weeks (Luecke et al., Ch. 20). Herbivory, algal growth, and nutrient fluxes have rapid dynamics and short return times of a few days (Vanni et al., Ch. 21).

Separate models were developed for all three modules. We used consistent state variables, equations, and parameters insofar as possible to facilitate exchanges of scenarios among the modules. Intraannual dynamics of planktivory and herbivory were of particular interest. Because of thermal effects on the bioenergetics of predation and because fish grow in mass through several orders of magnitude during their first year of life (with associated effects on consumption and vulnerability to predation), it was necessary for all three modules to operate with time steps of a day or less. We attempted to derive conditions that would



**Figure 22-1.** Hierarchical structure of the simulation models. The piscivory module (Post and Rudstam, Ch. 19) includes effects of stock and harvest policy. The planktivory module (Luecke et al., Ch. 20) is the nexus of interactions forced by primary production and fish predation. The herbivory–algae–nutrients module (Vanni et al., Ch. 21) includes effects of weather and nutrient input.

maximize the potential benefits to water quality from fisheries management, by determining herbivore states that minimized algal biomass, fish community structures that promoted such desirable herbivore assemblages, and stock and harvest policies that would lead to the targeted fish composition.

This chapter has two goals. First, we report results of a workshop held in January 1990 to link the three modules and examine the implications of contrasting nutrient loading and piscivory scenarios for water quality. Second, we take stock of our collective modeling efforts to date and identify priorities for the future.

## Methods

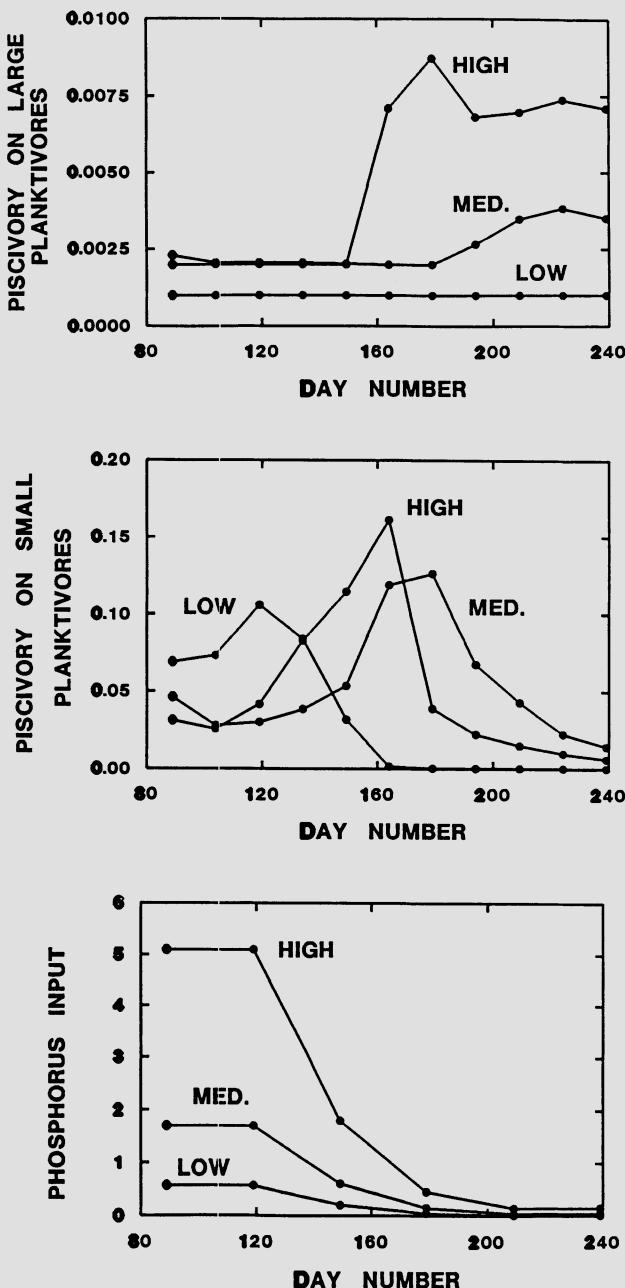
Models analyzed for this chapter were described in the preceding chapters by Vanni et al. (Ch. 21, herbivory–algae–nutrient module), Luecke et al.

(Ch. 20, planktivory module), and Post and Rudstam (Ch. 19, piscivory module). Phosphorus input scenarios spanned a range from those typical of oligotrophic lakes to those found in relatively eutrophic systems (Figure 22.2). Loading rates known from Lake Mendota lie within the range used in our modeling exercise (Lathrop, Ch. 6). We used a seasonal schedule of phosphorus input rates typical of Lake Mendota (Lathrop, Ch. 6; Vanni et al., Ch. 21).

Scenarios for piscivory on large and small planktivores during a growing season ranged from the lowest piscivore densities known from Lake Mendota to the highest densities management can plausibly achieve (Figure 22.2). The low-piscivory scenario represents a yellow perch-dominated system. Few walleyes are present, biomass of adult perch is high ( $5.6 \text{ g m}^{-2}$ ), and piscivory on small planktivores [young-of-year (YOY) perch] is dominated by cannibalism by older perch. Since perch are relatively small, the main consumption of YOY fish will occur when the YOY are small, early in the year. The medium-piscivory scenario represents a system with roughly equal biomasses of walleye and yellow perch. The high-piscivory scenario represents a walleye-dominated system. Walleyes are abundant, biomass of adult perch is small ( $0.6 \text{ g m}^{-2}$ ), and piscivory is dominated by walleye. Peak mortality rates on YOY perch occur later in the season when the biomass of perch and temperature are high.

Scenarios differed in the seasonal timing of piscivory as well as the absolute predation rates (Figure 22.2). Previous chapters have shown that the timing of peaks in predation can have important consequences for subsequent dynamics of lower trophic levels. Nutrient input peaks in the spring and is relatively low in midsummer, when piscivory peaks in the medium and high scenarios. Bartell et al. (1988) have discussed seasonal changes in the relative effects of predation and nutrients on plankton. During spring, the Lake Mendota food web experiences high nutrient inputs while low temperature constrains fish predation. During summer, nutrient inputs are relatively low but predation rates are relatively high.

We analyzed the modules in a  $3 \times 3$  factorial design: low-, medium-, and high-piscivory scenarios crossed with low-, medium-, and high-nutrient input scenarios. Our objective was to compare summer (June–August) mean herbivore and algal biomass as a function of predation and nutrient input. The exchange of scenarios among modules was accomplished as follows. Piscivory rates were generated using the piscivory module and used as forcing functions for the planktivory module. Phosphorus input scenarios were applied to the herbivory module to generate production scenarios used as forcing functions for the planktivory module. The planktivory module, forced by the appropriate piscivory and production rates, was used to generate a schedule of herbivory rates. The herbivory module was then run using the appropriate herbivory rates and nutrient input rates to calculate herbivore and algal biomasses.



**Figure 22-2.** Scenarios used as forcing functions for coupling the piscivory, planktivory, and herbivory–algae–nutrients modules. The upper and middle panels show mortality rates (piscivory plus harvest,  $\text{d}^{-1}$ ) on large and small planktivores, respectively, versus day of the year for the high-, medium-, and low-piscivory scenarios. The lower panel shows phosphorus input rate ( $\mu\text{g L}^{-1} \text{d}^{-1}$ ) versus day number for the high, medium, and low loading scenarios.

## Results

Biomass of *Daphnia* responded positively to increasing piscivory (Figure 22.3). The most dramatic increase in mean summer *Daphnia* biomass occurred when piscivory was increased from medium to high levels. *Daphnia* biomass also responded positively to phosphorus. The greatest increase occurred at high piscivory when phosphorus input was raised from low to medium levels.

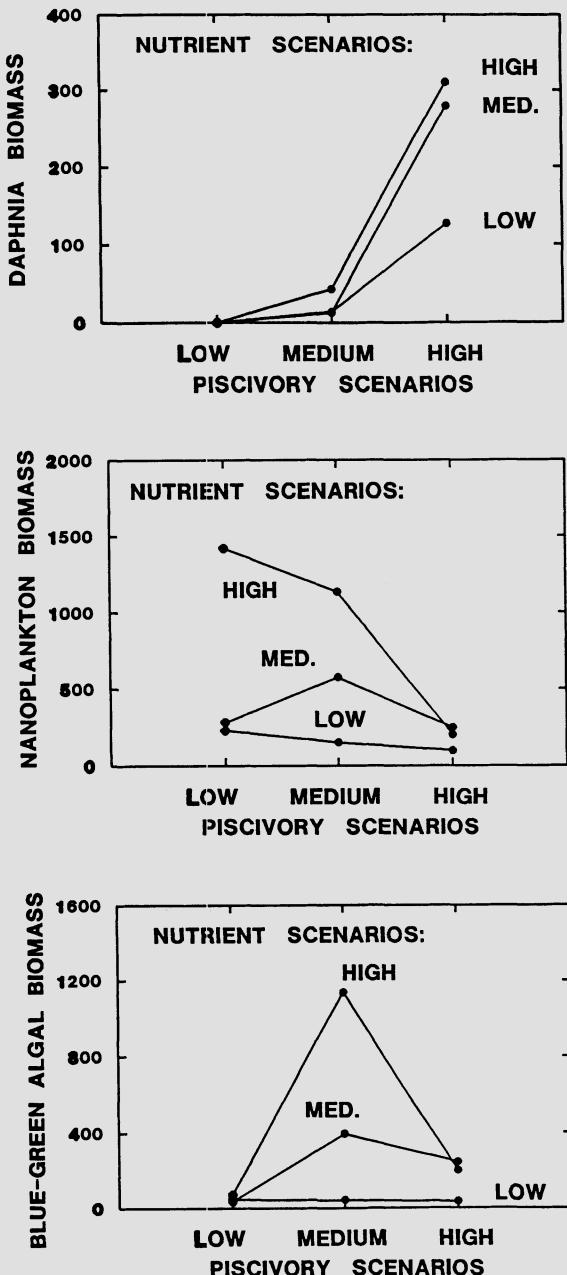
Mean summer biomass of edible nanoplankton responded positively to increasing phosphorus input (Figure 22.3). The response of nanoplankton biomass to piscivory depended upon phosphorus input. Nanoplankton biomass declined with increasing piscivory at low and high phosphorus loads, with the steepest decline occurring at the highest nutrient inputs. In these cases, high piscivory leads to low planktivory and high herbivore biomasses, which reduce the biomass of nanoplankton. At medium phosphorus input, the response to piscivory was unimodal, increasing from low to medium piscivory and decreasing from medium to high piscivory. Similar unimodal responses occur in other lake ecosystem models (Carpenter and Kitchell 1984, 1987) and in enclosure experiments in lakes (Bergquist and Carpenter 1986).

Mean summer biomass of blue-green algae is low at all piscivory levels when phosphorus input is low (Figure 22.3). At medium and high phosphorus loading, the highest biomass of blue-green algae occurs at intermediate levels of piscivory. At high levels of piscivory, high grazer densities constrain the biomass of blue-green algae. At low piscivory levels, grazing is negligible and algal composition is dictated by competitive interactions. The high growth rates and low half-saturation coefficients of the nanoplankton allow them to dominate when grazing rates are low.

## Discussion

This modeling exercise corroborates and quantifies the well-established argument that reduced nutrient loads will reduce algal biomass in Lake Mendota. Significant reduction of algal biomass by predation requires the highest levels of piscivory. A modest increase in piscivory (e.g., from low to medium scenarios) actually increased levels of blue-green algae when phosphorus inputs were medium or high. The conclusion that extreme fish manipulations are needed to affect water quality is consistent with the empirical and theoretical arguments of Kitchell et al. (1988), Carpenter and Kitchell (1988), and Carpenter (1989). Johnson et al. (Ch. 16) and Post and Rudstam (Ch. 19) discuss the challenges of achieving sufficiently high piscivore densities in Lake Mendota.

At medium piscivory, variations in nutrients cause maximal variation in blue-green algal biomass. In heavily fished lakes like Lake Mendota, the



**Figure 22-3.** Mean summer biomass ( $\mu\text{g C L}^{-1} \text{d}^{-1}$ ) versus piscivory level for the three nutrient loading scenarios. *Daphnia* biomass (upper panel), nanoplankton biomass (middle panel), and blue-green algal biomass (lower panel) are presented.

medium-piscivory scenario may approximate the typical long-term condition (Johnson and Staggs, Ch. 17). Nutrient inputs, on the other hand, have varied widely (Lathrop, Ch. 6). Therefore we would expect blue-green algal biomass to show higher summer-to-summer variability than *Daphnia* biomass. The 14-year record analyzed by Lathrop and Carpenter (Ch. 7 and 8) supports this inference. Coefficients of variation among summers (June–August) are 112% for blue-green algal biomass and 48% for *Daphnia* biomass.

Breaking the modeling problem into modules and exchanging scenarios among them was an efficient approach that facilitated rapid model development. However, the resulting structure allowed us to transfer information vertically among modules in only a limited number of ways. For a given module, the other modules are forcing functions, even though a dynamic interaction is sometimes more appropriate. The different hierarchical levels represented by the modules are not as neatly separated in the lake. Separation may misrepresent time lags and feedbacks among state variables with different return times placed in different modules. For example, with the module approach it is difficult to let year class formation in fish be dependent on food supply.

We recognize that it is now time to develop a single, whole-ecosystem model for Lake Mendota, integrated from fish to phosphorus. Analogues exist in whole-system models for a variety of other lakes (Scavia and Robertson 1979; Jorgenson 1983; Chapra and Reckhow 1983; Bartell et al. 1988). The progress in estimating parameters, testing model structures, and analyzing interactions summarized in these chapters provides a valuable foundation for the larger model we envision.

Key questions about the sustainability of desired food web structures in Lake Mendota revolve around the role of the littoral zone. Aquatic macrophytes are the subject of intensive management (Nichols et al., Ch. 9), which is often independent of fishery management efforts. If biomanipulation alters the long-term average clarity of Lake Mendota, we can expect expansion of macrophyte beds (Gulati et al. 1990). Because the macrophyte beds provide fishes with invertebrate food resources and a refuge from predation, littoral zone dynamics probably have important effects on the stability and variability of fish dynamics in the lake. The next generation of models for Lake Mendota should address fish populations in relation to the dynamic nature of littoral vegetation in the lake.

Our analysis has dealt with mean summer conditions because we were constrained by time and the structures of the models. It is important to recognize that variation on shorter time scales is substantial and, in the case of algal blooms, has significant impacts on water clarity and the public's perception of the lake. The more detailed analyses of previous chapters identify two important modes of variability, one derived from the instabilities of fish populations, the other from the instabilities of nutrient–alga–grazer dynamics.

The variability of fish population dynamics is renowned (Steele and Henderson 1984; Strong 1986; Hall 1988). Numerous modes of oscillatory dynamics are known from age- and size-structured fish population models that include nonlinear terms for density-dependent recruitment or cannibalism (Levin and Goodyear 1980; Carpenter 1988; Caswell 1989). Post and Rudstam (Ch. 19) show that a similar range of dynamics emerges from the piscivory module, in which size-dependent prey vulnerability and temperature-dependent consumption rates are considered explicitly on a daily time step.

In Lake Mendota we can expect substantial year-to-year variance in walleye and yellow perch stocks, even under a constant climatic regime (Post and Rudstam, Ch. 19). The trophic cascade transmits this variance to planktonic trophic levels at the same frequency, but with reduced amplitude (Carpenter 1988, 1989; Carpenter and Leavitt 1991). Attenuation of the variance results from compensatory interactions at the middle of the food web. Examples include replacement of vulnerable zooplankton species by smaller animals less susceptible to predation, and the capacity of invertebrate predators with rapid numerical responses to suppress herbivore populations (Luecke et al., Ch. 20). Post and Rudstam (Ch. 19) argue that planktivore biomass and the oscillatory tendencies of the walleye–yellow perch system can be suppressed only with rather high stocking levels or rather severe restrictions on harvest.

The interaction of phosphorus, phytoplankton, and grazers is destabilized by increases in phosphorus and planktivory, leading to dominance by blue-green algae and low densities of edible nanoplankton and grazers (Carpenter, Ch. 23). The instabilities of this system of equations underlie the seasonal dynamics modeled by Vanni et al. (Ch. 21). Time series analysis reveals a predator–prey oscillation of edible algae and *Daphnia* in Lake Mendota (Lathrop and Carpenter, Ch. 8). Springs with high concentrations of edible algae produce high peaks in *Daphnia* concentration, followed by severe crashes of *Daphnia* and high blue-green concentrations during summer (Lathrop and Carpenter, Ch. 8). The patterns in the long-term observations support the syndrome of destabilization followed by blue-green algal blooms that emerges from the simulation models.

Collectively, the models presented here suggest that we should anticipate highly variable behavior from Lake Mendota. Evidence of stability would surprise us. Even under the most rigorous phosphorus and food web controls we can envision, occasional severe blooms of blue-green algae will occur. It is impossible to infer the state of the lake from an isolated bloom or even a year of monitoring data. Continued monitoring is absolutely essential to assessing the lake’s trajectory and improving our capacity to model and forecast the likely consequences of management actions.

*Acknowledgments.* We are grateful for the support of the Wisconsin Department of Natural Resources (WDNR) grant NRG-90785.

## References

- Bartell SM, Brenkert AL, O'Neill RV, Gardner RH (1988) Temporal variation in regulation of production in a pelagic food web model. In Carpenter SR (ed) *Complex interactions in lake communities*, Springer-Verlag, New York, pp 101–118
- Bergquist AM, Carpenter SR (1986) Limnetic herbivory: Effects on phytoplankton populations and primary production. *Ecology* 67:1351–1360
- Carpenter SR (ed) (1988) *Complex interactions in lake communities*. Springer-Verlag, New York
- Carpenter SR (1989) Replication and treatment strength in whole-lake experiments. *Ecology* 70:453–463
- Carpenter SR, Kitchell JF (1984) Plankton community structure and limnetic primary production. *Am. Nat.* 124:159–172
- Carpenter SR, Kitchell JF (1987) The temporal scale of variance in limnetic primary production. *Am. Nat.* 129:417–433
- Carpenter SR, Kitchell JF (1988) Consumer control of lake productivity. *BioScience* 38:764–769
- Carpenter SR, Leavitt PR (1991) Scales of temporal variation in a paleolimnological record. *Ecology* 72:277–285
- Caswell H (1989) *Matrix population models*. Sinauer Associates, Sunderland, Massachusetts
- Chapra SC, Reckhow KH (1983) *Engineering approaches for lake management*. Vol. 2: Mechanistic modeling. Butterworths, Boston
- Gulati RD, Lammens EHRR, Meijer M-L, van Donk E (eds) (1990) *Biomanipulation, tool for water management*. Kluwer Academic Publishers, Dordrecht
- Hall CAS (1988) An assessment of several of the historically most influential theoretical models used in ecology and of the data provided in their support. *Ecol. Modelling* 42:5–31
- Jorgensen SE (1983) *Application of ecological modelling in environmental management*. Elsevier Scientific Publishers, Amsterdam
- Kitchell JF, Bartell SM, Carpenter SR, Hall DJ, McQueen DJ, Neill WE, Scavia D, Werner EE (1988) Epistemology, experiments, and pragmatism. In Carpenter SR (ed) *Complex interactions in lake communities*, Springer-Verlag, New York, pp 263–280
- Levin SA, Goodyear CP (1980) Analysis of an age-structured fishery model. *J. Math. Biol.* 9:245–274
- O'Neill RV, DeAngelis DL, Waide JB, Allen TFH (1986) *A hierarchical concept of ecosystems*. Princeton University Press, Princeton, New Jersey
- Scavia D, Robertson A (1979) Perspectives on lake ecosystem modeling. *Ann Arbor Science*, Ann Arbor, Michigan
- Steele JH, Henderson EW (1984) Modeling long-term fluctuations in fish stocks. *Science* 224:985–987
- Strong DR (1986) Density vagueness: Abiding the variance in the demography of real populations. In Diamond J, Case TJ (eds) *Community ecology*, Harper and Row, New York, pp 257–268



**Plate 8.** A Secchi disk is used to indicate water transparency during an intense bloom of blue-green algae.

# 23

## Destabilization of Planktonic Ecosystems and Blooms of Blue-Green Algae

**Stephen R. Carpenter**

### Introduction

Blooms of blue-green algae are a serious water quality problem in many productive lakes (Plate 8; Cooke et al. 1986; Paerl 1988). Causes of blue-green blooms involve many factors, including mixing, trace metals, macronutrients, dissolved organic matter, microbial activity, and herbivory (Paerl 1988; Carpenter 1989). Of the many factors implicated, phosphorus loading and grazing are especially pertinent to management of nuisance blue-green blooms (Cooke et al. 1986; Shapiro and Wright 1984). The role of phosphorus is firmly established. Blue-green blooms can be triggered by adding phosphorus to whole lakes (Schindler 1988). While low nitrogen to phosphorus ratios favor blue-green dominance (Smith 1983), these nutrients commonly covary (Carpenter et al. 1990) and phosphorus is generally the more critical element for ecosystem dynamics (Schindler 1977).

Effects of grazers on blue-green algae are more variable than those of phosphorus (Lathrop and Carpenter, Ch. 7 and 8). In several whole-lake food web perturbations, large grazers have suppressed blue-green algae (Shapiro and Wright 1984; Carpenter et al. 1987; Vanni et al. 1990). Grazers are clearly effective in fishless ponds (Hrbacek 1962) and in lakes during spring clear-water periods (Lampert et al. 1986; Benndorf et al. 1988). Yet, in other cases large grazers do not effectively control blue-green algae (Benndorf 1990). Benndorf (1990) suggests a threshold phosphorus loading above which grazing cannot suppress blue-green algal blooms. At this threshold, ecosystem dynamics undergo a discontinuous

change. Current ideas of trophic cascading (Carpenter and Kitchell 1988) and predation–nutrient interactions in lakes (McQueen et al. 1986; Carpenter et al. 1990) do not address such discontinuities. This chapter derives a model, similar to earlier models of the trophic cascade (Carpenter and Kitchell 1987), to explore the possibility of discontinuous changes in ecosystem stability.

My goal is a testable, relatively simple model of plankton dynamics capable of predicting algal blooms in lakes. The model incorporates biotic properties of the algae and characteristics of the lake ecosystem. In developing the model, I attempted to simulate plankton dynamics using a relatively small number of directly measurable parameters. The number of parameters was reduced by focusing on selected strong interactions (Paine 1980) and taking advantage of allometric relationships among parameters (Peters 1983). The resulting simplicity facilitates understanding and testing. This paper analyzes the conditions under which blooms are expected, demonstrates qualitative correspondence between dynamics of the model and actual lakes, interprets recent events in Lake Mendota, shows where improved parameter estimates are needed, and suggests experimental work necessary to evaluate the model.

## The Model

Four state variables are included (Figure 23.1A): herbivorous zooplankton ( $Z$ ), nanoplankton ( $A$ , relatively small, edible phytoplankton), blue-green algae ( $B$ , relatively large, less edible, bloom-forming phytoplankton), and phosphorus ( $P$ ). The model is intended to represent algal dynamics in a mixed water column, such as the epilimnion of a stratified lake or the entire water mass of a shallow lake. All state variables are expressed as phosphorus concentrations, and phosphorus is the currency of the model. In this paper, algal phosphorus was converted to chlorophyll assuming a ratio of unity by mass (Reynolds 1984). Zooplankton phosphorus was converted to biomass assuming a tissue concentration of 1.8% P (Peters and Rigler 1973).

Model results (see below) show that dominance by blue-green algae hinges on the stability of the phosphorus–nanoplankton–zooplankton interaction. The simpler, three-state variable subsystem (Figure 23.1B) will be explained first. Dynamic equations are:

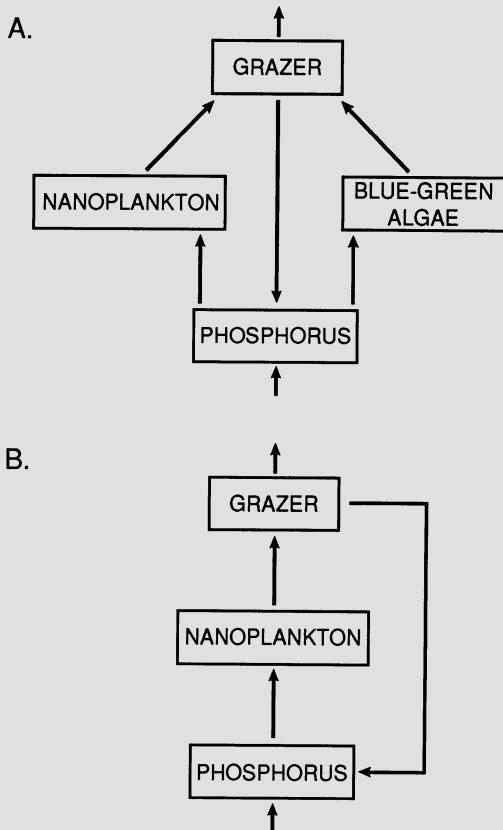
$$dZ/dt = a\phi AZ - DZ \quad (1)$$

$$dA/dt = A\Gamma\sigma - sA - \phi AZ \quad (2)$$

$$dP/dt = I - A\Gamma\sigma + E\phi AZ - QP \quad (3)$$

where  $a$  is assimilation efficiency,  $D$  is zooplankton death rate,  $s$  is nanoplankton sinking rate,  $I$  is phosphorus input rate,  $E$  is the fraction of

**Figure 23-1.** A. State variables and fluxes of the four-state variable model. B. State variables and fluxes of the three-state variable model.



ingested phosphorus that is excreted by zooplankton, and  $Q$  is the outflow rate of water from the lake. The feeding function is

$$\phi = c / [1 + cTA] \quad (4)$$

where  $c$  is attack rate and  $T$  is handling time. The self-shading function limiting algal growth is

$$\sigma = 1 - (A/U) \quad (5)$$

where  $U$  is maximal algal biomass. The algal growth function is

$$\Gamma = VP/(H + P) \quad (6)$$

where  $V$  is maximum growth rate and  $H$  is the phosphorus concentration at which growth is  $V/2$ . Mass balance requires that

$$1 \geq a + E \quad (7)$$

The fraction of phosphorus that is ingested but not assimilated or excreted ( $1 - a - E$ ) is assumed to be egested and lost to the system by sedimentation.

The four-state variable model (Figure 23.1A) adds the dynamics of B, the blue-green algae, to the above equations.

$$dZ/dt = Z\phi'(a_A c_A A + a_B c_B B) - DZ \quad (8)$$

$$dA/dt = A\Gamma_A\sigma - s_A A - c_A\phi'AZ \quad (9)$$

$$dB/dt = B\Gamma_B\sigma - s_B B - c_B\phi'AZ \quad (10)$$

$$dP/dt = I - A\Gamma_A\sigma - B\Gamma_B\sigma + EZ\phi'(c_A A + c_B B) - QP \quad (11)$$

$$\phi' = 1 / [1 + c_A T_A A + c_B T_B B] \quad (12)$$

$$\sigma = 1 - [(A + B)/U] \quad (13)$$

$$\Gamma_A = V_A P / (H_A + P) \quad (14)$$

$$\Gamma_B = V_B P / (H_B + P) \quad (15)$$

The subscripts A and B denote parameters or functions specific to nanoplankton and blue-green algae, respectively. Mass balance conditions analogous to equation 7 pertain to  $a_A$  and  $a_B$ .

The parameters of equations 1–15 were derived from six master parameters: P input ( $I$ ), water outflow rate ( $Q$ ), algal diameter ( $d'$ ) or volume ( $v'$ ), zooplankton length ( $L$ ), zooplankton death rate ( $D$ ), and depth of the epilimnion ( $Z_E$ ). Unless otherwise indicated, all numerical results in this paper employed the  $Z_E$  and outflow rate of Lake Mendota, Wisconsin (Brock 1985; Lathrop, Ch. 6). The effects of the other master parameters were determined by varying them systematically across ranges of values known from lakes. The parameter  $I$  represents P influx to the epilimnion from all sources, including allochthonous input, input from littoral sediments, vertical eddy diffusive flux, and entrainment flux by thermocline migration. Methods for measuring  $I$  are given by Stauffer (1985, 1987; Stauffer and Lee 1973). During summer in Wisconsin lakes,  $I$  ranges from about  $0.1 \mu\text{g P liter}^{-1} \text{d}^{-1}$  in oligotrophic northern lakes (Carpenter, unpubl. data) to as much as  $4 \mu\text{g P liter}^{-1} \text{d}^{-1}$  in eutrophic southern lakes (Stauffer 1985, 1987; Stauffer and Lee 1973). Typical diameters of lake nanoplankton are 2 to  $5 \mu\text{m}$  (Reynolds 1984). Colonies of bloom-forming blue-green algae range from ca. 50 to 2,000  $\mu\text{m}$  in diameter (Reynolds 1984). Mean lengths of crustacean grazers in lakes range from 0.3 to 2.5 mm (Carpenter et al. 1990). Crustacean death rates are typically between 0.05 and  $0.3 \text{ d}^{-1}$  (Downing and Rigler 1984; Threlkeld 1976).

Algal maximum growth rate  $V$  was estimated from

$$V = 1.855 - 0.266 \log v' \quad (16)$$

(Reynolds 1984). Half-saturation coefficients  $H$  are proportional to twice the log of cell diameter (Malone 1980). While  $H$  also depends on other factors, for the purposes of this model the main point is that colonial blue-green algae have higher  $H$  than nanoplankton. This relationship can be achieved by scaling  $H$  with algal size. For a mixed assemblage

dominated by nanoplankton (log diameter ca. 1.08),  $H = 14$  (Brown et al. 1978). Therefore, I used

$$H = 12.96 \log d' \quad (17)$$

The resulting half-saturation coefficients are within the range of 11 to  $364 \mu\text{g PL}^{-1}$  found in culture studies (Reynolds 1984).

Algal maximum biomass  $U$  (as chlorophyll) was obtained from Reynolds' (1984) equation

$$U = [1.04(P_{\text{MAX}}/R)/(\varepsilon_s Z_E)] - (\varepsilon_w + \varepsilon_p) \quad (18)$$

The ratio  $P_{\text{MAX}}/R$  ranges from 7 to 25; a value of 16 was used in calculations reported here. The chlorophyll-specific light extinction coefficient of algal suspensions ( $\varepsilon_s$ ) is 0.017 for a wide range of lakes (Reynolds 1984; Brock 1985; Elser 1987). Across a variety of Wisconsin lakes, light extinction by water and nonalgal substances ( $\varepsilon_w + \varepsilon_p$ ) is about 0.5 (Brock 1985; Elser 1987), which contributes negligibly to equation 18.

Sinking rates ( $s$ ) were obtained from Stokes' law as applied to phytoplankton in a mixed water column by Reynolds (1984):

$$s = 2g(d'/2)^2\delta/9\eta FZ_E \quad (19)$$

where  $g$  is the gravitational constant ( $9.8 \text{ m s}^{-2}$ ) and viscosity  $\eta$  is  $0.001 \text{ kg m}^{-1} \text{ s}^{-1}$ . Calculations reported here assume a density difference between nanoplankton and water of  $\delta = 100 \text{ kg m}^{-3}$  and a form resistance coefficient  $F = 1.0$ . Under these assumptions, for  $d'$  in  $\mu\text{m}$ ,  $Z_E$  in m, and  $s$  in  $\text{d}^{-1}$ , equation 19 reduces to

$$s = 0.0188(d'/2)^2/Z_E \quad (20)$$

Equation 20 yields reasonable sinking loss rates for nanoplankton less than about  $20 \mu\text{m}$  in diameter. The gelatinous investments and flotation capabilities of colonial blue-green algae cause them to have sinking rates substantially lower than equation 20 would predict (Reynolds 1984). Apparently natural selection has acted to stabilize the sinking rates of blue-green colonies at fairly low values. A uniform sinking loss rate of  $0.05 \text{ d}^{-1}$  was used for blue-green algae.

Parameters of the feeding function  $\phi$  were based on the empirical equations of Peters and Downing (1984). The attack rate  $c$  was calculated from feeding rates at a very low algal concentration,  $0.1 \text{ mg wet mass/L}$ . The handling time  $T$  was calculated from feeding rates at a saturating food concentration,  $45 \text{ mg wet mass/L}$ . From equation 7 of Peters and Downing (1984), the feeding rate on cells of volume  $v'$  is

$$f = -0.719 + 0.587 \log W - 0.165 (\log v')^2 + 0.887 \log v' \quad (21)$$

where animal dry mass  $W = 9.86 L^{2.1}$ . The attack rate in units of  $(\text{zoopl. } P)^{-1} \text{ d}^{-1}$  is

$$c = 10^{(f-0.486)} * 0.556 / W \quad (22)$$

The handling time  $T$  in units of (zoopl.  $P$ ) d (algal  $P$ ) $^{-1}$  is

$$T = W / [10^{(f+1.317)} * 0.178] \quad (23)$$

Equations 22 and 23 imply that blue-green algae experience lower attack rates and longer handling times than nanoplankton. Simulations reported here assume an excretion coefficient  $E$  of 0.4 (Peters and Rigler 1973). I assumed that 10% of nanoplankton P was egested, so by mass balance  $a = 1.0 - 0.1 - E = 0.5$  for nanoplankton. This value is smaller than assimilation efficiencies for nanoplankton carbon, because carbon is not excreted. I assumed that 40% of blue-green algal P was egested, so by mass balance  $a_B = 0.2$ . This is within the wide range (10–100%) of carbon assimilation efficiencies reported for crustaceans feeding on blue-green algae (Schindler 1968; Arnold 1971; Lampert 1977; Holm et al. 1983).

## Numerical Analyses

To verify that the model could approximate the dynamics of lakes, simulations were performed for oligotrophic Paul Lake and eutrophic Lake Mendota, Wisconsin. These represent the range of conditions that the model should simulate if it is to be useful. For Paul Lake in 1985,  $Z_E = 3.7\text{ m}$ ,  $Q = 0.0003\text{ d}^{-1}$ ,  $I = 0.5\mu\text{g L}^{-1}\text{ d}^{-1}$ ,  $d' = 5\mu\text{m}$  for nanoplankton and  $75\mu\text{m}$  for blue-green colonies,  $L = 1.1\text{ mm}$ , and  $D = 0.1\text{ d}^{-1}$  (Carpenter et al. 1987; Carpenter, unpubl. data). For Lake Mendota in 1979,  $Z_E = 10.2\text{ m}$ ,  $Q = 0.0005\text{ d}^{-1}$ ,  $I = 2\mu\text{g L}^{-1}\text{ d}^{-1}$ ,  $d' = 5\mu\text{m}$  for nanoplankton and  $75\mu\text{m}$  for blue-green colonies,  $L = 0.95\text{ mm}$ , and  $D = 0.1\text{ d}^{-1}$  (Brock 1985; Lathrop, Ch. 6; Lathrop and Carpenter, Ch. 7). The estimate of  $I$  for Lake Mendota is a composite of the mean external loading and sedimentation rates for 1976 and 1977 (Brock 1985; Lathrop, Ch. 6) and vertical flux rates for July and August 1971 (Stauffer and Lee 1973).

To establish the relationship between stability of the model and blue-green blooms, further simulations of Lake Mendota were calculated. For the purposes of this paper, a blue-green algal bloom condition was defined to occur when blue-green algae comprised more than three-quarters of a total chlorophyll concentration in excess of  $30\mu\text{g/L}$ . Days of bloom per growing season (150 d) were computed for a range of P input rates and grazer sizes.

Stability of the three-state variable model was determined by computing eigenvalues of the Jacobian matrix around the equilibria. For a given set of parameters, the equilibrium  $Z^*$ ,  $A^*$ ,  $P^*$  was obtained by setting equations 1–3 to zero:

$$Z^* = (\Gamma\sigma - s)/\phi \quad (24)$$

$$A^* = D/(ac - DcT) \quad (25)$$

$$0 = -QP^{*2} + P^*(I - QH - A^*\sigma V + EA^*V\sigma - EA^*S) \\ + IH - EA^*SH \quad (26)$$

$P^*$  was set equal to the positive root of equation 26. The eigenvalues were obtained numerically by the QR method after converting the Jacobian matrix to Hessenberg form (Press et al. 1986).

Stability of the system was assessed using the eigenvalues and results of long-term simulations. Dynamics were assigned to one of three categories. Asymptotic stability occurred when the largest eigenvalue was real and negative, and the system approached equilibrium monotonically. Damped oscillations occurred when the system oscillated with decreasing amplitude as it approached equilibrium. The largest eigenvalue was complex, with a negative real part. Unstable dynamics occurred when the system did not approach equilibrium and oscillated indefinitely. The largest eigenvalue was complex, with a positive real part. I will refer to these dynamics as unstable, while recognizing that the oscillations may approach a limit cycle or strange attractor.

Sensitivity analyses were performed to determine the effects of errors in parameters on apparent stability of the system. Sensitivity analyses followed the general procedures of Bartell et al. (1988). Each sensitivity analysis was based on 500 randomly chosen parameter sets. In each parameter set, values were selected at random from normal distributions with means equal to the nominal values and coefficients of variation of 5%. The real part of the dominant eigenvalue was calculated for each parameter set. The dominant eigenvalues were then regressed against the parameter values. The relative partial sum of squares (RPSS) for each parameter value is the percentage of variation in the eigenvalue explained by that parameter after effects of other parameters have been accounted for. Thus RPSS measures the relative improvement in estimation of the eigenvalue that could be obtained by improved precision in measurement of the parameter (Bartell et al. 1988). Pearson product-moment correlations between the eigenvalues and the parameters were also calculated.

## Results

The four-state variable model yielded reasonable simulations of Paul Lake in 1985 and Lake Mendota in 1979 (Table 23.1). In view of the approximations employed to estimate the parameters and the variability of the field measurements, the correspondence is satisfactory. More rigorous tests of the model are possible and will be informative (see

**Table 23-1.** Comparison of model results with limnological data from eutrophic Lake Mendota (1979; Brock 1985) and oligotrophic Paul Lake (1985; Carpenter et al. 1987).

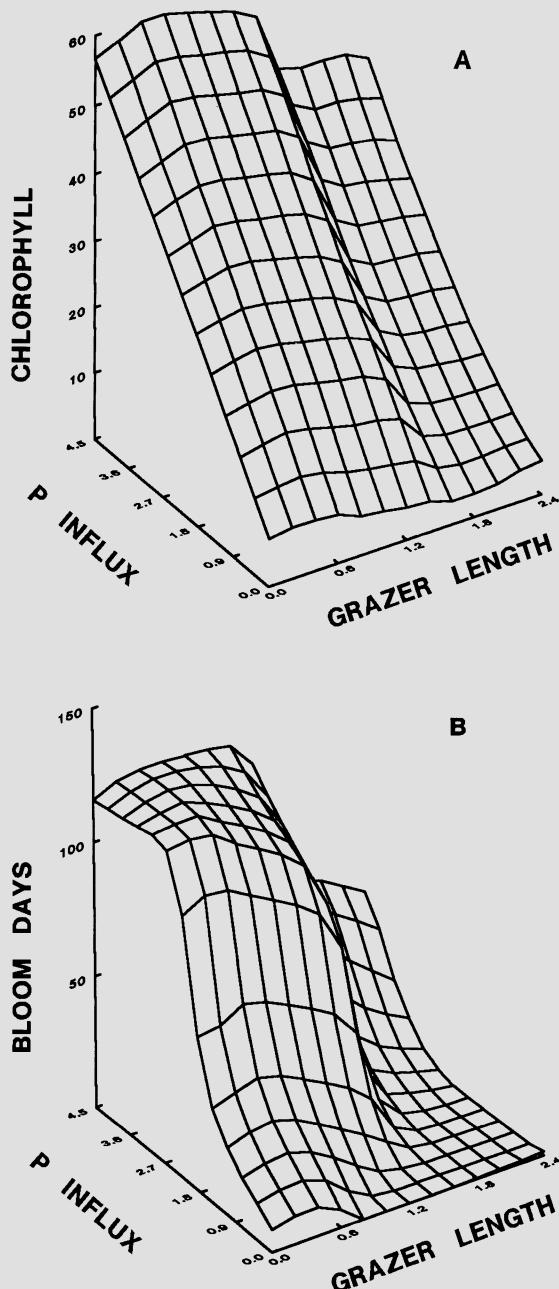
Variable	Mendota		Paul	
	Model	Lake	Model	Lake
Total P ( $\mu\text{g/L}$ )	42	52	13	15
Chlorophyll ( $\mu\text{g/L}$ )	34	33	3.5	3.1
% of summer days with blue-green algal blooms	63	82	0	0
Grazer biomass ( $\mu\text{g/L}$ )	103	95	302	211

Discussion). For the purposes of this chapter, Table 23.1 verifies that the model produces reasonable values across a range of lake trophic states.

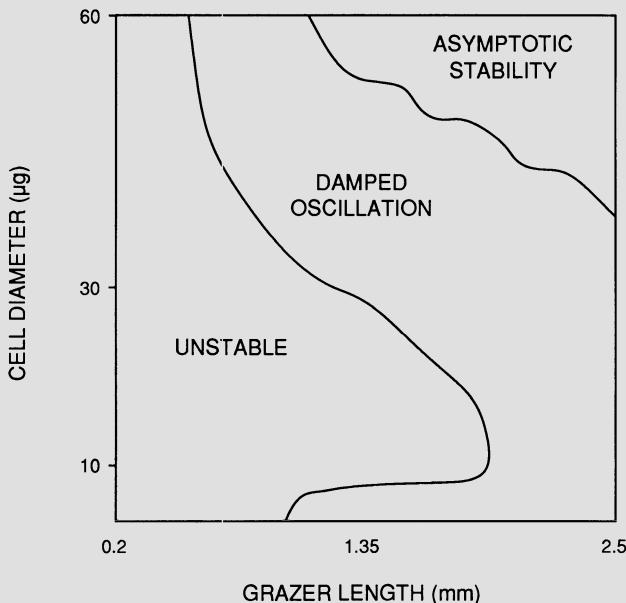
In the four-state variable model, mean summer chlorophyll concentration rises steadily as P influx rises (Figure 23.2A). At any given P influx rate, chlorophyll declines as grazers become larger. The relatively planar shape of the chlorophyll response surface contrasts with the changing slopes of the bloom response surface (Figure 23.2B). Bloom days per summer are quite low for the region with P influx below  $1.8 \mu\text{g L}^{-1} \text{d}^{-1}$  and grazers larger than 1.2 mm. As P influx rises from 1.8 to  $2.7 \mu\text{g L}^{-1} \text{d}^{-1}$  and grazer length decreases from 1.6 to 1.2 mm, bloom days per summer rise steeply, reaching a plateau in the region where P influx is relatively high and grazers are relatively small.

In regions of parameter space where blooms are rare, the competitive superiority of the nanoplankton (higher  $V$ , lower  $H$ ; Tilman 1977) is asserted, and they predominate (Figure 23.2B). In regions of parameter space where blooms are common, blue-green algae rise to dominance during times when nanoplankton concentrations and zooplankton growth rates are declining (Carpenter 1989). The zooplankton become limited by the low food quality of the prevailing blue-green algae (low ingestion and assimilation rates). Nutrients are sequestered in the blue-green biomass. Low free nutrient availability and grazing by the remaining zooplankton hold the nanoplankton at low levels. In lakes, declining nanoplankton concentrations and declining zooplankton growth rates commonly occur at the end of the spring clear-water phase, and blue-green dominance often begins at that time (Reynolds 1984; Brock 1985). Some evidence exists that blue-green algae invade the water column from benthic colonies at the end of the clear-water phase when prospects for dominance of the phytoplankton are optimal (Lynch 1980; Trimbee and Prepas 1988; Carpenter 1989).

In studying these simulations, I noticed that blooms were rare when the nanoplankton and grazers were relatively stable, and that blooms commonly followed severe oscillations of nanoplankton and grazers (Carpenter 1989). Apparently destabilization of the nutrient–nanoplankton–grazer



**Figure 23-2.** Results of the four-state variable model. A. Mean summer chlorophyll ( $\mu\text{g L}^{-1}$ ) as a function of P input ( $I$ ,  $\mu\text{g P L}^{-1} \text{d}^{-1}$ ) and grazer length ( $L$ , mm). B. Days of blue-green algal bloom per summer as a function of P input ( $I$ ) and grazer length ( $L$ ). Where the days of bloom per summer exceed about 10, the three-state variable subsystem is unstable (class 4, Table 23.1).

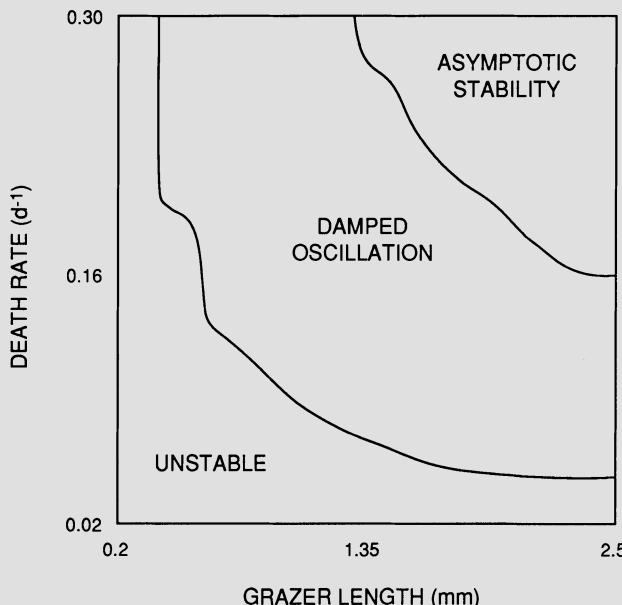


**Figure 23-3.** Model dynamics as a function of grazer length ( $L$ ) and cell diameter ( $d'$ ) in the three-state variable model. Regions where the model exhibits instability, damped oscillations, and asymptotic stability are shown.

interaction led to blue-green algal blooms. This idea was explored by analyzing the stability properties of the three-state variable model in detail.

In the three-state variable model, no positive equilibria occurred for cell diameters larger than  $60\text{ }\mu\text{m}$  (Figure 23.3). Grazing rates on large phytoplankters are too low to sustain the herbivore population. However, the sizes of actual phytoplankton assemblages are well within the range where positive equilibria occurred in the model (Reynolds 1984). For example, in three phytoplankton communities studied for 3 years each by Elser and Carpenter (1988), mean diameter of all algae ranged from 7.4 to  $18.8\text{ }\mu\text{m}$ , and mean diameter of algae considered edible never exceeded  $10\text{ }\mu\text{m}$ .

Grazer length and death rate interact to influence system stability (Figure 23.4). The system is stable for moderate to large grazer lengths and death rates. With small grazers and low death rates, the system is oscillatory. Size-selective predation by fishes (Brooks and Dodson 1965) tends to destabilize the system. Fish predation increases the death rate of large grazers, thereby causing mean grazer size to decline. Since small grazers suffer lower losses to fish predation, death rates drop. The net effect is to move the system from a relatively stable domain (large grazer

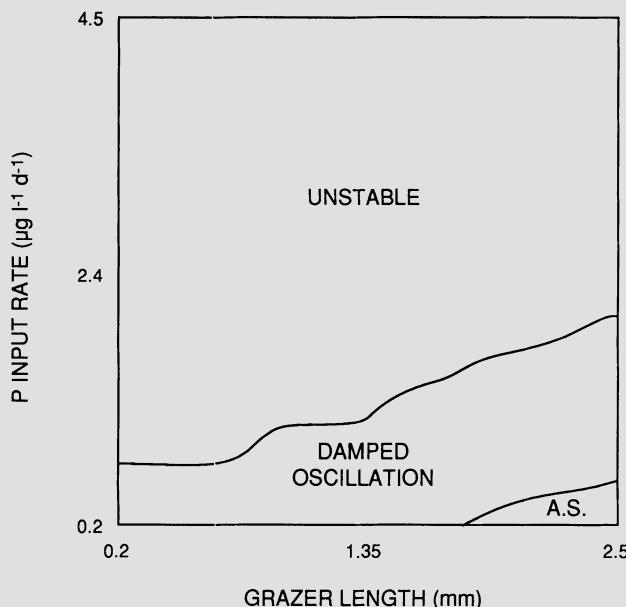


**Figure 23-4.** Model dynamics as a function of grazer death rate ( $D$ ) and grazer length ( $L$ ) in the three-state variable model. Regions where the model exhibits instability, damped oscillations, and asymptotic stability are shown.

lengths and death rates) to a relatively unstable one (small grazer lengths and death rates).

System stability responds jointly to P input and grazer length (Figure 23.5). For very low P inputs, primary production is insufficient to sustain grazers. This effect is important in ultraoligotrophic lakes (Neill 1988). In Wisconsin lakes, P fluxes are large enough to sustain grazers, and analyses reported here are confined to this range of trophic conditions. The system is stable for the lowest P inputs considered. The onset of oscillations occurs at higher P inputs as grazer size increases. Systems with relatively large grazers can maintain stable plankton dynamics in the face of relatively large P inputs. Large grazers are prevalent in systems with little size-selective planktivory by fishes. Such lakes are predicted to have stable plankton dynamics at higher P loads than lakes with abundant planktivores.

Sensitivity analyses were calculated for three regions of Figure 23.5: a region of asymptotic stability (P input  $0.6 \mu\text{g L}^{-1} \text{d}^{-1}$  and grazer length 2.1 mm), a region of damped oscillations (P input  $1.0 \mu\text{g L}^{-1} \text{d}^{-1}$  and grazer length 1.5 mm), and an unstable region (P input  $3 \mu\text{g L}^{-1} \text{d}^{-1}$  and grazer length 1.0 mm). In Table 23.2, negative correlations mean that system stability increases as parameter values increase. Positive correlations mean that system stability decreases as parameter values increase.



**Figure 23-5.** Model dynamics as a function of P input ( $I$ ) and grazer length ( $L$ ) in the three-state variable model. Regions where the model exhibits instability, damped oscillations, and asymptotic stability (A.S.) are shown.

The RPSS measures the percentage of variation in system stability accounted for by variation in each parameter.

Under stable conditions, control of system stability was distributed fairly evenly over five parameters ( $H$ ,  $V$ ,  $c$ ,  $a$ , and  $D$ ). In the region of damped oscillations, P input and grazer attack rate ( $c$ ) had relatively powerful effects on system stability. P input influenced stability only in the region of damped oscillations, where increased P input was strongly destabilizing. In the unstable region, control of system stability shifted to maximum algal growth rate ( $V$ ) and handling time ( $T$ , the inverse of maximum feeding rate). Four parameters had negligible effects in all scenarios:  $Q$ ,  $s$ ,  $E$ , and  $U$ . Effects of  $H$  were relatively weak.

## Discussion

### Relationship to Previous Theory

The results of my analyses add to those from earlier studies of destabilization in simpler producer-consumer systems (Rosenzweig 1971; Steele and Henderson 1981; Antonios and Hallam 1984). Rosenzweig (1971) studied destabilization in six different two-state variable models (producer-

**Table 23-2.** Results of sensitivity analyses to determine effects of parameter variations on the dominant eigenvalue. Sensitivities are presented for three regions of parameter space (see Figure 23.5): (1) asymptotically stable, P input  $0.6 \mu\text{g L}^{-1} \text{d}^{-1}$  and grazer length 2.1 mm; (2) damped oscillations, P input  $1.0 \mu\text{g L}^{-1} \text{d}^{-1}$  and grazer length 1.5 mm; and (3) unstable, P input  $3 \mu\text{g L}^{-1} \text{d}^{-1}$  and grazer length 1.0 mm. For each parameter set, correlation coefficients between parameters and eigenvalues and relative partial sums of squares (RPSS) are presented. Where no RPSS is shown, RPSS < 0.1%.

Parameter	Stable		Damped Oscillation		Unstable	
	r	RPSS	r	RPSS	r	RPSS
<b>Nutrient fluxes</b>						
$I$ , input	0.163	1.6	0.551	30.0	0.030	–
$Q$ , outflow	-0.012	–	0.031	–	-0.003	–
<b>Algal dynamics</b>						
$H$ , half-saturation coefficient	0.341	9.7	0.190	1.5	-0.009	–
$V$ , max. growth rate	-0.363	12.2	-0.272	6.5	0.419	20.5
$s$ , sinking rate	0.062	–	-0.083	–	0.093	–
$U$ , maximum biomass	-0.005	–	0.109	0.2	0.247	2.1
<b>Herbivory</b>						
$c$ , attack rate	0.467	13.5	0.544	27.0	0.108	2.5
$T$ , handling time	-0.071	0.2	0.128	3.8	0.595	34.3
$a$ , assimilation coefficient	0.438	15.2	0.353	11.0	-0.449	19.8
$E$ , excretion coefficient	0.021	0.1	0.234	3.1	0.006	–
$D$ , death rate	-0.333	10.3	-0.286	8.8	0.447	19.7

consumer). Arditi and Ginzburg (1989) analyzed a class of two-state variable models that included interactions among predators. Antonios and Hallam (1984) studied destabilization in a closed, three-state variable system (nutrient–producer–consumer). Like Arditi and Ginzburg (1989), they focused on effects of interactions among consumers. Their assumption of a closed system allowed them to eliminate one state variable and analyze the resultant two-state variable model.

Steele and Henderson (1981) analyzed four different herbivore–alga–nutrient models. One of their models (their Figure 4a) is identical to equations 1 and 2 of this chapter except for the presence of the sinking term in equation 2. They argued that the instabilities exhibited by this model were not characteristic of the marine system they studied. Multiple equilibria were thought to be a more realistic representation of their system. They noted that multiple stable equilibria are possible if there is interference competition among herbivores (Rosenzweig 1972; Antonios and Hallam 1984), if grazing follows a sigmoid functional response, or if the mortality term in equation 1 (this chapter) is  $-DZ^2$ .

Destabilization is a sufficient and plausible representation of the dynamics of eutrophic lakes as they pass from spring blooms of edible algae, to spring clear-water phase, to summer blooms of inedible algae. The additional assumptions required by models with alternative stable states are not necessary to explain the dynamics observed in lakes. In support of the model structure analyzed here, I argue that features necessary to stabilize herbivore–alga models (interference competition; sigmoid functional response;  $-DZ^2$  mortality; Steele and Henderson 1981) are not likely to obtain in lake food webs with planktivorous fishes and cladoceran herbivores. Interference competition is known to occur between *Daphnia* and rotifers, which differ greatly in size (Gilbert 1988). However, it is reasonable that interference among the similar-sized herbivores represented in this model could be neglected. Studies using *Daphnia* have concluded that a hyperbolic functional response is more appropriate than linear and sigmoid alternatives (Porter et al. 1982), and the assumptions that underlie the hyperbolic functional response seem appropriate to generalist filter feeders (Hassell 1978). A  $-DZ^2$  mortality term is likely if a carnivore population's density closely tracks the population density of the herbivore (Steele and Henderson 1981, p. 680). In lakes, invertebrate predators like *Leptodora* could produce such mortality terms (Luecke et al., Ch. 20), but fish predation is better represented by the  $-DZ$  term used in equation 1.

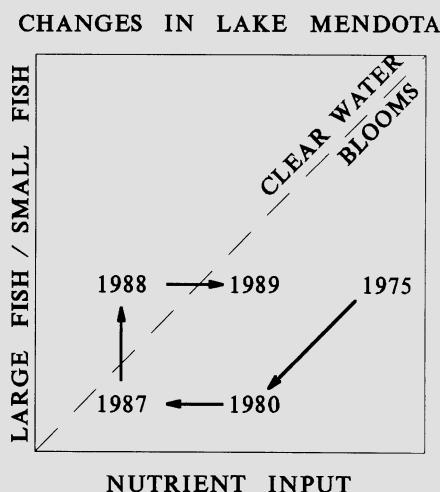
Destabilizations resulting from nutrient flux and herbivory are the most interesting from a practical standpoint, because nutrient inputs and herbivory in lake ecosystems can be managed to some extent (Cooke et al. 1986; Carpenter and Kitchell 1988). Rosenzweig (1971) showed that nutrient enrichment could destabilize producer–consumer interactions by raising carrying capacity for the prey. He also showed that, under fixed nutrient input, destabilization occurred if feeding rate of the predators increased (Rosenzweig 1972). Brauer et al. (1976) showed similar destabilizations caused jointly by enrichment and exploitation of the predator population. Steele and Henderson (1981), Antonios and Hallam (1984), and Arditi and Ginzburg (1989) elaborated the effects of predator functional response on stability. My model is also destabilized by high nutrient input and rapid grazing rates, but the mechanisms are more complicated. Since the state variables are biomass (as P), it is the mass specific feeding rates (equations 4 and 12) that are important for stability. Mass specific feeding rates [i.e., mass ingested (predator mass) $^{-1}$  d $^{-1}$ ] are highest for small zooplankton and lowest for large zooplankton (Peters and Downing 1984). Previous models based on population densities are destabilized by high per capita (i.e., mass ingested predator $^{-1}$  d $^{-1}$ ) feeding rates of the predators. Per capita feeding rates are highest for large zooplankton and lowest for small zooplankton (Peters and Downing 1984).

In four oligotrophic lakes, Walters et al. (1987) found no evidence of instability. Seasonal dynamics of phytoplankton and zooplankton over an 11-year period were best described by equilibrium models. Their results are consistent with the model presented here, which predicts equilibrial dynamics in lakes with very low P inputs.

### Implications for Lake Mendota

The general prediction that chlorophyll concentrations should rise as P input increases and grazers become smaller is consistent with evidence from many lakes (Carpenter et al. 1990). The model also predicts transitions between states of infrequent blooms and states of frequent blooms as changes occur in P input and grazer size. The interface between stable (infrequent bloom) and unstable (frequent bloom) states is analogous to Benndorf's (1990) P loading threshold, above which grazing does not effectively control phytoplankton. Benndorf's threshold is a constant P flux, independent of grazer composition. In contrast, this model predicts that the P loading threshold depends on grazer size structure. Also, the model predicts that algal blooms are preceded by destabilization of the herbivore-nanoplankter interaction. If that interaction can be stabilized, e.g., by altering grazer death rates, then a system may tolerate relatively high P loads without developing blooms (Steele and Henderson 1981).

Based on these results, I offer the following interpretations and expectations for recent and forthcoming changes in Lake Mendota (Figure 23.6). Zooplankton size structure and death rates are predictable from the ratio of piscivores to planktivores, or some similar index of fish community structure (Carpenter and Kitchell 1988). For simplicity, Figure 23.6 uses the ratio of large fishes to small fishes to represent the

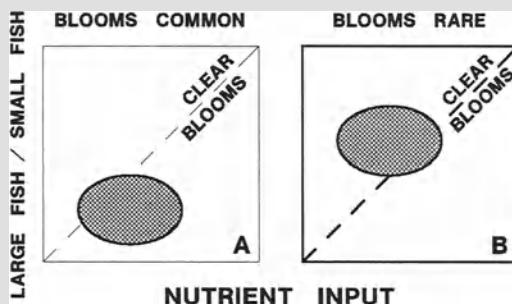


**Figure 23-6.** Simplified conceptual diagram showing changes in Lake Mendota from 1975 to 1989 on axes defined by the ratio of large fishes to small fishes and nutrient input. The dashed diagonal line shows the threshold for transitions between relatively clear water and frequent blooms.

piscivore/planktivore ratio. The demarcation between clear water and bloom conditions is a diagonal line in a plot of the fish ratio versus nutrient input. When piscivores are prevalent (so planktivory is low and grazers are large) and/or nutrient input is low, blooms are rare. Where small fish are prevalent (so planktivory is high and grazers are small) and/or nutrient input is high, blooms are common. Between 1975 and 1987, nutrient levels generally declined (Lathrop, Ch. 6) and planktivory increased with the reestablishment of cisco in the late 1970s (Magnuson and Lathrop, Ch. 11). The system remained below the diagonal line, and algal blooms were common (Lathrop and Carpenter, Ch. 7). The 1987 cisco die-off and low runoff in 1988 moved the system across the diagonal to the region of relatively clear water (Lathrop and Carpenter, Ch. 7; Vanni et al., Ch. 13). In 1989 relatively high runoff moved the system across the diagonal again into the region of frequent blooms.

This hypothesis has significant implications for the future of Lake Mendota. Fluctuations in nutrient input will continue to be no more predictable than the weather. While attempts to reduce nutrient loading must continue, we can expect high loading in some years. We can also expect the eventual resurgence of cisco populations, which have recovered from past die-offs (Magnuson and Lathrop, Ch. 11). In view of continuing uncertainty about future loading rates and fish community dynamics, pragmatic management strategies will seek to reduce the probability of blue-green blooms while recognizing that prevention is unrealistic.

The probability distribution of lake ecosystem states can be viewed as an ellipse on axes of fish community structure and nutrient loading (Figure 23.7). The probability of blue-green algal blooms is the propor-



**Figure 23-7.** Simplified conceptual diagram showing the probability distribution of possible states of Lake Mendota on the same axes used in Figure 23.6. Each ellipse contains 95% of the possible states of the lake under a given management regime. A. Low ratio of large fish to small fish. Most of the area of the ellipse is below the diagonal line, and blooms will be common in most years. B. High ratio of large fish to small fish. Most of the area of the ellipse is above the diagonal line, and clear water will prevail in most years.

tion of the ellipse that lies below the diagonal line. Fish community structure can influence the odds of blue-green blooms, independent of substantial variation in nutrient loading. When small planktivorous fishes are prevalent, the probability of blooms is relatively high (Figure 23.7A). When large piscivorous fishes are prevalent, the probability of blooms is relatively low (Figure 23.7B). During the past 15 years, fluctuations in fish community size structure have been driven almost entirely by the waxing and waning of populations of planktivorous fishes (Magnuson and Lathrop, Ch. 11). Enhancements of piscivore populations may drive the probability ellipse upward and lower the risk of blue-green algal blooms. Such increases in piscivory are the goal of this management program; prospects for success are addressed by models in other chapters of this volume.

### **Further Tests of the Model**

While the model yields reasonable simulations of Lake Mendota and general patterns that agree qualitatively with comparative and experimental ecosystem studies, more rigorous tests will be informative. My analysis suggests that certain especially influential parameters should be emphasized in future experimentation. P influx to the epilimnion during summer is measured much less frequently than P concentrations and P loading. Vertical fluxes (eddy diffusion, hypolimnetic entrainment, sedimentation) are measured infrequently, yet can be substantially more important than external loading in stratified lakes during summer (Stauffer and Lee 1973; Stauffer 1987). The attack rate ( $c$ ) strongly influences model behavior in systems on the edge of instability. Such systems are likely to provide the most informative tests of the model. Relatively little information exists on grazing rates at low food concentrations. Such data are essential for reliable estimates of attack rate. Grazer size and death rates, and maximal rates of algal growth and grazing, can exhibit substantial variation from site to site, and reliable measurements will be valuable for testing the model. Several parameters have weak effects on the dynamics, and crude estimates are probably adequate. These are the efflux rate  $Q$ , algal sinking rate  $s$ , P excretion efficiency  $E$ , maximum algal biomass  $U$ , and half-saturation coefficient  $H$ .

This paper used seasonal mean values for grazer lengths and death rates, and obtained reasonable simulations of ecosystem dynamics at seasonal time scales. At daily to weekly time scales, system dynamics may depend in part on fluctuations in grazer size and death rate driven by population dynamics, spatial patterns, and diet shifts of planktivorous fishes. The model offers the opportunity to evaluate quantitatively these short-term processes and their implications for system dynamics.

The most powerful tests of the model will come from ecosystems shifted across stability boundaries by nutrient and food chain manipula-

tions. Such experiments should engender the nutrient and grazer interactions implied by the model, and could include the rate measurements essential for quantitative tests. Removals and/or additions of fishes and nutrients are the most practical means of performing these manipulations. Since these are among the tools available to lake managers, the results may also have useful applications. Nutrient and food web processes have been conceptually separated by aquatic ecologists for several decades (Persson et al. 1988). Parallel separations exist between limnology and fish ecology, and between water quality and fisheries management (Carpenter and Kitchell 1988). The model proposed here bridges all of these gaps, and provides a quantitative vehicle for testing and elaborating the joint effects of predation and nutrient flux on lake ecosystem dynamics.

**Acknowledgments.** I thank Fred Brauer and John Steele for comments on the models and the manuscript, Peter Leavitt and Mike Vanni for detailed reviews, and Kathy Cottingham and Dan Schneider for spotting errors in the text. This research was supported by grants from the Wisconsin Department of Natural Resources (WDNR) (NRG-90785), the National Science Foundation (NSF) (BSR 86-06271), and the Graduate School of the University of Wisconsin (UW).

## References

- Antonios MN, Hallam JG (1984) Nutrient and density-dependent effects in a producer-consumer model. *Math. Biosci.* 69:243–256
- Arditi R, Ginzburg LR (1989) Coupling in predator-prey dynamics: Ratio dependence. *J. Theor. Biol.* 139:311–326
- Arnold DE (1971) Ingestion, assimilation, survival, and reproduction by *Daphnia pulex* fed seven species of blue-green algae. *Limnol. Oceangr.* 16:906–920
- Bartell SM, Brenkert AL, O'Neill RV, Gardner RH (1988) Temporal variation in regulation of production in a pelagic food web model. In Carpenter SR (ed) *Complex interactions in lake communities*, Springer-Verlag, New York, pp 101–118
- Benndorf J (1990) Conditions for effective biomanipulation: Conclusions derived from whole-lake experiments in Europe. In Gulati RD, Lammens EHRR, Meijer M-L, van Donk E (eds) *Biomanipulation, tool for water quality management*, Kluwer Academic Publishers, Dordrecht, pp 187–204
- Benndorf J, Schultz H, Benndorf A, Unger R, Penz E, Kneschke H, Kossatz K, Dumke R, Hornig U, Kruspe R, Reichel S (1988) Food web manipulation by enhancement of piscivorous fish stocks: Long-term effects in the hypertrophic Bautzen Reservoir. *Limnologica* 10:97–110
- Brauer F, Soudack AC, Jarosch HS (1976) Stabilization and destabilization of predator-prey systems under harvesting and nutrient enrichment. *Int. J. Control* 23:553–573
- Brock TD (1985) *A eutrophic lake: Lake Mendota, Wisconsin*. Springer-Verlag, New York

- Brooks JL, Dodson SI (1965) Predation, body size, and the composition of plankton. *Science* 150:28–35
- Brown EJ, Harris RF, Koonce JF (1978) Kinetics of phosphate uptake by aquatic micro-organisms: Deviations from a simple Michaelis-Menten equation. *Limnol. Oceanogr.* 23:26–34
- Carpenter SR (1989) Temporal variance in lake communities: Blue-green algae and the trophic cascade. *Landscape Ecol.* 3:175–184
- Carpenter SR, Frost TM, Kitchell JF, Kratz TK, Schindler DW, Shearer J, Sprules WG, Vanni MJ, Zimmerman AP (1990) Patterns of primary production and herbivory in 25 North American lake ecosystems. In Cole J, Findlay S, Lovett G (eds) Comparative analyses of ecosystems: Patterns, mechanisms, and theories, Springer-Verlag, New York, pp 67–96
- Carpenter SR, Kitchell JF (1987) The temporal scale of limnetic primary productivity. *Am. Nat.* 124:157–172
- Carpenter SR, Kitchell JF (1988) Consumer control of lake productivity. *BioScience* 38:764–769
- Carpenter SR, Kitchell JF, Hodgson JR, Cochran PA, Elser JJ, Elser MM, Lodge DM, Kretchmer D, He X, von Ende CN (1987) Regulation of lake primary productivity by food web structure. *Ecology* 68:1863–1876
- Cooke GD, Welch EB, Peterson SA, Newroth PR (1986) Lake and reservoir restoration. Butterworths, Boston
- Downing JA, Rigler FH (1984) A manual on methods for the assessment of secondary productivity in fresh waters. 2nd edn. Blackwell, Oxford
- Elser JJ (1987) Evaluation of size-related changes in chlorophyll-specific light extinction in some north temperate lakes. *Arch. Hydrobiol.* 111:171–182
- Elser JJ, Carpenter SR (1988) Predation-driven dynamics of zooplankton and phytoplankton communities in a whole-lake experiment. *Oecologia* 76: 148–154
- Gilbert JJ (1988) Susceptibilities of ten species of rotifers to interference from *Daphnia pulex*. *Ecology* 69:1826–1838
- Hassell MP (1978) The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton, New Jersey
- Holm NP, Ganf GG, Shapiro J (1983) Feeding and assimilation rates of *Daphnia pulex* and *Aphanizomenon flos-aquae*. *Limnol. Oceanogr.* 28:677–687
- Hrbacek J (1962) Species composition and the amount of zooplankton in relation to the fish stock. *Rozpr. Cesk. Akad. Ved Rada Mat. Prir. Ved* 72:1–116
- Lampert W (1977) Studies on the carbon balance of *Daphnia pulex* de Ceer as related to environmental conditions. II. The dependence of carbon assimilation on animal size, temperature, food concentration and diet species. *Arch. Hydrobiol. (Suppl.)* 48:310–335
- Lampert W, Fleckner W, Rai H, Taylor BE (1986) Phytoplankton control by grazing zooplankton: A study on the spring clear-water phase. *Limnol. Oceanogr.* 31:478–490
- Lynch M (1980) *Aphanizomenon* blooms: Alternate control and cultivation by *Daphnia pulex*. In Kerfoot WC (ed) Evolution and ecology of zooplankton communities, University Press of New England, Hanover, New Hampshire, pp 299–304
- Malone TC (1980) Algal size. In Morris I (ed) The Physiological Ecology of Phytoplankton, University of California Press, Berkeley, pp 433–463

- McQueen DJ, Post JR, Mills EL (1986) Trophic relationships in freshwater pelagic ecosystems. *Can. J. Fish. Aquat. Sci.* 43:1571–1581
- Neill WE (1988) Complex interactions in oligotrophic lake food webs: Responses to nutrient enrichment. In Carpenter SR (ed) *Complex Interactions in Lake Communities*, Springer-Verlag, NY, pp 31–44
- Paerl HW (1988) Growth and reproductive strategies of freshwater blue-green algae (cyanobacteria). In Sandgren CD (ed) *Growth and reproductive strategies of freshwater phytoplankton*, Cambridge University Cambridge, England, pp 261–315
- Paine RT (1980) Food webs, linkage interaction strength, and community infrastructure. *J. Anim. Ecol.* 49:667–685
- Persson L, Andersson G, Hamrin SF, Johansson L (1988) Predator regulation and primary production along the productivity gradient of temperate lake ecosystems. In Carpenter SR (ed) *Complex interactions in lake communities*, Springer-Verlag, New York, pp 45–68
- Peters RH (1983) *The ecological implications of body size*. Cambridge University Press, New York
- Peters RH, Downing JA (1984) Empirical analysis of zooplankton filtering and feeding rates. *Limnol. Oceanogr.* 29:763–784
- Peters RH, Rigler FH (1973) Phosphorus release by *Daphnia*. *Limnol. Oceanogr.* 18:821–839
- Porter KG, Gerritsen J, Orcutt JD (1982) The effect of food concentration on swimming patterns, feeding behavior, ingestion, assimilation, and respiration by *Daphnia*. *Limnol. Oceanogr.* 27:935–949
- Press WH, Flannery BP, Teukolsky SA, Vetterling WT (1986) *Numerical recipes: The art of scientific computing*. Cambridge University Press, Cambridge, England
- Reynolds CS (1984) *The ecology of freshwater phytoplankton*. Cambridge University Press, Cambridge, England
- Rosenzweig ML (1971) Paradox of enrichment: Destabilization of exploitation ecosystems in ecological time. *Science* 171:385–387
- Rosenzweig ML (1972) Stability of enriched aquatic ecosystems. *Science* 175:562–565
- Schindler DW (1968) Feeding, assimilation and respiration rates of *Daphnia magna* under various environmental conditions and their relation to production estimates. *J. Anim. Ecol.* 37:369–385
- Schindler DW (1977) Evolution of phosphorus limitation in lakes. *Science* 195:260–262
- Schindler DW (1988) Experimental studies of chemical stressors on whole-lake ecosystems. *Verh. Internat. Verein. Limn.* 23:11–41
- Shapiro J, Wright DI (1984) Lake restoration by biomanipulation: Round Lake, Minnesota the first two years. *Freshwat. Biol.* 14:371–383
- Smith VH (1983) Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. *Science* 221:669–671
- Stauffer RE (1985) Nutrient internal cycling and the trophic regulation of Green Lake, Wisconsin. *Limnol. Oceanogr.* 30:347–363
- Stauffer RE (1987) Vertical nutrient transport and its effects on epilimnetic phosphorus in four calcareous lakes. *Hydrobiologia* 154:87–102

- Stauffer RE, Lee GF (1973) The role of thermocline migration in regulating algal blooms. In Middlebrooks EJ (ed) Modelling the eutrophication process. Ann Arbor Science, Ann Arbor, Michigan, pp 73–81
- Steele JH, Henderson EW (1981) A simple plankton model. *Am. Nat.* 117:676–691
- Threlkeld ST (1976) Starvation and the size structure of zooplankton communities. *Freshwat. Biol.* 6:489–496
- Tilman D (1977) Resource competition between planktonic algae: An experimental and theoretical approach. *Ecology* 58:338–348
- Trimbee AM, Prepas EE (1987) Evaluation of total phosphorus as a predictor of the relative biomass of blue-green algae, with emphasis on Alberta lakes. *Can. J. Fish. Aquat. Sci.* 44:1337–1342
- Vanni MJ, Luecke C, Kitchell JF, Allen Y, Temte J, Magnuson JJ (1990) Effects on lower trophic levels of massive fish mortality. *Nature* 344:333–335
- Walters CJ, Krause E, Neill WE, Northcote TG (1987) Equilibrium models for seasonal dynamics of plankton biomass in four oligotrophic lakes. *Can. J. Fish. Aquat. Sci.* 44:1002–1017

# 24

## An Analogy for Plankton Interactions

Peter R. Leavitt

### Introduction

Algal succession in Lake Mendota is similar to that of other eutrophic lakes (Pearsall 1932; Sommer et al. 1986). During spring, high biomass of edible algae (cryptophytes, diatoms) is reduced by elevated standing stocks of large herbivores, especially *Daphnia* (Vanni et al., Ch. 13; Luecke et al., Ch. 14). This clear-water phase (CWP) is short-lived, however, and both *Daphnia* density and fecundity decline as their resource base is overgrazed. Collapse of the *Daphnia* population may open a window of colonization for cyanophytes which often dominate for the rest of the summer (Carpenter, Ch. 23; Lathrop and Carpenter, Ch. 7).

The Plankton Ecology Group (PEG; Sommer et al. 1986) has described the CWP as an “equilibrium phase which persists until inedible algal species develop in significant numbers” (p. 435 in Sommer et al. 1986). The equilibrium is short-lived (<1 month) in eutrophic lakes but may be summer-long in less productive systems. Post-CWP algal succession is less complicated in Lake Mendota than that described by the PEG model, where edible cryptophytes and inedible green algae give way to diatoms prior to cyanophage dominance (Sommer et al. 1986). While the PEG model provides a useful reference of standardized events, it cannot address the cause of the interannual variability seen in lakes nor suggest methods to prevent noxious blooms of blue-green algae.

This chapter develops a simple conceptual model that describes how plankton interactions during the CWP regulate subsequent algal succession. I use a physical analogy to represent the CWP as a dynamic system

in which nutrients have a “potential energy for algal growth.” Predictions from the analogy are compared with recent observations from Lake Mendota and contrasted to the PEG model. Alternative lake management strategies are evaluated in light of the model.

## The Model

The model is a physical analogue of interactions between nutrient loading, phytoplankton, and zooplankton, specifically *Daphnia*. The model is restricted to plankton interactions during and shortly after the spring CWP. The CWP holds special significance because initial colonization by cyanophytes establishes blooms that exceed most others during the stratified period (Lathrop and Carpenter, Ch. 7; Carpenter 1989).

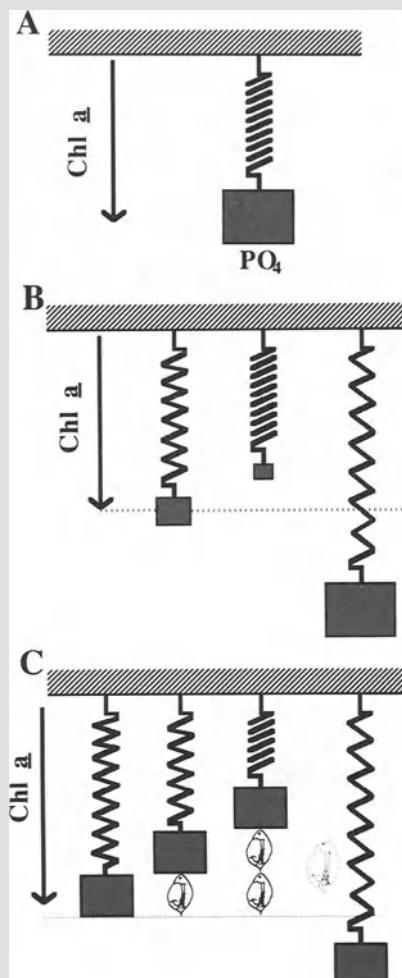
Consider a block suspended from a ceiling by a spring. The distance from the ceiling to the block is proportional to the mass of the block, all else being equal. If the block is lifted and held at a new position closer to the ceiling, it has a potential energy proportional to its mass and the distance displaced. When released, the block falls past its original position, until the spring arrests descent. The extent of “overshoot” is proportional to the former potential energy of the block. The maximum possible overshoot occurs after a block that is held against the ceiling is released.

The block-and-spring model is an analogy for plankton interactions during the CWP (Figure 24.1A). The mass of the block represents the quantity of nutrients potentially available for algal growth—specifically, the vernal load of total phosphorus (TP, exclusive of fish). The distance from the ceiling to the block represents the standing stock of phytoplankton expected for a given TP supply. In its simplest form, the distance is a measure of mean summer chlorophyll (chl) content of surface waters. Thus the block (nutrient load) and its distance to the ceiling (algal biomass) are linked through time. The spring itself has no direct analogue in a lake, but represents ecosystem resistance to change (reviewed in DeAngelis et al. 1989).

Increased nutrient supply is represented in the model by increased block mass (Figure 24.1B). The greater the block mass, the greater its distance from the ceiling. This is analogous to: the greater the vernal nutrient supply, the greater the expected algal biomass in the summer. Strong linear relationships exist between vernal TP and mean summer chl (e.g., Schindler 1976).

Effects of grazing by *Daphnia* in the CWP can be represented with the block-and-spring model (Figure 24.1C). For a given nutrient supply, there is a summer chl concentration that is expected in the absence of intense herbivory. This is represented as the distance of the block from the ceiling (dashed line). During the CWP, *Daphnia* dominate and the chl is

**Figure 24-1.** Block-and-spring model. Mass of suspended block represents vernal load of total phosphorus (TP), excluding fish. Distance of the block to the ceiling represents expected mean surface chl concentration during summer. Grazing by *Daphnia* reduces chl produced. Loss of *Daphnia* increases chl by increasing nutrient availability and selecting for surface-bloom-forming taxa.



reduced, proportional to the intensity of herbivory. In the block-and-spring model, the distance from the block to the ceiling decreases as chl standing stock is reduced. In the model, a block elevated toward the ceiling has high potential energy, for movement in this case. By analogy, nutrients in the CWP have a high potential energy—to stimulate algal growth—because intense grazing by *Daphnia* suppresses algal standing crop and prevents cycling of nutrients into phytoplankton biomass.

If released, a block falls to a point beyond its initial position. The degree of overshoot is proportional to the potential energy the block held when supported close to the ceiling. Block release is equivalent to the rapid decline in density and fecundity that *Daphnia* exhibit at the end of the CWP.

Starvation of *Daphnia* removes constraints on nutrient uptake and incorporation into algal biomass. According to the model, this should result in an unusually high chl standing crop (overshoot). The intensity of this post-CWP bloom should be proportional to both the vernal nutrient load and the intensity of herbivory during the CWP. The rate of zooplankton death will also influence the magnitude of summer algal bloom. In the analogy, a series of small reductions in block elevation results in less overshoot than a single reduction because of spring resistance. The maximum possible overshoot is defined as the chl concentration produced if the entire nutrient pool is converted to phytoplankton biomass. This distance defines the scope for algal growth.

### Evidence from Lake Mendota

According to the block-and-spring model, the severity of algal blooms in summer is proportional to both the rate and the extent of the *Daphnia* population crash, all else being equal. This initial colonization may be a key event in the seasonal succession of phytoplankton because it establishes colonial cyanophytes that are insensitive to herbivory (Carpenter, Ch. 23; Carpenter 1989).

In Lake Mendota, *Daphnia* standing stock and subsequent rate of decline are typically greatest in spring (Lathrop and Carpenter, Ch. 8). As predicted above, total blue-green biovolume, algal biovolume, and chl are usually higher in the post-CWP peak than at any other point in the summer (Figures 7.2 and 7.3 in Lathrop and Carpenter, Ch. 7). In fact, time series analyses show that *Daphnia* standing stock in the CWP predicts the abundance of blue-green algae 1–3 months later (Lathrop and Carpenter, Ch. 8). Similarly, data from 1987 to 1989 suggest that the “window of colonization” may be abbreviated and cyanophyte blooms avoided if the rate of *Daphnia* decline is reduced in early summer (Vanni et al., Ch. 13; Luecke et al., Ch. 14).

Three mechanisms can produce excessive post-CWP algal blooms: increased nutrient availability, direct nutrient contributions from dying zooplankton, and selection for buoyancy-regulating, colonial cyanophytes. Unusually high *Daphnia* densities during the CWP may increase both the rate of supply and the availability of nutrients for inedible algae. *Daphnia* convert some edible algae to available nutrients (Lehman 1980; Sterner 1989; Vanni et al., Ch. 13). Presumably, grazing releases nutrients from nonalgal sources as well (e.g., bacteria, detritus, rotifers). *Daphnia* also release stable phosphatase enzymes that facilitate uptake by algae of otherwise unavailable organic-bound phosphorus (Boavida and Heath 1984).

With continued herbivory, nutrients are not cycled and remain in the available pool. Thus nutrient supply rate is maximized when herbivore

populations rapidly collapse. Algal biomass may become excessive because of additional phosphorus (phosphatase effects, nonalgal sources) and because luxury consumption of nutrients by colonial cyanophytes (Reynolds 1984) maximizes uptake and reduces phosphorus allocations to bacteria or sedimentation losses.

Synchronous starvation of *Daphnia* will increase nutrient supply both as loss from live animals and through mineralization of dead *Daphnia*. *Daphnia* lose half their body weight during starvation, yet maintain a constant percentage of phosphorus in their bodies (Hessen 1990). Therefore as much as half of the phosphorus bound in zooplankton tissues could be released into the water prior to *Daphnia* death. Mineralization of the remaining zooplankton biomass could also increase available nutrients. During the CWP, rapidly sinking herbivore corpses might deliver these nutrients directly to blue-green algae, which typically colonize from benthic sources (Carpenter 1989).

Mesocosm experiments conducted in Lake Mendota in 1989 show that loss of *Daphnia* at densities typical of CWP could significantly stimulate algal growth (Table 24.1) (Leavitt, unpubl. data). In these experiments, up to 100 *Daphnia L<sup>-1</sup>* were added to replicate 5,000-L bags which enclosed epilimnetic waters. Herbivores reduced algal biomass within 24 h but starved to death within 10 days (at 25°C). At the end of the trial (21 days), total phosphorus in plus zooplankton treatments was threefold greater than both ambient lake levels and *Daphnia*-free controls. Most phosphorus was sequestered in colonial cyanophytes (Leavitt, unpubl. data).

*Daphnia* in Lake Mendota comprise up to 15% of CWP total phosphorus (excluding fish), assuming 1.4% phosphorus by weight (calculated from Lathrop and Carpenter, Ch. 8). Nutrient release from this pool may

**Table 24-1.** Change in mean *Daphnia* density (animals L<sup>-1</sup>) and total phosphorus concentration (TP, mg L<sup>-1</sup>) as a result of *Daphnia* death during 21 days. Pre-treatment = lake before *Daphnia* additions; Lake = lake samples after 21 days; +D = *Daphnia* added to bags; -D = no *Daphnia* added to bags. Initial = day 0, final = day 21. Standard deviation of mean TP indicated in parentheses.

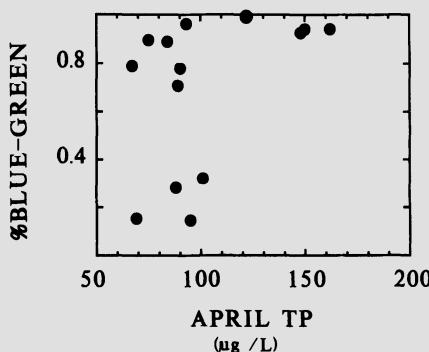
Treatment	N	Mean daphnia L <sup>-1</sup>		
		Initial	Final	TP (mg L <sup>-1</sup> )
Lake	5	1.0	1.2	0.029 (0.003)
+D	6	88.0	0.3	0.102 (0.014)
-D	5	0.5	4.9	0.027 (0.005)
Pretreatment	3	—	—	0.040 (0.002)

be significant because small changes in nutrient supply can have large effects on algal community composition (Figure 24.2). Bloom-forming cyanophytes completely dominate the phytoplankton during years when TP exceeds  $100 \mu\text{g L}^{-1}$ . However, blue-green dominance is unpredictable when nutrient concentrations are below this threshold. Therefore, relatively small changes in nutrient supply may be critical in determining the likelihood of surface blooms.

Excessive grazing by *Daphnia* may lead to surface blooms of colonial cyanophytes if herbivory is not maintained. Intense herbivory will favor large inedible algae at the expense of smaller, more competitive (for nutrients) phytoplankton (Benndorf 1990). Large colonial algae are often buoyancy-regulating, unlike the smaller cells. Therefore, after rapid loss of large grazers, colonial algae dominate and would tend to concentrate chl in surface waters, especially during calm weather. Filamentous cyanophytes dominate both because they are inedible and because live *Daphnia* excrete nutrients at a nitrogen:phosphorus ratio ( $\sim 20\text{N}:1\text{P}$ , by weight) that may selectively enhance growth of blue-green algae (Smith 1983; Sterner 1989, 1990).

### Implications for Lake Management

The PEG model of autogenic plankton succession describes the CWP as an equilibrium that exists until inedible algae colonize (Sommer et al. 1986). This view does not convey the dynamic nature of the CWP. Similarly, post-CWP algal biomass is presented as a dichotomy, high or low, in which transitions between states occur because of changes in nutrient supply (Sommer et al. 1986). Variation in timing or magnitude of successional events is expressed as deviations from a single pathway of autogenic plankton succession. Sommer et al. (1986) note that weak zooplanktivory by fish allows higher herbivore biomass, resulting in



**Figure 24-2.** Relation between total phosphorus (TP,  $\mu\text{g L}^{-1}$ , excluding fish) in April and importance (% of total algal biovolume) of blue-green algae in the post-CWP bloom. Data from Lathrop (1990).

reduced algal standing crop. However, the PEG model does not offer a predictive relationship on interactions between food web manipulations and nutrient load.

In contrast, the block-and-spring model of plankton interactions represents the CWP as a dynamic system in which nutrients have high potential energy—for stimulating algal growth. This potential determines the severity of post-CWP blooms and is proportional to nutrient load (mass of the block), *Daphnia* biomass in the CWP (degree of displacement from initial state), and rate of herbivore death (rate of block release). In this model, post-CWP conditions are distributed along a continuum of summer algal biomass.

Nutrient load delimits summer algal biomass within a broad range (Lathrop, Ch. 6) and defines the importance of *Daphnia* in stimulating post-CWP blooms. Under oligotrophic conditions (small block mass), relatively few herbivores are needed to exert maximum effect (displacement of block). However, both the scope for algal growth (maximum distance ceiling to block) and the potential of nutrients (displacement of block) are small. Consequently, herbivory has relatively little effect on post-CWP blooms.

More productive lakes have greater nutrient supply (scope for algal growth) and require more intense herbivory to achieve a given level of water clarity. However, the elevated herbivore biomass of the CWP combined with high nutrient load increases the potential of nutrients to stimulate post-CWP blooms.

The optimum amount of herbivory required for clear water in eutrophic lakes should vary from year to year. Grazing pressure must increase with elevated nutrient load, but must lessen in other years to prevent zooplankton population crashes. To some extent this occurs naturally—standing crop of edible algae is a good predictor of *Daphnia* biomass (Lathrop and Carpenter, Ch. 8). However, direct management of CWP *Daphnia* populations may be required to guarantee high summer water quality.

The block-and-spring model suggests that maintenance of acceptable water quality will be equally accomplished by reduction of nutrient supply or by establishment of stable *Daphnia* populations (cf. Benndorf 1987, 1990). Large, rapid collapses of herbivore populations are to be avoided in eutrophic systems because they may directly fuel post-CWP algal blooms. Resource limitation and *Daphnia* population crashes could be avoided either by reducing peak CWP zooplankton densities or by increasing energy flow to *Daphnia*.

In theory, a tightly regulated cold-water fishery could be established in which zooplanktivory would be optimized when *Daphnia* were superabundant. Predation by zooplanktivores would truncate peak herbivore levels and reduce grazer-imposed starvation, the principal source of

daphnid mortality in spring (Luecke et al., Ch. 14). Ideally, CWP peaks of *Daphnia* biomass would be reallocated to later in the growing season, such as occurred naturally in 1988 (Vanni et al., Ch. 13). Benndorf (1990) presented a similar argument, stating that the goal of biomanipulations should be to establish a fishery of few, but not absent, zooplanktivores. In this case, zooplankton are continuously cropped (but at low efficiency) through maintenance of high piscivore/planktivore ratios.

Evidence from Lake Mendota suggests regulation of zooplanktivory by fish in spring will not be an effective management technique. Cisco (*Coregonus artedii*) in Lake Mendota exhibit their greatest predation on *Daphnia* during the CWP (Luecke et al., Ch. 14). However, zooplanktivory by cisco prior to the CWP selects for a less effective grazer, *D. galeata mendotae*. The dominant summer *Daphnia* species is apparently set during spring (Luecke et al., Ch. 14; Lathrop and Carpenter, Ch. 8). Therefore, management of springtime fisheries with vernally active zooplanktivores is unlikely to reduce the rate of *Daphnia* starvation without adversely affecting herbivory during the summer.

Increased daphnid production may be the only practical means to maintain water clarity in the absence of reduced nutrient supply. Herbivore fecundity may be increased through addition of nutrient supplements (e.g., vitamins, metabolizable lipids) or establishment of a more nutritious forage base.

Zooplankton husbandry was recommended by Steel (1972) and Shapiro (1984) when considering factors required to maintain clear water. Shapiro (1984) stated that a resource base of edible phytoplankton is needed to sustain high *Daphnia* densities. In eutrophic systems where pH is quite high, this may be achieved through acid–base buffering to allow chlorophyte dominance (Shapiro 1984). Alternately, Steel (1972) recommended returning organic detritus to eutrophic reservoirs in London to supplement *Daphnia* nutrition and suppress algal biomass.

Supplements that promote growth and survival of *Daphnia* are difficult to identify. *Daphnia* only attain high densities when edible cryptophytes and diatoms dominate, suggesting that these algae are most nutritious. Ahlgren et al. (1990) showed flagellates are rich in essential lipids that other algal taxa lack. Diatoms are similarly rich in lipids (Reynolds 1984). *Daphnia*, like other Cladocera, are incapable of manufacturing their own lipid reserves and instead metabolize sources from their food (Peters 1987; Goulden and Henry 1986). Additional research is needed to evaluate the use of lipid-rich supplements to increase *Daphnia* survivorship.

In conclusion, summer water quality is a function of nutrient load and plankton dynamics both in the spring and in the summer. High nutrient loads combined with intense grazing pressure produce conditions in which nutrients have a high potential for producing surface blooms of undesirable algae. Maintenance of clear water requires reductions in the scope for algal growth (nutrient load) as well as promotion of factors that damp oscillations in total grazing pressure.

## References

- Ahlgren G, Lundstedt L, Brett M, Forsberg C (1990) Lipid composition and food quality of some freshwater phytoplankton for cladoceran zooplankters. *J. Plankt. Res.* 12:809–818
- Benndorf J (1987) Food web manipulation without nutrient control: A useful strategy in lake restoration? *Schweiz. Z. Hydrol.* 49:238–248
- Benndorf J (1990) Conditions for effective biomanipulation: Conclusions derived from whole-lake experiments in Europe. In Gulati R (ed) *Biomanipulation*. Kluwer Publishers, The Netherlands, pp 187–203
- Boavida MJ, Heath RT (1984) Are the phosphatases released by *Daphnia magna* components of its food? *Limnol. Oceanogr.* 29:641–645
- Carpenter SR (1989) Temporal variance in lake communities: Blue-green algae and the trophic cascade. *Landscape Ecol.* 3:175–184
- DeAngelis DL, Mulholland PJ, Palumbo AV, Steinman AD, Huston MA, Elwood JW (1989) Nutrient dynamics and food-web stability. *Annu. Rev. Ecol. Syst.* 20:71–95
- Goulden CE, Henry LL (1986) Lipid energy reserves and their role in Cladocera. In Strickler JR, Meyers DG (eds) *Trophic interactions within aquatic systems*. AAAS Selected Symp. 85. Westview Press, pp 167–185
- Hessen DO (1990) Carbon, nitrogen and phosphorus status in *Daphnia* at varying food concentrations. *J. Plankt. Res.* 12:1239–1249
- Lathrop RC (1990) Response of Lake Mendota (Wisconsin, U.S.A.) to decreased phosphorus loadings and the effect on downstream lakes. *Int. Ver. Theor. Angew. Limnol.* 24:457–463
- Lehman JJ (1980) Release and cycling of nutrients between planktonic algae and herbivores. *Limnol. Oceanogr.* 25:620–632
- Pearsall WH (1932) Phytoplankton in the English lakes. II. The composition of the phytoplankton in relation to dissolved substances. *J. Ecol.* 20:241–262
- Peters R (1987) Metabolism in *Daphnia*. *Mem. Ist. Ital. Hydrobiol.* 45:193–243
- Reynolds CS (1984) *The ecology of freshwater phytoplankton*. Cambridge University Press, Cambridge, England
- Schindler DW (1976) Biogeochemical evolution of phosphorus limitation in nutrient-enriched lakes of the Precambrian Shield. In Nriago JO (ed) *Environmental biochemistry*, Ann Arbor Science, Ann Arbor, Michigan, pp 647–664
- Shapiro J (1984) Blue-green dominance in lakes: The role and management significance of pH and CO<sub>2</sub>. *Int. Rev. Ges. Hydrobiol.* 69:765–780
- Smith VH (1983) Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. *Science* 221:669–671
- Sommer U, Gliwicz ZM, Lampert W, Duncan A (1986) The PEG-model of seasonal succession of planktonic events in fresh waters. *Arch. Hydrobiol.* 106:433–471
- Steel JA (1972) The application of fundamental limnological research in water supply system design and management. *Symp. Zool. Soc. Lond.* 29:41–67
- Sterner RW (1989) The role of grazers in phytoplankton succession. In Sommer U (ed) *Plankton ecology: Succession in plankton communities*, Springer-Verlag, Berlin, pp 107–170
- Sterner RW (1990) The ratio of nitrogen to phosphorus resupplied by herbivores: Zooplankton and the algal competitive arena. *Am. Nat.* 136:209–229

# **25**

## **Individual-Based Modeling: Application to Walleye Stocking**

**Charles P. Madenjian, Brett M. Johnson, and  
Stephen R. Carpenter**

To effect the biomanipulation, the Wisconsin Department of Natural Resources (WDNR) has undertaken an intensive walleye stocking program for Lake Mendota since 1987. Over 1.5 million walleye fingerlings have been stocked into the lake from 1987 through 1989. Walleye stocking, albeit at a reduced level, is expected to continue through 1993, at which time the Lake Mendota stocking program will be terminated. Success of the biomanipulation is directly related to success of walleye stocking.

Stocking success is directly proportional to survival of the stocked fish. Walleye stocking success has shown an enormous amount of variation among lakes in the United States and Canada (Laarman 1978). A substantial portion of this variation cannot be attributed only to size of walleyes at stocking or to the number of walleyes stocked (Laarman 1978). Johnson et al. (1988) suggested that size of prey fish relative to the size of walleye at time of stocking was an important factor in regulating success of stocked walleyes. If prey fish were too large to be eaten, then growth of walleyes was relatively slow during their first growing season because walleyes consumed chiefly invertebrates. If prey fish were small enough to be vulnerable to walleye predation, then walleye growth was rapid.

Size of young-of-year (YOY) walleyes (YOY walleye refers to a walleye in its first year of life) at the end of the growing season has been identified as a critical factor in determining survival of these fish over their first winter (Forney 1976, 1980). Walleyes greater than 175 mm in total length at the end of the first growing season in Oneida Lake (New

York) were more likely to survive their first winter than smaller walleyes (Forney 1976, 1980). One possible explanation for this phenomenon is that susceptibility to predation is sharply reduced as YOY walleye length approaches 175 mm (Forney 1976). Similarly, walleye population surveys conducted in Lake Mendota indicated that overwinter survival of YOY walleyes was substantially greater for years in which a large percentage of the YOY population had achieved a total length of at least 175 mm (Johnson et al. 1992b). Finally, the walleye population in western Lake Erie has supported both recreational and commercial fisheries since 1975 (Hushak et al. 1986). Walleye survival through the first year of life has remained sufficiently high to maintain a commercial fishery for the last 15 years. Mean length of the YOY walleye cohort at the end of the growing season has exceeded 175 mm since 1961 (Muth and Wolfert 1986).

Individual-based modeling appears to be especially appropriate to investigate the effects of varying size and time of stocking on stocking success. An individual-based model (IBM) for a population is a simulation model in which a set of individuals that represent the population of interest is tracked over time (Huston et al. 1988). Furthermore, IBMs that have been used to model growth of piscivorous fish specifically address interactions between predator and prey fish at the level of individual fish. The IBM approach has been applied to largemouth bass (*Micropterus salmoides*) populations in southern United States reservoirs in order to explain variation in growth between individuals within a single YOY cohort (Adams and DeAngelis 1987). A similar IBM approach has been used to model growth of YOY walleye in Oneida Lake (Madenjian and Carpenter 1991) and Lake Mendota (Madenjian et al. 1991). Provided the model can accurately portray YOY walleye growth, it then can be used to explore the effects of various stocking strategies on first-year growth.

In this chapter we employed an IBM to evaluate various walleye stocking regimes for Lake Mendota. Through a series of simulation experiments, we investigated the effects of walleye size at stocking and timing of stocking on first-year growth in the lake. Based on these simulations, recommendations for management of walleye stocking were formulated. The economic costs of culturing walleye fingerlings to various sizes prior to stocking were considered in the recommendation process.

### **Individual-Based Model for Piscivorous Fish Populations**

Individual-based models differ from conventional models for fish populations in that individual fish are tracked with time in IBMs, whereas state variables are used in most conventional models. These state variables usually represent some characteristic of the fish population, such as mean size or number of individuals. An IBM could be used to predict the

length-frequency distribution of a fish cohort through time. Such predictions are verifiable because fish length-frequency distributions can be measured directly in the field.

Bimodality in the size distribution of YOY largemouth bass populations during certain years in several southern United States reservoirs served as an impetus to develop an IBM for piscivorous fish (Adams and DeAngelis 1987). During some years, the population of largemouth bass at the end of the growing season could be divided into two size groups. Presumably the smaller individuals of the cohort were too small to consume fish, and had subsisted chiefly on invertebrates. Piscivorous fish will grow faster on a fish diet than on an invertebrate diet (Hewett and Johnson 1987). Larger individuals of the cohort were sufficiently large to eat fish, and therefore had grown at a faster rate. The IBM developed by Adams and DeAngelis successfully predicted the size bimodality expressed in certain YOY largemouth bass populations.

## Methods

### Lake Mendota Data

Yellow perch (*Perca flavescens*) and bluegill (*Lepomis macrochirus*) are the two most important prey species for walleye in Lake Mendota (Ch. 16). Yellow perch typically spawn in April in Lake Mendota, whereas bluegill peak spawning occurs in June.

This chapter deals exclusively with the 1989 growing season. Length-frequency data for YOY yellow perch and bluegill were inadequate for years 1987 and 1988. Furthermore, application of an IBM to observations from either 1987 or 1988 would have been complicated because the stocking period extended over an interval of approximately 40 days. During 1989, 500,000 walleye fingerlings, at an average total length of 50 mm, were stocked into Lake Mendota from 27 June to 29 June.

Methods for sampling larval, juvenile, and adult fish in Lake Mendota during 1989 have been described by Post et al. (Ch. 15) and by Johnson et al. (Ch. 16). To briefly summarize, larval fish were collected from May to June (usually at 1-week intervals) using a larval purse seine similar to the one described by Post and Prankevicius (1987). Small-mesh (6-mm ace) fyke nets were employed to sample YOY perch and bluegill populations during July and August. YOY walleyes, yellow perch, and bluegills were electroshocked during September and October. Total lengths of fish were recorded and length-frequency distributions were determined for each species. YOY walleye stomach contents were examined and prey fish were identified to species, if possible. Water temperature of Lake Mendota was monitored throughout the growing season.

### Model Description

The essential features of the model are as follows. The initial length-frequency distribution of YOY walleyes modeled in the computer simulation was based on a sampling of fingerling walleyes immediately before release into Lake Mendota. Growth of 500 individual walleyes was simulated from date of stocking (28 June 1989) until 20 October 1989. All 500 of the simulated YOY walleyes survived the growing season. The underlying assumption was that no size-selective mortality was operating on the YOY walleye cohort. Size-selective mortality is difficult to detect and even more difficult to quantify (Post and Prankevicius 1987). There was no evidence from IBM applications to Oneida Lake and Lake Mendota (Madenjian and Carpenter 1991) and western Lake Erie (Madenjian 1991) populations that size-selective mortality had a significant impact on YOY walleye size distributions during the growing season.

On each day of the simulation, numbers of encounters with YOY yellow perch and bluegills were determined for each of the walleyes by randomly choosing from a Poisson distribution. Average encounter rates were determined by calibrating the model with the YOY walleye length-frequency distribution at the end of the growing season. Lengths of each of the yellow perch and bluegills encountered by a particular walleye were assigned by randomly selecting from a normal distribution with mean and standard deviation equal to those parameters estimated from sampling the YOY perch and bluegill populations in the lake for that day of the year. Thus, prey growth schedules were inputs to the IBM.

We assumed that the YOY walleyes preferred perch over bluegills (Forney 1974; Swenson 1977). This assumption was implemented by processing yellow perch encounters before the bluegill encounters for each walleye individual. Each encounter with a prey fish was processed in the following manner. The size of each encountered prey fish was compared to the size of the particular walleye. If the ratio of the length of the yellow perch or bluegill to the length of the walleye was less than 0.46 or 0.32, respectively, then the perch or bluegill was vulnerable to predation by that particular walleye. A vulnerable prey fish was consumed by the walleye, provided that consumption of that perch did not result in the walleye exceeding its maximum daily ration. Maximum daily ration was modeled as a function of water temperature and an allometric function of walleye weight, using the relationships outlined by Hewett and Johnson (1987) and updated for YOY fish by Post (1990).

If the walleye individual did not consume any fish on a particular day, the walleye received 30% of its maximum daily ration. This feeding represented an intake of invertebrate food items. The 30% invertebrate ration was arrived at by calibrating the model with the YOY walleye size distribution at the end of the growing season. A constant proportion,

the gross growth efficiency (gge), of the weight of food (either fish or invertebrates) consumed was then converted into walleye biomass. Gross growth efficiency was assigned the value of 0.25 (Adams and DeAngelis 1987). This simple approach to fish bioenergetics obviated the estimation of a suite of parameters needed to apply a detailed bioenergetics model. The bioenergetics of YOY fish are not as well understood as adult fish bioenergetics (Post 1990). For a more detailed description of the individual-based model used in this chapter, see studies by Madenjian and Carpenter (1991) and Madenjian et al. (1991).

### Stocking Strategies

Various stocking strategies for walleye fingerlings into the 1989 Lake Mendota system were explored via IBM simulations. Mean total length of the stocked walleye fingerlings was allowed to vary from 35 to 75 mm, in 5-mm increments; date of stocking was allowed to range from 10 June to 10 July, in 3-day increments. Thus,  $11 \times 11$  or 121 IBM simulation trials were performed to map the mean length and number of big fish (NBF) surfaces over the combinations of fingerling size and date of stocking. For every simulation, the shape of the initial length-frequency distribution of YOY walleyes was identical to that observed just prior to the actual stocking in Lake Mendota in 1989. However, the initial length-frequency distribution used in each simulation was positioned along the length axis in order to correspond with the selected mean length for that particular simulation. Growth of the stocked YOY walleyes was simulated from time of stocking until 20 October for each combination of stocking date and size of fingerlings at stocking time. Mean length of the YOY walleye cohort and the NBF at the end of the simulation run were recorded. NBF refers to the number of walleye individuals with a total length of 175 mm or greater.

### Economic Analysis

Typically, walleye eggs are collected from adult females in spring, eggs are hatched at hatcheries, and fry are stocked in growout ponds or troughs (Buttner and Kirby 1986). In the north-central region of the United States, fry are stocked into growout ponds or troughs in May. Within 6 to 8 weeks, the YOY walleyes are approximately 50 mm in total length. In the majority of stocking programs, walleye fingerlings are harvested from the growout ponds at the 50-mm size and then stocked into lakes, reservoirs, or rivers.

An optimization problem of interest to walleye fisheries managers is to stock walleye fingerlings, for a given day of stocking, at a size such that cost per big fish (in Lake Mendota, a YOY fish greater or equal to

175 mm in total length) in the lake by the end of the first growing season is at a minimum. In other words, for a given stocking day, managers want to stock walleyes at a length that would generate the most large fish at the end of the first growing season per dollar invested in culturing the walleye fingerlings. We used results from the IBM simulations in order to solve this optimization problem for stocking walleye fingerlings in Lake Mendota on 28 June 1989. We considered a range in stocking length from 50 to 75 mm.

Three linear cost scenarios were explored: (1) an increase from 6 to 12 cents for stocking a 75-mm rather than a 50-mm fingerling on 28 June, (2) an increase from 6 to 18 cents for stocking the larger fingerling, and (3) an increase from 6 to 24 cents for stocking the larger fingerling. These cost scenarios covered a reasonable range of expected costs for stocking walleye fingerlings between 50 and 75 mm in length (see Madenjian et al. 1991). Cost per big fish at the end of the growing season was calculated by dividing cost per stocked fingerling by the proportion of big fish in the stocked cohort at the end of the first growing season:

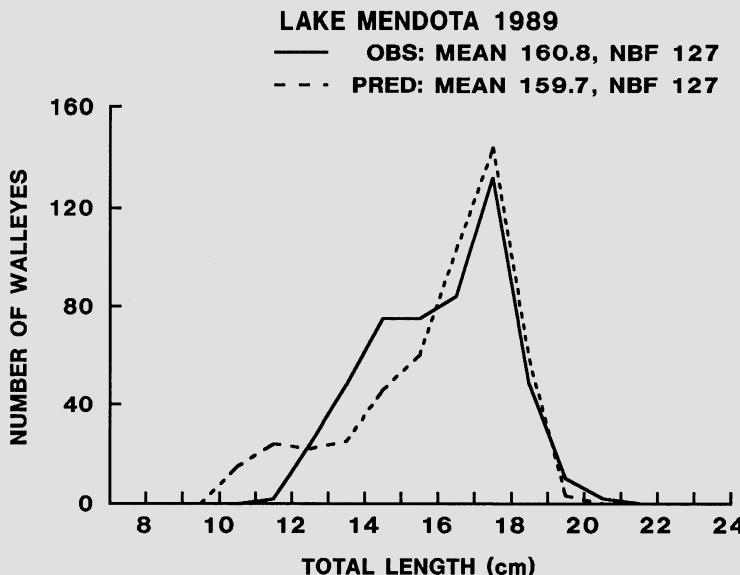
$$\begin{aligned} \text{cost per big fish} &= \frac{\text{cost per stocked fingerling}}{\text{proportion of big fish in cohort}} \\ &= (\text{cost per stocked fingerling}) (500/\text{NBF}) \end{aligned} \quad (5)$$

The proportion of large individuals in the stocked cohort at the end of the first growing season was equal to NBF determined from the IBM simulation divided by 500.

## Results

The predicted size distribution of YOY walleyes in Lake Mendota in late October 1989 was in good agreement with the observed size distribution (Figure 25.1). The model predicted that YOY yellow perch would remain relatively invulnerable to YOY walleye predation during the 1989 growing season and that bluegills would be the most common prey fish eaten by YOY walleyes. This prediction was corroborated by analysis of stomach contents from YOY walleyes collected in September and October. Bluegills or unidentified *Lepomis* individuals comprised 71% of the total number of fish observed in YOY walleye stomachs, with yellow perch comprising only 13%, and the remaining fish were either minnows (Cyprinidae), unidentifiable fish, silversides (Atherinidae), or smallmouth bass (*Micropterus dolomieu*).

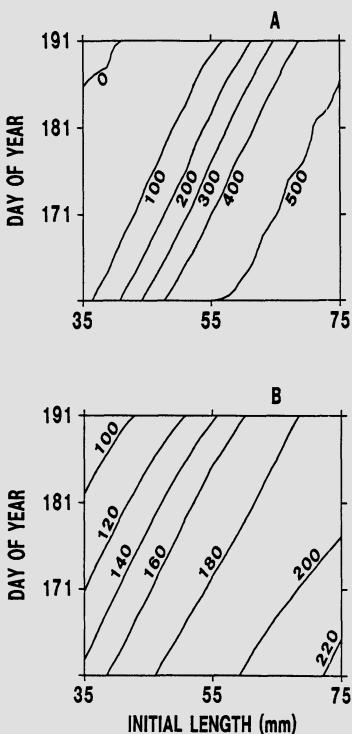
NBF and mean total length of the walleye YOY cohort at the end of the simulation period (ending on 20 October) increased as the fingerling size at stocking increased or as the stocking day of year decreased (Figure 25.2). In general, the NBF gradient was steeper with respect to size



**Figure 25-1.** Observed (OBS) and predicted (PRED) length-frequency distributions of YOY walleyes at the end of the 1989 growing season in Lake Mendota. Predictions were based on an individual-based model. MEAN refers to the mean total length (mm) of the YOY population at the end of the growing season, and NBF refers to the number of big fish (total length  $\geq 175$  mm) within a population of 500 YOY walleyes at the end of the growing season. Data taken from Madenjian et al. (1991).

at stocking than with date of stocking (Figure 25.2A). During 1989, walleye fingerlings at an average length of 50 mm were stocked into Lake Mendota on 28 June. Results from the simulation experiments indicated that small perturbations from the actual size at stocking and time of stocking for walleye fingerlings in Lake Mendota could precipitate substantial increases in NBF. For example, if the average length of the walleyes stocked into the lake on 28 June was 60 mm rather than 50 mm, the result would be more than a threefold increase in NBF at the end of the simulation period (Figure 25.2A). Similarly, if the date of stocking was moved forward in time from 28 June (day 179) to 14 June (day 165), and 50-mm-long fingerlings were stocked, then simulations revealed that NBF at the end of the growing season would increase from 127 to 395 individuals (Figure 25.2A). Mean total length of the YOY walleye cohort increased from 160 to 181 mm when the stocking date was moved from 28 June to 14 June, but average length at stocking remained 50 mm (Figure 25.2B).

Cost per big fish was minimized when average length of stocked walleye fingerlings was 62 mm (Figure 25.3). This result was the same for



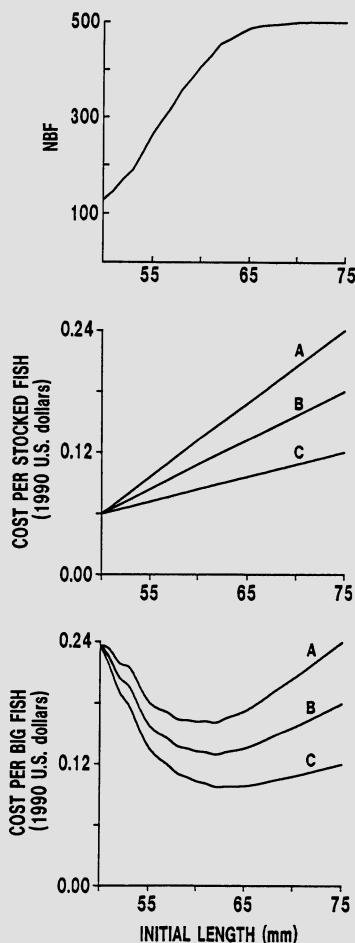
**Figure 25-2.** Isopleths for (A) NBF and (B) final length (mean total length of YOY walleyes at the end of the growing season) as a function of timing of stocking of walleye fingerlings (day of year) and mean total length of walleye fingerlings at time of stocking (initial length). NBF refers to the number of big fish (individuals with a total length  $\geq 175$  mm) within a population of 500 YOY walleyes. NBF units in number of individuals, final length units in mm. Data taken from Madenjian et al. (1991).

all the cost scenarios. Even when cost of stocking a 75-mm fingerling was four times greater than that for stocking a 50-mm fingerling at the same time of the year (on 28 June), cost per big fish showed a minimum value at a stocking length of 62 mm. Cost per big fish was between 36% and 62% less expensive when the average stocking length was 62 mm rather than 50 mm, depending on the cost scenario.

## Discussion

The IBM simulations presented in this chapter were used to explore alternative stocking strategies for the 1989 stocking of walleye fingerlings in Lake Mendota. The IBM could also be used to forecast, prior to the start of the growing season, the proportion of big fish and mean total length for the YOY walleye population at the end of the growing season in response to various combinations of time of stocking and size of walleyes at stocking. Some prediction of growth schedules and abundances of YOY populations of the prey species would be necessary in order to make the forecasts before the start of the growing season. Sampling of fish larvae and monitoring of water temperatures prior to

**Figure 25-3.** Top graph: Response of NBF to mean total length of fingerling walleyes at time of stocking (initial length). Time of stocking was held constant at 28 June (day 179). NBF refers to the number of big fish (individuals with a total length  $\geq 175$  mm) within a population of 500 YOY walleyes. Middle graph: Hypothetical cost scenarios for stocking walleye fingerlings ranging in average length from 50 to 75 mm in June in the north-central United States. A, B, and C correspond to a quadrupling, tripling, and doubling, respectively, of cost for producing a 75-mm fingerling rather than a 50-mm fingerling. Bottom graph: Cost per big fish at the end of the growing season as a function of initial length. Curves were derived from top and middle graphs. Data taken from Madenjian et al. (1991).



stocking of walleyes, as well as how much year-to-year variation to expect in the growth schedules of the YOY prey populations in the body of water of interest, would be useful in this regard. The results of the IBM simulations, coupled with results from the economic analysis, could then be used to determine the “optimal” stocking size for that particular year.

The most notable biological finding of this simulation study was that the proportion of larger fish in the walleye YOY cohort at the end of the growing season could be substantially increased by stocking earlier in the year or stocking at a slightly larger size. Based on previous discussion in this chapter, the increase in the proportion of larger fish would be converted into an increase of the overwinter survival of the YOY walleye cohort. Consequently, stocking success would be enhanced.

The stocking strategies discussed in this chapter were based on minimizing cost per large walleye at the end of the growing season. Based on

over 20 years of studying the walleye population in Oneida Lake, Forney (1976) concluded that overwinter survival of YOY walleye increased sharply as walleye total length increased to 175 mm at the end of the first growing season. Our analysis could be interpreted as assuming a step overwinter survival function (survival as a function of length at the end of the growing season), with the step occurring at a length of 175 mm. Overall results of the study are fairly robust to this assumption. Specifically, use of a smooth survival curve, provided it rose sharply in the vicinity of 175 mm, would not significantly alter the conclusions from our analyses.

We have modeled NBF at the end of the growing season as a function of the initial sizes of walleye and prey individuals, timing of stocking, the growth schedules for prey species, and abundances of prey species. However, success of walleye stocking may also depend on factors that are not considered in the present formulation of the IBM; these factors include variation in condition factor of the stocked fish and duration of the transportation time from the growout facilities to the body of water destined for stocking. As more information becomes available on the effects of these other factors on YOY walleye growth, these factors can be included in the model.

The IBM used in this analysis did not account for density-dependent effects within the cohort of stocked fish. Walleye stocking experiments by Forsythe (1977) indicated that walleye fingerlings are typically stocked into lakes and impoundments at densities far below a value at which overcrowding effects become important. From 1987 through 1989, walleye fingerlings were stocked into Lake Mendota at a density of 127 fingerlings  $\text{ha}^{-1}$ ; Forsythe observed overcrowding effects (including depletion of prey fish) at stocking densities of 1,040 fingerlings  $\text{ha}^{-1}$  or greater.

An age-structured model for the Lake Mendota walleye fishery has been used to explore various stocking and harvesting scenarios (Johnson et al., Ch. 16, and 1992a). Recruitment rate was assumed constant in this model. However, as pointed out earlier in this chapter, recruitment to the adult population may be strongly determined by growth rate, particularly during the first year of life. To accommodate size-dependent recruitment, the IBM presented in this chapter could be incorporated into a detailed model of the walleye fishery, and that detailed model could then be used as a predictive tool by fisheries managers for evaluation of stocking and harvest policies. Such a model would describe the entire walleye recruitment sequence from fingerling to adult.

A more encompassing model than the age-structured model by Johnson et al. (1992a) is the Post and Rudstam (Ch. 19) model for interactions between yellow perch and walleye populations in Lake Mendota. Post and Rudstam have used their model to investigate the long-term effects of various fishing pressures and walleye stocking rates on the stability of the lake fishery system. An individual-based model for YOY walleye growth may be included in this general model to add more detail to first-year

growth and survival of walleye in Lake Mendota. Interestingly, the predator-prey encounter model used in the IBM has been shown to converge to the type II functional response used by Post and Rudstam in their yellow perch-walleye interaction model (Madenjian and Carpenter 1991).

Madenjian and Carpenter (1991) have proposed that an IBM is the most appropriate approach to model certain stages of the fish recruitment process. For stocked walleye fingerlings in Lake Mendota, an IBM could be used to capture the individual variation in YOY growth which is crucial to overwinter survival. Modeling of subsequent stages may not require detail to the individual level. More information on the walleye fishery would be needed to apply such an elaborate model to the Lake Mendota walleye population.

At the time of preparation of this book, the WDNR was reviewing the results of this IBM simulation study and considering some intensification of the walleye fingerling culture. Presently Wisconsin hatcheries are stocked with eggs from walleyes collected in northern Wisconsin. Plans for collecting eggs from walleyes in southern rather than northern Wisconsin, and thus making the eggs available to the hatcheries approximately 2 weeks earlier, are being reviewed (J. Klingbiel, WDNR, Madison, Wisconsin, pers. comm.). This change in the walleye egg collection scheme could be accomplished with minimal additional cost (J. Klingbiel, pers. comm.). Furthermore, hatching and raising of minnow fry in the walleye growout ponds may also provide some enhancement of walleye fingerling growth at modest additional costs.

We hope that the results of our analyses will lead to a bridging of the gap between hatchery managers and fisheries managers. Hatcheries have been treated as a separate entity outside the system used for managing fish resources in lakes, reservoirs, or rivers. Presently, hatchery managers aim to produce as many fingerlings as possible, rather than focusing on acceleration of fingerling growth prior to stocking (B.L. Johnson, U.S. Fish and Wildlife Service, LaCrosse, Wisconsin, pers. comm.). If hatcheries are incorporated in the overall fisheries management scheme, perhaps more research effort could be allocated to areas such as earlier spawning of the piscivore to be stocked and to intensification of growth of the fingerlings in the growout ponds.

Analyses presented in this chapter can be applied toward improving success of stocking walleyes in Lake Mendota during the remaining years of the biomanipulation study. The IBM approach should also be appropriate for improving the effectiveness of other biomanipulation programs in which piscivorous fish are stocked as YOY fish. More generally, we contend that the IBM approach signifies a noteworthy innovation for exploring strategies for stocking piscivorous fishes. The model is fairly simple, and few parameters need be estimated for its application. Again, the model appears to adequately explain the variation in YOY

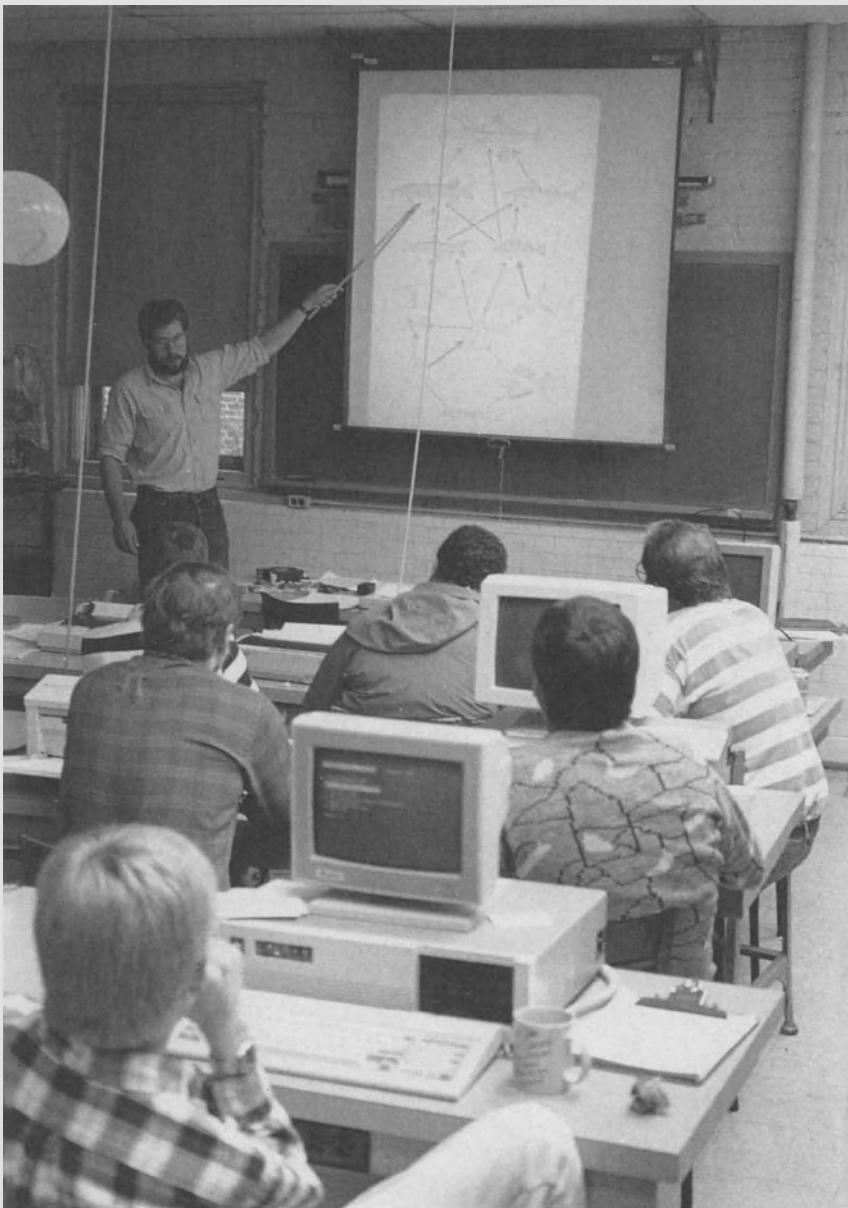
piscivorous fish growth, which has a direct bearing on stocking success. The IBM approach is well suited to evaluate management plans for stocking piscivorous fish.

*Acknowledgments.* D. Bonneau, D. Ellison, J. Klingbiel, L. Mitzner, J. Schneider, R. Stein, and D. Wahl provided information on costs for rearing walleye fingerlings and evaluations of walleye stocking programs. Thanks to J. Kitchell, J. Post, and R. Wright for their reviews of this chapter. This report was funded in part by the Federal Aid in Sport Fish Restoration Act under Project F-95-P and the WDNR. The research was also supported by the Graduate School of the University of Wisconsin, and by a Guyer Postdoctoral Fellowship (to C. Madenjian) from the Department of Zoology at the University of Wisconsin.

## References

- Adams SM, DeAngelis DL (1987) Indirect effects of early bass-shad interactions on predator population structure and food web dynamics. In Kerfoot WC, Sih C (eds) *Predation. Direct and indirect impacts on aquatic communities*, University Press of New England, Hanover, New Hampshire, pp 103–117
- Buttner JK, Kirby J (1986) Response of zooplankton and walleye fry to cladoceran inoculation and fertilization of earthen ponds. N.Y. Fish Game J. 33:34–39
- Forney JL (1974) Interactions between yellow perch abundance, walleye predation, and survival of alternate prey in Oneida Lake, New York. Trans. Am. Fish. Soc. 103:15–24
- Forney JL (1976) Year-class formation in the walleye (*Stizostedion vitreum vitreum*) population of Oneida Lake, New York, 1966–73. J. Fish. Res. Board Can. 33:783–792
- Forney JL (1980) Evolution of a management strategy for the walleye in Oneida Lake, New York. N.Y. Fish Game J. 27:105–141
- Forsythe TD (1977) Predator-prey interactions among crustacean plankton, young bluegill (*Lepomis macrochirus*), and walleye (*Stizostedion vitreum*) in experimental ecosystems. Dissertation. Michigan State University, East Lansing
- Hewett SW, Johnson BL (1987) A generalized bioenergetics model of fish growth for microcomputers. Technical Report No. WIS-SG-87-245, University of Wisconsin Sea Grant Institute, Madison
- Hushak LJ, Morse GW, Apraku KK (1986) Regional impacts of fishery allocation to sport and commercial interests: A case study of Ohio's portion of Lake Erie. No. Am. J. Fish. Manage. 6:472–480
- Huston M, DeAngelis D, Post W (1988) New computer models unify ecological theory. BioScience 38:682–691
- Johnson BM, Luecke C, Stewart RS, Staggs MD, Gilbert SJ, Kitchell JF (1992a) Forecasting effects of harvesting regulations and stocking on prey fish communities in a eutrophic lake. No. Am. J. Fish. Manage. 12 (in press)

- Johnson BM, Stein RA, Carline RF (1988) Use of a quadrat rotenone technique and bioenergetics modeling to evaluate prey availability to stocked piscivores. *Trans. Am. Fish. Soc.* 117:127–141
- Johnson BM, Stewart RS, Gilbert SJ (1992b) Ecology of fishes in the Madison lakes. *Fish Management Report* 148, Wisconsin Department of Natural Resources, Madison (in press)
- Laarman PW (1978) Case histories of stocking walleyes in inland lakes, impoundments, and the Great Lakes—100 years with walleyes. *Am. Fish. Soc. Spec. Publ.* 11:254–260
- Madenjian CP (1991) Limits to growth of young-of-the-year walleye (*Stizostedion vitreum vitreum*): An individual-based model perspective. *Can. J. Fish. Aquat. Sci.* 48:1492–1499
- Madenjian CP, Carpenter SR (1991) Individual-based model for growth of young-of-the-year walleyes: A piece of the recruitment puzzle. *Ecol. Appl.* 1:268–279
- Madenjian CP, Johnson BM, Carpenter SR (1991) Stocking strategies for fingerling walleyes: An individual-based model approach. *Ecol. Appl.* 1:280–288
- Muth KM, Wolfert DR (1986) Changes in growth and maturity of walleyes associated with stock rehabilitation in western Lake Erie, 1964–1983. *No. Am. J. Fish. Manage.* 6:168–175
- Post JR (1990) Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): In situ estimates and bioenergetic models. *Can. J. Fish. Aquat. Sci.* 47:554–560
- Post JR, Prankevicius AB (1987) Size-selective mortality in young-of-the-year yellow perch (*Perca flavescens*): Evidence from otolith microstructure. *Can. J. Fish. Aquat. Sci.* 44:1840–1847
- Swenson WA (1977) Food consumption of walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) in relation to food availability and physical conditions in Lake of the Woods, Minnesota, Shagawa Lake, and western Lake Superior. *J. Fish. Res. Board Can.* 34:1643–1654



**Plate 9.** Workshops were a primary means of technology transfer. Here, Brett Johnson leads a demonstration of bioenergetics modeling techniques.

# **26**

## **Development, Evaluation, and Transfer of New Technology**

**Lars G. Rudstam and Brett M. Johnson**

### **Introduction**

A selling point of the Lake Mendota biomanipulation project was the evaluation of two technologies developed by the Center for Limnology at the University of Wisconsin (UWCFL)—bioenergetics modeling and hydroacoustic assessment of fish populations—and the subsequent transfer of these technologies to the Wisconsin Department of Natural Resources (WDNR). An important result of the Lake Mendota project has been a large increase in contact and cooperation between the university and WDNR accomplished partly through monthly discussion group meetings followed by important after-hours informal discussions at the Student Union Terrace on the shores of Lake Mendota. The increased contact between UWCFL and WDNR facilitated technology transfer and we are increasingly dealing with collective evaluation and development rather than with a transfer of technology from the university to fisheries management.

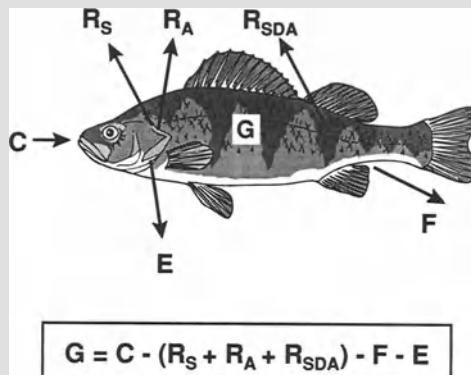
The cooperation between UWCFL and WDNR also resulted in unplanned transfer of techniques between the two parties. In addition to bioenergetics and hydroacoustics, the Lake Mendota project has evaluated and developed a number of other management techniques described in more detail elsewhere in this book. A need for improved sampling techniques for larval fishes resulted in the adoption of a fine-mesh purse seine by UWCFL (Post et al., Ch. 15; Plate 6). Purse seining provided estimates of year class strength of most of Lake Mendota's planktivores and was used in a study of trophic ontogeny of key

planktivore species (Schael et al., 1991). Other techniques include evaluation of mark-recapture methods for walleye (Johnson et al., Ch. 16), a new stomach pump for sampling piscivore stomachs (Gilbert and Johnson, in press), creel survey techniques (Johnson and Staggs, Ch. 17) and the use of individual-based models for guiding stocking practices (Madenjian et al., Ch. 25). Several additional benefits to fisheries management not anticipated at the start of the project are described in the following chapter (Staggs, Ch. 27).

We have divided this chapter into three sections. The first part describes bioenergetic models and the successful transfer of this technology to WDNR. Several workshops specifically designed to introduce bioenergetic models to WDNR personnel have been conducted and bioenergetic models are now used by fisheries managers to address specific management issues. The second section describes the potentials of hydroacoustics and the specific problems encountered in Lake Mendota: survey design, methane bubbles, and extraction of species-specific abundance data. We also include a comparison with other fish assessment techniques (mark-recapture and creel surveys, vertical gill nets). The final remarks include a summary of the transfer process for bioenergetics and hydroacoustics, some general comments on the benefits gained from collaboration between a management agency and a university research group, and some thoughts on how to make this happen.

## Bioenergetics Modeling

Knowledge of the effect of food availability, ration, and diet on fish growth and estimation of food demand by a fish population is central to modern fisheries management (Ney 1990). Bioenergetic models use first principles ("what comes in will come out") to calculate either growth given a consumption rate or consumption given a growth rate (Figure 26.1; Kitchell 1983). The bioenergetic models developed at the University of Wisconsin (the "Wisconsin model"; Ney 1990) treat different parts of the energetic equation as functions of fish weight and temperature, a dependency that is well established (Brett and Groves 1979; Peters 1983). Hewett and Johnson (1987) present a flexible, user-friendly computer program and parameters for 10 fish species including yellow perch, walleye, and northern pike. Since then, another 14 species have been added to this list, partly as a result of a seminar during the fall of 1989 with participation from both UWCFL and WDNR. The model structure has undergone extensive sensitivity analysis (Kitchell et al. 1977; Bartell et al. 1986) and model predictions do correspond to field data at least in some cases (Rice and Cochran 1984; Hayward 1990; Hewett et al., 1991, but see Boisclair and Leggett 1989, 1990).



**Figure 26-1.** The basic components of the bioenergetic equation overlaid on a Lake Mendota perch. Consumption (C), respiration (R), egestion (F), and excretion (E) are functions of temperature and fish weight and based on laboratory experiments on whole animal physiology. Respiration is often divided into three components:  $R_S$  standard metabolism,  $R_A$  active metabolism, and  $R_{SDA}$  standard dynamic action, the increase in metabolic rates associated with digestion. Given information on occupied temperature, diet, and energy content of prey and predator, the model calculates consumption from observed (or hypothesized) growth (G). This is achieved by iteratively fitting one parameter, P, the proportion of maximum consumption rate, to allow the fish to grow as observed.

These models are cost efficient compared to direct measurements in the field. Daily consumption rates can be estimated using stomach samples collected every 2 to 4 h over at least 24 h and the application of a gastric evacuation model (Elliott and Persson 1978). However, several evacuation rate models are currently used (Jobling 1986; Persson 1986) and daily rations can be quite variable from one day to the next (Smagula and Adelman 1982; Johansson and Persson 1986; Hodgson et al. 1989). Growth integrates consumption over space and time, and bioenergetic calculations may therefore be less subject to estimation error than direct estimates of food consumption. Perhaps most importantly, bioenergetic models can be used to evaluate alternative management scenarios and to guide field sampling.

UWCFL and the Wisconsin Sea Grant Institute have taken an active role in transferring the bioenergetic models to practicing fisheries managers. To date (1 January 1991), 12 workshops have been conducted across the continent (in Wisconsin, Minnesota, North Carolina, Vermont, and Ontario; Plate 9). Four workshops were directed at WDNR fisheries managers and researchers in Ashland, Brule, Woodruff, and Madison. One of us (B.M.J.), trained in an early workshop, has now been recruited

to the bioenergetic teaching team which helps provide a management perspective to current workshops.

A workshop usually lasts for 2 days. The first day includes an introduction to the physiological basis of bioenergetic models and to some of the model applications. After this introduction the participants are walked through the software package with several exercises designed to show a range of problems that can be addressed with bioenergetic models (e.g., effects of changes in occupied temperature as a result of global warming or warm water discharge from a power plant, effects of changes in diet, effects of seasonal changes in energy content of the fish, impact on the forage base, growth under different daily rations, etc.; Johnson 1988). The second day is spent working through specific problems using data sets brought by the participants. This second day is valuable, both because participants can explore the possibilities and limitations of the models for their own management problems and because the instructors learn about existing problems and possible future model modifications. The result is a productive interplay between model development and model application. Following such workshops, WDNR fisheries managers have applied bioenergetic models to questions about piscivore growth rates in Lake Superior and hatchery practices for rearing muskellunge.

Development and application of bioenergetic models have been an integral part of the Lake Mendota project from the beginning. These models are used in several chapters of this book either directly to estimate consumption by adult and larval fishes (Luecke et al., Ch. 14; Post et al., Ch. 15), merged with a more traditional fish population model to evaluate impact of walleye stocking and harvest regulations (Johnson and Staggs, Ch. 17; Johnson et al. 1992), or as a component of more complex models (Post and Rudstam, Ch. 19; Luecke et al., Ch. 20; Madenjian et al., Ch. 25). Specific models have been developed for larval yellow perch (Post 1990) and for coregonid fishes (Rudstam et al., in prep.; Luecke et al., Ch. 14).

We have also used these models as a tool to guide field sampling programs. For example, model analysis indicated the time of year when it is most important to know the temperature occupied by walleyes in Lake Mendota to assess the impact of walleyes on their forage base (Johnson et al. 1991). Weekly maximum and minimum lake temperatures at depths with sufficient dissolved oxygen were obtained from temperature profiles (Lathrop, unpubl. data) to construct hypothetical thermal histories for Lake Mendota walleyes. Simulations at the two temperature regimes showed that estimated daily consumption rate can be in error by at least 50% during June, when the lake is stratified but the hypolimnion is not anoxic, and in August, when maximum temperatures are high enough to reduce consumption. But errors in annual consumption estimates due to thermal history should be less than 15%. Because quantifying thermal history precisely would be a costly and time-consuming task, modeling

suggested that a prudent strategy would be to devote most of the available sampling effort to determine temperatures occupied by walleyes during June and August.

## Hydroacoustics

Hydroacoustics is the science of underwater sound transmission and the sound scattering processes of fish. Echo sounders have been used for fish stock assessment in both lakes and seas for over two decades (Clay and Medwin 1977; Johannesson and Mitson 1983). An echo sounder transmits a sound pulse into the water and receives the echo from any target with different acoustic properties than water—the larger this difference, the greater the amount of acoustic energy that is reflected by the target and the greater the target strength. Air bubbles like the gas-filled swim bladder of fish are strong targets and echo sounders are therefore particularly useful for observing fish.

Hydroacoustics is cost efficient because large areas can be covered in a short time. Any management questions that require knowledge of the amount, size, and spatial/temporal distribution of fish in a lake can benefit from the use of hydroacoustic methods. Examples of specific management questions of interest in Wisconsin include estimations of forage base for Lake Michigan salmonids and other open-water predators, entrainment into power plants, interactions between native cisco and introduced smelt in northern Wisconsin, and changes in diel distribution patterns of prey mediated by introducing (stocking) predators. The main limitation of acoustics in small lakes is that the volume of water about 1 m above the bottom and 1 to 2 m below the surface cannot be sampled with available techniques. Thus, acoustics is presently less useful for littoral fishes or in very shallow lakes, but the new generation of echo sounders has variable pulse length (allowing for better vertical resolutions) and we have used such sounders to map macrophyte distributions in shallow water (1–3 m depth). Another limitation of acoustics is that different fish species cannot be separated (but see below).

Two methods exist for extracting fish abundance information from the acoustic signals—echo integration and analysis of echo peaks. Echo integration is proportional to the returning sound pressure, which is proportional to fish density for both schooling and single fish as long as the size structure is constant. When the size structure and target strengths of the fish population are known, we can convert echo integration numbers to absolute fish densities (Johannesson and Mitson 1983). Echo integration coupled with trawl sampling is commonly used in marine fish stock assessment. In lakes, echo integration is often combined with the analysis of echo peaks from single fish (e.g., Burczynski and Johnson 1987; Rudstam et al. 1987; Jurvelius et al. 1988). Programs and pro-

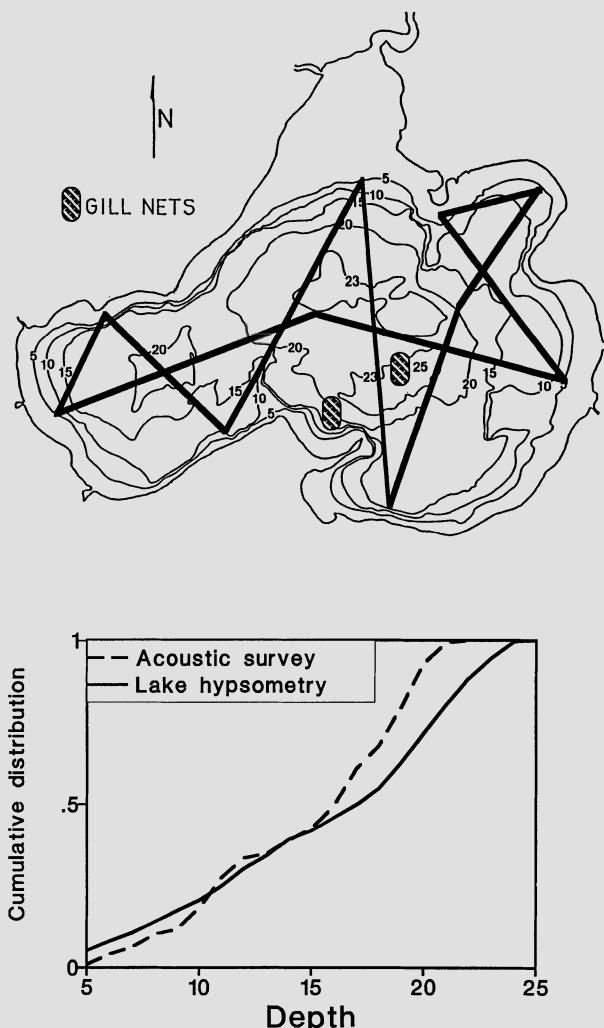
cessors for this type of analysis have been developed independently at several institutions and may use single-beam (Lindem 1983; Clay 1983) or dual-beam sonar data (Traynor and Ehrenberg 1979). By combining these two methods, it is possible to extract target strength distribution from *in situ* measurements on single fish and use these measurements to calibrate echo integration data from fish schools (where single fish cannot be resolved). This approach requires that at least some individual fish be resolved and the assumption that fish observed individually are representative of the fish in schools. The Lake Mendota project has used two single-beam methods, one developed at the University of Wisconsin by Clay and coworkers partly with support from the Lake Mendota project (Deconvolution: Clay 1983; Rudstam et al. 1987; Jacobson et al., in press) and one developed by Lindem at the University of Oslo (Hydro Acoustic Data Acquisition System, HADAS: Lindem 1983, 1990). Dual-beam and different single-beam methods give similar fish size and abundances under a variety of conditions (Hartmann et al. 1987; Rudstam et al. 1988). The acoustic data discussed below for Lake Mendota are from a 70 KHz SIMRAD EY/M single-beam sonar (11.4° half-power beam angle, 0.6 ms pulse length).

### **Survey Design**

The survey design used in Lake Mendota from 1981 through 1987 involved repeating a north-south and an east-west transect across the lake. Jacobson et al. (1990) showed that the variability between two runs of the same transect was much lower than the variability between two transects. Since we are interested in applying our fish population estimates to the whole lake, a variance calculated from repeated surveys of the same transects will underestimate the true variance. Also, this design oversampled the deeper parts of the lake compared to the shallower parts, and horizontal inshore-offshore gradients in fish abundance are likely to occur. Therefore we changed the sampling design in 1988 to cover a larger part of the lake and to sample depth strata 5 m and deeper approximately in relation to their occurrence (Figure 26.2). We did not attempt to sample shallower areas, because our current method excludes the top 2 m and the bottom 1 m of water and macrophyte beds tend to obscure fish echoes in shallow water. It follows that our acoustic estimates, even with the new (1988-89) survey design, are only representative of waters deeper than 5 m (about 75% of the lake surface).

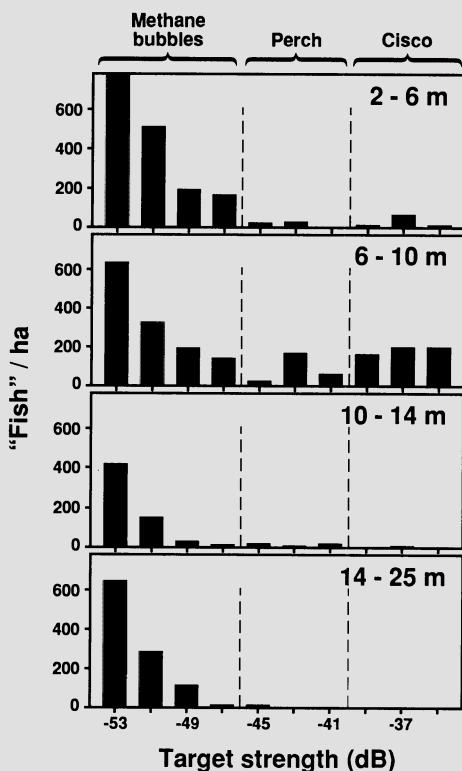
### **Contamination of Acoustic Data by Methane Bubbles**

Methane is produced through anaerobic bacteria in the sediment. In eutrophic lakes like Lake Mendota, bubbles are released from the sedi-



**Figure 26-2.** Map of Lake Mendota indicating sonar transects used in 1988 and 1989. The corresponding hypsographic curves for this survey design and for the whole lake are also shown. This design samples different depth strata approximately according to their occurrence from 5 m depth and deeper.

ment and rise to the surface (Brock 1985). These bubbles cannot be distinguished with acoustics from fish swim bladders. The release of bubbles starts in June in Lake Mendota and continues until fall overturn. The target distribution in the anoxic hypolimnion where fish are absent reveals that these bubbles are relatively small and will not contaminate target strengths larger than  $-47\text{ dB}$  (Figure 26.3, fish sizes over 12 cm). The bubbles should increase in size as they rise to the surface because of



**Figure 26-3.** Examples of output from an acoustic transect on Lake Mendota, 23 August 1981, between 22:00 and 23:00 CST. Fish were most abundant between 6 and 12 m depth in vertical gill nets (cisco and perch). Water below 12 m depth was anoxic; no fish were caught at these depths and the observed echoes represent methane bubbles. These small bubbles (targets less than  $-46\text{ dB}$ ) increase somewhat in size as they rise to the surface. Note that target strengths are given as negative numbers and on a logarithmic scale; a target strength of  $-53\text{ dB}$  is smaller than a target strength of  $-38\text{ dB}$ .

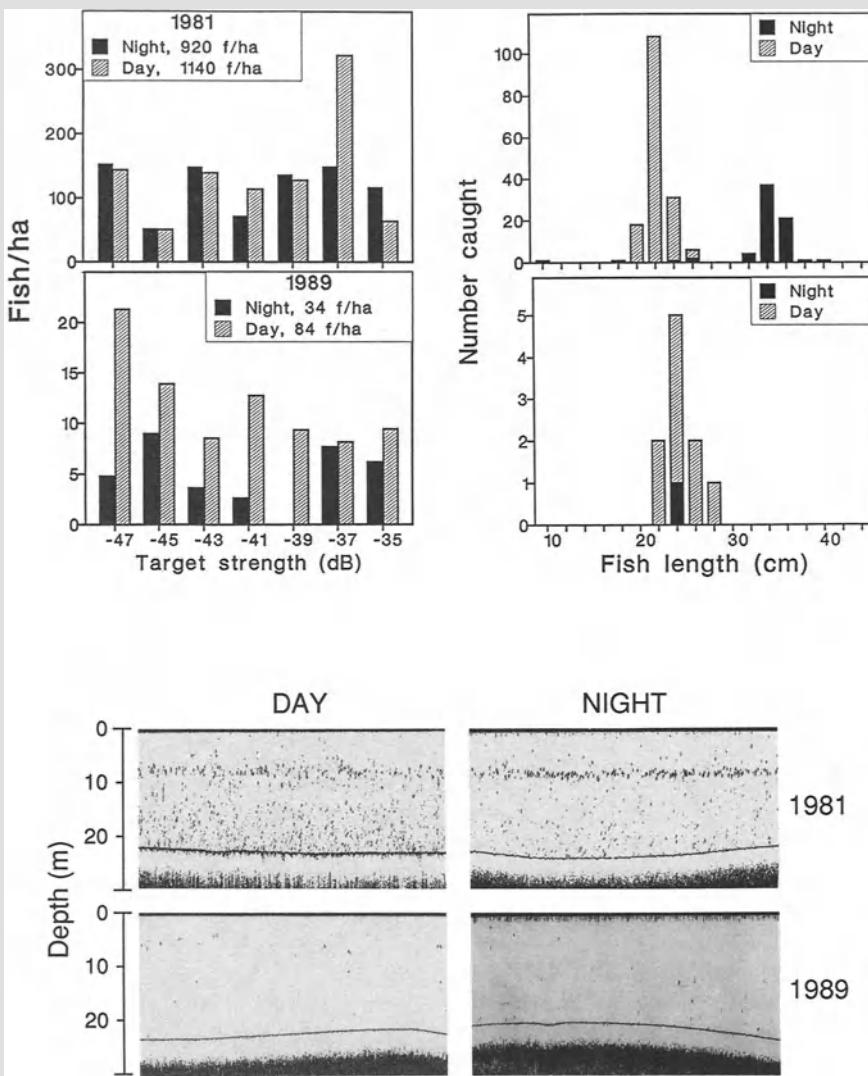
pressure changes. Based on Boyle's law, we expect a doubling in volume as the bubble rises from the sediment surface at 20 m depth to 5 m depth. This corresponds to an increase in area of a factor of 1.6 and an increase in acoustic target strength of approximately 2 dB. We do see higher densities of bubbles (small targets  $-55$  to  $-47\text{ dB}$ ) closer to the surface, indicating that bubbles with smaller target strengths than  $-56\text{ dB}$  in deep water increase in size and target strength in shallow water. We also observe an increase in the  $-47\text{ dB}$  target strength group (Figure 26.3). Bubble size is complicated, however, and depends also on surface tension, on the diffusion of methane to the water and therefore on the methane concentration in the water, on the stability of the boundary layer and therefore on the amount of organic material that adheres to the surface of the bubbles, and on the extent that larger bubbles split into smaller ones. In addition, bubbles will resonate at certain acoustic frequencies (depending on bubble size; Clay and Medwin 1977). Fortunately, most open-water fish in Lake Mendota are relatively large and give echoes greater than those observed from bubbles. For applications of acoustics to small fish in lakes with substantial production of methane bubbles, it may be necessary to derive a filter (based on the theoretical

change of bubble size with depth and associated change in acoustic properties) and remove contributions from methane bubbles.

### Extracting Species-Specific Information

Acoustic size distributions generally show good correspondence with fish sizes observed in vertical gill nets and trawls (Lindem and Sandlund 1984; Rudstam et al. 1987, 1988; Jacobson et al., 1990). The dominant open-water fish species in Lake Mendota are cisco and yellow perch (Rudstam et al., Ch. 12). In this lake, cisco are longer than 25 cm as age I+ in the fall, and perch age I+ to V+ range from 12 to 25 cm (Luecke et al, Ch. 14). For Lake Mendota, we used two acoustic size groups: targets between  $-46$  and  $-40$  dB (or 12 to 25 cm) and targets larger than  $-40$  dB (or larger than 25 cm, equation from Lindem and Sandlund (1984),  $TS$  (target strength) =  $20\log L$  (length) - 68, notice that  $TS$  is negative and  $-46$  dB is a smaller target than  $-40$  dB). The smaller fish were predominantly perch, although young-of-year (YOY) cisco, freshwater drum, and white bass will also be included. The larger fish were predominantly cisco before the 1987 die-off, and a mixture of cisco and large perch, white bass, and freshwater drum after the cisco die-off (Luecke et al., Ch. 14). Interference from methane bubble production complicates the use of acoustics for fish sizes smaller than 12 cm in late summer and fall (see above).

It is also possible to use differences in behavior of fish species to extract species-specific abundance information from acoustics data. In Lake Mendota, gill nets primarily catch cisco during the night and perch during the day (Rudstam and Magnuson 1985), and perch have been observed to migrate inshore and rest on the bottom at night (Hasler and Bardach 1949). In some lakes, cisco school close to shore during the day (Engel and Magnuson 1976; Rudstam and Trapp 1987). Consequently, we originally hoped that night acoustic surveys would record mainly cisco and day surveys would record mainly perch. However, this does not appear to be the case in Lake Mendota. A comparison of day and night acoustic size distributions collected since 1981 in Lake Mendota shows that cisco- and perch-size targets are present in the open water both day and night (Figure 26.4), although the perch-size targets are less abundant during the night than during the day. The ratio of day to night abundances is 1.0 (SE = 0.2, N = 6) for cisco-size targets (using surveys between 1981 and 1986, before the 1987 cisco summer kill, Rudstam et al., Ch. 12) and 2.3 (SE = 0.3, N = 14) for perch-size targets (using surveys between 1981 and 1989). We interpret this as evidence that cisco do not migrate between inshore and offshore regions to Lake Mendota and that part of the perch population stays in the water column during the night (see also Hasler and Tibbles 1970; McCarty 1990). However, since part of the perch



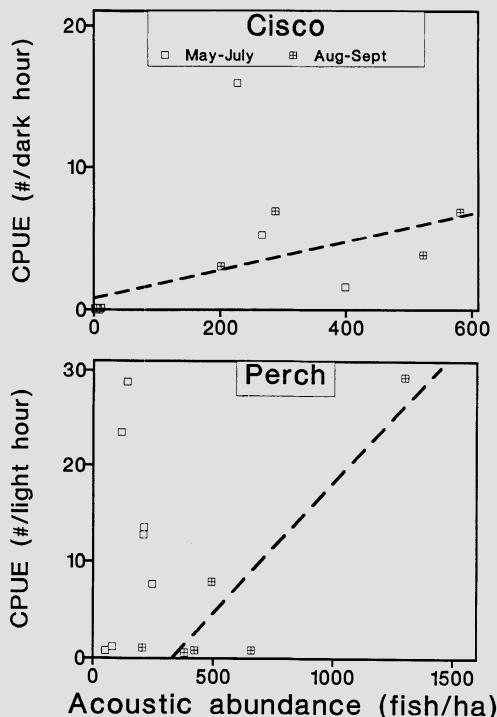
**Figure 26-4.** Day and night target strength distributions for the 2- to 14-m depth layer in Lake Mendota based on acoustic data from August 1981 and July 1989, and associated catches in vertical gill nets. The two fish size classes caught in gill nets are represented by peaks at target strengths of  $-37$  dB (about 36-cm fish) and  $-43$  dB (about 18-cm fish). Most ciscos were caught at night and most perch were caught at day. Day and night echo charts are also shown. No cisco was caught in July of 1989.

population probably is inshore at night, it is necessary to use day acoustic surveys for perch abundances (as done in Luecke et al., Ch. 14).

### Comparison with Other Assessment Techniques

*Gill Nets.* Since 1981, the open-water fish populations in Lake Mendota have been sampled with vertical gill nets in the deeper part of the lake (Figure 26.2). Catch per unit effort (CPUE) in gill nets is often used as an index of fish abundance. In Lake Mendota, fish abundances determined from acoustics explained 64% of the variability in CPUE for cisco and 83% for perch when CPUE was computed on nets set in August and September in water deeper than 15 m (Figure 26.5). With only 6 years of data, these correlations are significant for perch but not for cisco ( $0.10 < p < 0.05$ ). If catch from different seasons is included, the amount of variance explained decreases to 29% for cisco ( $N = 15$ ,  $p < 0.05$ ) and to 8% for perch ( $N = 13$ , not significant). These rather poor correlations are partly explainable by the different spatial extent of net and acoustic samples. Net data are from only one station whereas the acoustic data represent an average for the whole lake. Poor correlations also reflect the problems associated with using a passive fishing gear like gill nets, where catches depend on fish activity (Hamley 1975; Rudstam et al. 1984). This is especially true when comparing catches over different seasons.

*Mark–Recapture Estimates and Creel Surveys.* An intensive mark–recapture study of perch in Lake Mendota was conducted in May of 1988. Over 20,000 male perch were fin-clipped (Johnson et al., Ch. 16). The resulting population estimate for Lake Mendota in spring of 1988 (modified Petersen estimate) was 432,000 male perch larger than 17 cm (95% confidence interval 355,000–527,000), or 860,000 perch with the observed 50:50 sex ratio. These larger fish are primarily from the 1985 year class that dominated the perch population in 1988 and 1989 (Luecke et al., Ch. 14). Recruitment of young perch was poor in 1987–89 (Luecke et al., Ch. 14; Post et al., Ch. 15). The average acoustic estimate of perch from the four day-surveys during 1988 is 319 fish/ha ( $SE = 71$ ) or 890,000 fish in the lake in waters 5 m and deeper. The acoustic abundances will include some white bass and freshwater drum, but gill net catches and creel surveys indicate that perch is the dominant open-water fish in 1988 and 1989 (Johnson and Staggs, Ch. 17). Bulegills are also common but are generally found closer to shore. Perch in the littoral zone (less than 5 m depth) are not included in the acoustic estimate, and these fish will contribute to the total population. Perch are more abundant in gill nets set at 10–12 m than in gill nets set at 6 and 2 m depth (McCarty 1990; Luecke et al. 1990). Assuming that perch densities in shallow water are the same as the lake average increases our population estimate to 1.2 million fish, still an excellent correspondence with the mark–recapture estimate.



**Figure 26-5.** Catch per unit effort (CPUE) in gill nets set in 16- to 23-m deep water plotted against acoustic density estimates for large- (25-cm and larger, cisco) and medium- (12- to 25-cm, perch) sized fish. The data are based on surveys in Lake Mendota from 1981 through 1989. Data from August to September (all years) and from April to June (1986–89) are separated. CPUE is calculated as catch per light hour (1 h before sunrise to 1 h after sunset) for perch and catch per dark hour (1 h before sunset to 1 h after sunrise) for cisco, as the two species have markedly different catch rates during day and night (Figure 26.4). The regression line of CPUE versus acoustic fish abundance only includes August and September surveys. The equations are  $CPUE(\text{Cisco}) = 0.01 \cdot (\text{fish/ha}) + .82$  ( $r^2 = 0.64$ ,  $N = 6$ ,  $0.1 < p < 0.05$ ) and  $CPUE(\text{Perch}) = 0.027 \cdot (\text{fish/ha}) - 8.8$  ( $r^2 = 0.83$ ,  $N = 6$ ,  $p < 0.05$ ).

A second comparison can be made by using the creel survey estimate of the number of perch harvested in Lake Mendota between May 1988 and October 1989 (400,000 perch; Johnson and Staggs, Ch. 17). Subtracting this number from the mark–recapture estimate yields 460,000 perch (if we assume no natural mortality) or 210,000 perch (if we assume a 30% annual natural mortality) in the lake at the end of 1989. These numbers do not include any recruitment (supported by our observations, see above). Acoustic estimates from September and October 1989 were 99 and 117 fish/ha or 315,000 perch (in water deeper than 5 m, 420,000 perch

in the whole lake assuming shallow densities are the same as the lake average), again an excellent correspondence.

The correspondence between the two methods is encouraging. Similar attempts at comparisons of acoustic and mark–recapture estimates are rare (Dahm et al. 1985; Mulligan and Kieser 1986; Hartmann et al. 1987) and generally show lower acoustic fish abundances than abundances obtained with mark–recapture or weir counts. This is attributed to the part of the fish populations residing in areas not sampled with acoustics i.e., inshore and close to the surface or bottom. The excellent correspondence between mark–recapture and acoustics in Lake Mendota is probably a result of the fish being restricted to the lower epilimnion by low oxygen from below and light from above (Rudstam and Magnuson 1985). This fish distribution is ideal for acoustic estimates of total fish abundance (Unger and Brandt 1989).

## Final Remarks

As promised in UWCFL's proposal to WDNR, two potential management tools (bioenergetics models and hydroacoustics) have been refined, evaluated, and made available to WDNR fisheries managers. Already, bioenergetics models have been applied to several management problems around the state. The direct transfer of technology in the form of workshops has provided a core of trained bioenergetics modelers within the WDNR. These managers will continue the technology transfer process by demonstrating the everyday applications of the models to their peers and by serving as resources for other managers interested in adding the technique to their management toolbox.

Though not currently incorporated into inland management programs, techniques for hydroacoustic assessments of fish abundance are more accessible to the manager with the advent of user-friendly analysis software and a demonstration of the potential of the method on Lake Mendota. We have only recently started with workshops on basic acoustic theory and on the use of hydroacoustics in the field. Unlike bioenergetics, acoustics requires specialized hardware including the echo sounder, recorder, and data processing units, and this hardware is not currently available to the local fisheries manager. Application of hydroacoustics is also limited to fish distributed in the open water, and many species of interest to fisheries managers (walleye, bass, bluegills, etc.) are not amenable to quantification with acoustic techniques. Within the open-water zone, though, acoustics can be profitably applied to any fisheries management questions that require knowledge of fish abundances, sizes, and spatial/temporal distributions.

The close cooperation between UWCFL and WDNR during the Lake Mendota project has facilitated the transfer and evaluation of bio-

energetics, hydroacoustics, and other technologies. Cooperative field sampling, monthly discussion group meetings, shared authorship of publications, workshops, and special seminars have all contributed to an enhanced working relationship between the two parties. As researchers and resource managers collaborate, there is an exchange of philosophies and approaches to problems that is broadening for both groups.

It is hard to pinpoint the reasons why this cooperation worked well within the Lake Mendota project. A genuine interest in research questions among the management group and in management questions within the university was probably important, as was a desire and determination to pursue collaborative efforts on the part of top-level administrators (Addis at WDNR, Kitchell and Magnuson at UWCFL) and excellent administrative support (Staggs), with close connection with the top WDNR administration. It is not a coincidence that one of us (B.M.J.) is both the project coordinator at the WDNR and a Ph.D. student at the UWCFL. Johnson was recruited to the position of liaison because of his interest in both research and management. Also critical to the project's success was the formation of an executive subcommittee composed of representatives from both the UWCFL and WDNR that allocated research funds, developed long-range plans, and ensured that project objectives were met. However, institutional and administrative arrangement can only improve the possibilities for collaboration; it is the people involved who make it happen. Our hope is that the cooperation within the Lake Mendota project has instilled a greater appreciation for the challenges and expertise of the other group and that we are part of the process of building a bridge over what Cullen (1990) describes as the turbulent boundary between water science and water management.

**Acknowledgments.** We thank Barry Johnson, Michael Staggs, and Jim Kitchell for helpful suggestions and acknowledge support from the Federal Aid in Sport Fish Restoration Act under Project F-95-P, the WDNR, the National Science Foundation (Grant No. DEB 801233 LTER-NTL), and the Swedish Council for Forestry and Agriculture Research (L.G.R.).

## References

- Bartell SM, Breck JM, Gardner RH, Brenkert AL (1986) Individual parameter perturbation and error analysis of fish bioenergetic models. *Can. J. Fish. Aquat. Sci.* 43:160–168
- Boisclair D, Leggett WC (1989) The role of activity in bioenergetic models of actively foraging fishes. *Can. J. Fish. Aquat. Sci.* 46:1859–1867
- Boisclair D, Leggett WC (1990) On the relationship between growth and consumption rates: Response to comments by R.S. Hayward (1989). *Can. J. Fish. Aquat. Sci.* 47:230–233

- Brett JR, Groves DD (1979) Physiological energetics. In Hoar WS, Randall DJ, Brett JR (eds) Fish physiology. Vol. VIII: Bioenergetics and growth. Academic Press, New York, pp 279–352
- Brock TD (1985) A eutrophic lake: Lake Mendota, Wisconsin. Springer-Verlag, New York
- Burczynski JJ, Johnson RL (1987) Application of dual-beam acoustic survey techniques to limnetic populations of juvenile sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 43:1776–1788
- Clay CS (1983) Deconvolution of the fish scattering PDF from the echo PDF for a single transducer sonar. J Acoust. Soc. Am. 73:1989–1994
- Clay CS, Medwin H (1977) Acoustical oceanography: Principles and application. John Wiley and Sons, London
- Cullen P (1990) The turbulent boundary between water science and water management. Freshwat. Biol. 24:201–209
- Dahm E, Hartmann J, Lindem T, Löffler H (1985) EIFAC experiments on pelagic fish stock assessment by acoustic methods in Lake Constance. EIFAC Occas. Pap. 15
- Elliott JM, Persson L (1978) The estimation of daily rate of food consumption of fish. J. Anim. Ecol. 47:977–993
- Engel S, Magnuson JJ (1976) Vertical and horizontal distribution of coho salmon (*Oncorhynchus kisutch*), yellow perch (*Perca flavescens*) and cisco (*Coregonus artedii*) in Pallette Lake, Wisconsin. J. Fish. Res. Board Can. 33:2710–2715
- Gilbert SJ, Johnson BM (in press) An efficient, easy-to-use stomach pump for live fish. Administrative Report, Wisconsin Department of Natural Resources, Madison
- Hamley JM (1975) Review of gill net selectivity. J. Fish. Res. Board Can. 32:1943–1969
- Hartmann J, Dahm E, Dawson J, Doering P, Jürgensen S, Lindem T, Löffler H, Raemhild G, Völzke V (1987) EIFAC experiments on pelagic fish stock assessment by acoustic methods in Lake Tegel. EIFAC Occas. Pap. 17
- Hasler AD, Bardach JE (1949) Daily migration of perch in Lake Mendota, Wisconsin. J. Wildl. Manage. 13:40–51
- Hasler AD, Tibbles JJ (1970) A study of depth distribution of perch (*Perca flavescens*) using a rolling gill net. Ber. Dtsch. Wiss. Komm. Meeresforsch. 21:46–55
- Hayward RS (1990) Comments on Boisclair and Leggett: Can eating really stunt your growth? Can. J. Fish. Aquat. Sci. 47:228–230
- Hewett SW, Johnson BL (1987) A generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin Sea Grant Institute, Madison
- Hewett SW, Kraft CE, Johnson BL (1991) Consumption, growth and allometry: A comment on Boisclair and Leggett (1989a,b,c,d). Can. J. Fish. Aquat. Sci. 48:1334–1337
- Hodgson JR, Carpenter SR, Gripentrog AP (1989) Effect of sampling frequency on intersample variance and food consumption estimates of nonpiscivorous largemouth bass. Trans. Am. Fish. Soc. 118:11–19
- Jacobson PT, Clay CS, Magnuson JJ (1990) Size, distribution, and abundance of pelagic fish by deconvolution of single-beam acoustic data. Rapp. P.-V. Réun. Cons. Int. Explor. Mer. 189:304–311

- Jobling M (1986) Mythical models of gastric emptying and implications for food consumption studies. Env. Biol. Fish. 16:35–50
- Johannesson KA, Mitson RB (1983) Fisheries acoustics. A practical manual for aquatic biomass estimation. FAO Fish. Tech. Pap. (240):249 p
- Johansson L, Persson L (1986) The fish community of temperate eutrophic lakes. In Riemann B, Søndergaard M (eds) Carbon dynamics of eutrophic, temperate lakes, Elsevier, Amsterdam, pp 237–266
- Johnson BL (1988) Using the bioenergetic model in the classroom. Bioenergetics Booter No. 1, University of Wisconsin Sea Grant Institute, Madison
- Johnson BM, Luecke C, Stewart RS, Staggs MD, Gilbert SJ, Kitchell JF (1992) Forecasting effects of harvest regulations and stocking on prey fish communities in a eutrophic lake. No. Am. J. Fish. Manage. (in press)
- Johnson BM, Stewart RS, Gilbert SJ (1991) Ecology of fishes in the Madison lakes. Wisconsin Department of Natural Resources, Federal Aid in Fish Restoration F-95-P, Madison
- Jurvelius J, Lindem T, Heikkinen T (1988) The size of a vendace, *Coregonus albula* L., stock in a deep lake basin monitored by hydroacoustic methods. J. Fish. Biol. 32:679–687
- Kitchell JF (1983) Energetics. In Webb PW, Weihs D (eds) Fish biomechanics, Praeger Press, New York, pp 312–338
- Kitchell JF, Stewart DJ, Weininger D (1977) Applications of a bioenergetic model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34:1922–1935
- Lindem T (1983) Successes with conventional *in situ* determinations of fish target strength. In Nakken O, Venema SC (eds) Symposium on fisheries acoustics, Bergen, Norway, 21–24 June 1982. FAO Fish. Rep. (300):104–111
- Lindem T (1990) Hydro Acoustic Data Acquisition System HADAS Instruction manual. Lindem Data Acquisition, Oslo
- Lindem T, Sandlund OT (1984) New method in assessment of pelagic freshwater fish stocks—coordinated use of echosounder, pelagic trawl and pelagic nets. Fauna 37:105–111
- Luecke C, Vanni MJ, Magnuson JJ, Kitchell JF, Jacobson PT (1990) Seasonal regulation of *Daphnia* populations by planktivorous fish: Implications for the spring clearwater phase. Limnol. Oceanogr. 35:1718–1733
- McCarty JP (1990) Diel periodicity of movement and feeding of yellow perch (*Perca flavescens*) in Lake Mendota, Wisconsin. Trans. Wisc. Acad. Sci. Arts Lett. 78:65–76
- Mulligan TJ, Kieser R (1986) Comparison of acoustic population estimates of salmon in a lake with a weir count. Can. J. Fish. Aquat. Sci. 43:1373–1385
- Ney JJ (1990) Trophic economics in fisheries: Assessment of demand-supply relationships between predators and prey. Rev. Aquat. Sci. 2:55–81
- Persson L (1986) Patterns of food evacuation in fishes: A critical review. Env. Biol. Fish. 16:51–58
- Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge, UK
- Post JR (1990) Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): In situ estimates and bioenergetic models. Can. J. Fish. Aquat. Sci. 47:554–560

- Rice JA, Cochran PA (1984) Independent evaluation of a bioenergetic model for largemouth bass. *Ecology* 65:732–739
- Rudstam LG, Binkowski FP, Miller MA (in prep) A bioenergetic model for analysis of food consumption by bloater in Lake Michigan
- Rudstam LG, Clay CS, Magnuson JJ (1987) Density and size estimates of cisco, *Coregonus artedii* using analysis of echo peak PDF from a single transducer sonar. *Can. J. Fish. Aquat. Sci.* 44:811–821
- Rudstam LG, Lindem T, Hansson S (1988) Density and in situ target strength of herring and sprat: A comparison between two methods of analyzing single-beam sonar data. *Fish. Res.* 6:305–315
- Rudstam LG, Magnuson JJ (1985) Predicting the vertical distribution of fish populations: An analysis applied to cisco (*Coregonus artedii*) and yellow perch (*Perca flavescens*). *Can. J. Fish. Aquat. Sci.* 42:1178–1188
- Rudstam LG, Magnuson JJ, Tonn WM (1984) Size selectivity of passive fishing gear: A correction for encounter probability applied to gill nets. *Can. J. Fish. Aquat. Sci.* 41:1252–1255
- Rudstam LG, Trapp TW (1987) Diel patterns of behavior and habitat utilization of cisco *Coregonus artedii* in two Wisconsin lakes. *Trans. Wisc. Acad. Sci. Arts Lett.* 75:70–78
- Schael DM, Rudstam LG, Post JR (1991) Gape limitation and prey selection in larval yellow perch (*Perca flavescens*), freshwater drum (*Aplodinotus grunniens*), and black crappie (*Pomoxis nigromaculatus*). *Can. J. Fish. Aquat. Sci.* (in press)
- Smagula CM, Adelman IR (1982) Day-to-day variation in food consumption by largemouth bass. *Trans. Am. Fish. Soc.* 111:543–548
- Traynor JJ, Ehrenberg JE (1979) Evaluation of the dual beam acoustic fish target strength method. *J. Fish. Res. Board Can.* 36:1065–1071
- Unger PA, Brandt SB (1989) Seasonal and diel changes in sampling conditions for acoustic surveys of fish abundance in small lakes. *Fish. Res.* 7:353–366

# **27**

## **Benefits on a Larger Scale**

**Michael D. Staggs**

One of the most troublesome questions raised by the Lake Mendota project has been whether the expenditure of \$1.2 million dollars over the study period has been rewarded with commensurate benefits for state aquatic management programs. The Wisconsin Department of Natural Resources (WDNR) Bureau of Fisheries Management, which initiated and funded the bulk of the project, has been consistently questioned by the public, the department administration, legislators, and even biologists within our own program about the cost/benefit ratio of this project. Critics are concerned with the high apparent cost and resulting trade-off in other more traditional management functions, the large number of fish stocked into one lake at the presumed expense of stocking programs in other areas of the state, perceived favoritism in selection of a study lake in the State Capitol area, and the validity of project goals and objectives, particularly those relating to potential improvements in water quality.

Other chapters in this book have detailed the project objectives (Kitchell, Ch. 1), administration and funding (Addis, Ch. 2), and some of the new technologies which have been developed (Rudstam and Johnson, Ch. 26). Although a detailed analysis of the cost/benefit ratio of the Lake Mendota project would be difficult and very subjective, this chapter will describe the larger benefits that have accrued from project work and allow the readers to judge for themselves whether the project has succeeded. Emphasis is placed on fisheries management questions and problems, but benefits for other WDNR programs are briefly addressed.

## Fisheries Sampling Techniques

Sampling procedures and data analysis techniques for fisheries surveys used by WDNR managers and researchers have varied extensively. Lack of standardization makes it difficult to compare fish populations across the state, and efficiency is lost as biologists must locally develop optimal sampling strategies. Sampling must often be repeated needlessly as managers find new surveys cannot be compared to old ones or those conducted on other waters.

One of the objectives of the Lake Mendota project was to evaluate traditional sampling methods and develop a useful set of index sampling techniques. Three years of intensive sampling using mark-recapture, creel survey, and a variety of catch/effort methods has shown that some traditional WDNR sampling methods are less useful than previously thought and have suggested some alternative techniques.

WDNR managers typically index game fish recruitment by shoreline electrofishing in fall (Hauber 1983). A specific quantitative relationship, the Serns index, between walleye young-of-year (YOY) catch/effort and population size (Serns 1982) is widely used throughout the state. This index was calibrated with mark-recapture estimates based on shoreline electrofishing circuits. Sampling the Lake Mendota walleye YOY population during 1986–89 quickly revealed that the Serns index did not apply to larger, southern Wisconsin lakes. Furthermore, even the mark-recapture methods did not adequately sample all of the walleye fingerlings. Currently, no single method appears to give a valid index of the abundance of walleye fingerlings, and in these larger lake systems it may be necessary to wait until the fish mature and can be adequately sampled in the spawning run to accurately determine year class contributions.

Standard shoreline seine stations have commonly been employed during WDNR comprehensive lake surveys to assess panfish and forage fish species abundance. Recent work in a northern Wisconsin lake has suggested that seine haul catches are extremely variable (Lyons 1986), and analysis of seine haul catches in Lake Mendota verified their limited usefulness in indexing population sizes. This led project biologists to experiment with other sampling gear such as small-mesh mini-fyke nets, purse seines, and trawls (Johnson et al. 1992c; Rudstam and Johnson, Ch. 26).

The two most common fish sampling methods used in Wisconsin are fyke nets fished during spawning runs, and shoreline electrofishing. However, significant questions have been raised concerning the representativeness of samples from these methods, particularly when deployed during spawning runs (e.g., Serns 1985). In Lake Mendota, spring fyke netting, fall and spring electroshocking, and summer experimental gill netting have all been used during the study. Size-specific mark-recapture estimates have allowed a comparison of the selectivity and efficiency of

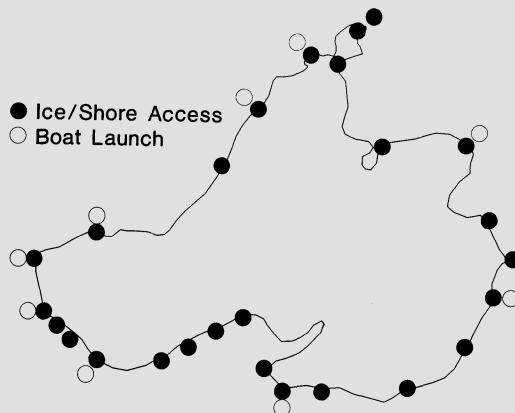
the various gear types for walleye, northern pike, and largemouth bass (Johnson et al., 1992b). This information was used to help design a standard walleye population estimation method for assessing tribal harvest impacts in northern Wisconsin (Hansen 1989) and for ongoing development of a standard fisheries management sampling and database system.

Field techniques for diet sampling are varied and usually developed locally with varying degrees of efficiency. Traditionally, diet analyses have not been frequently used by WDNR biologists because of the time needed for field sampling and sample processing. However, increasing interest in predator competitive interactions, control of panfish and rough fish, and (food web) impacts make bioenergetic analysis (Rudstam and Johnson, Ch. 26) and diet sampling an attractive alternative. During the Lake Mendota project, biologists have developed an easy-to-use standard diet sampling apparatus (Gilbert and Johnson 1992) and conducted a workshop on its use. Spin-off projects throughout the state are examining diets in conjunction with control of invading species in the St. Louis River, introduction of chinook salmon in Lake Superior, and impacts of high walleye density on the fish community of the Turtle–Flambeau Reservoir.

Gill nets are not often used to sample fish populations in inland Wisconsin lakes, primarily because they are unpopular with the public. However, the benefits of quantifiable gear selectivity and efficiency (e.g., Hamley and Regier 1973), the ability to fish randomly throughout the lake and year, and the vulnerability of all sizes and maturity stages make this gear desirable for obtaining representative samples of some fish species. Experimental gill netting has been evaluated throughout the study period during the Lake Mendota project and found to have many of the advantages stated above (Johnson et al. 1992c). Unfortunately, the relatively high mortalities previously discovered for gill nets for species such as walleye were confirmed (Johnson et al. 1992b).

## Routine Resource Inventories

Long time series of fisheries data are rare for Wisconsin waters because of lack of gear standardization, personnel changes over the years, large numbers of waters, and changing management priorities. As a result, fisheries managers do not have access to an adequate historical database for interpreting current survey information on their waters. One of the objectives of the Lake Mendota project was to develop a set of minimum sampling needs for long-term monitoring of the fisheries community on Lake Mendota and other similar waters. Results collected during 1986–89 provided the basis for a reduced-effort sampling program which can be used to monitor the future impacts of the predator biomass increase (Johnson et al. 1992c). The finding that the Lake Mendota ecosystem can



**Figure 27-1.** Location of fishing access points on Lake Mendota.

be highly variable was not surprising and underscores the need for long-term, routine monitoring of important community indicators.

### Creel Surveys

Design and implementation of inland creel surveys in Wisconsin has been standardized since 1978 (Staggs 1989). However, the method is cumbersome for large waters with multiple access points or large night or ice fisheries, such as Lake Mendota (Figure 27.1). Also, the standard computer program did not include variance estimates. The comprehensive access point creel survey designed for Lake Mendota in 1987 utilized a state-of-the-art “bus-route” clerk scheduling method (Robson and Jones 1989) and variance estimates (Johnson and Staggs, Ch. 17). The Lake Mendota creel survey was the first 24 h/day survey in Wisconsin providing an accurate picture of night harvest of walleye. The results contradicted a long-standing belief of managers that late-night harvest of walleyes during difficult-to-survey periods was a large share of the total harvest. This survey methodology has since been exported to surveys on two large northern Wisconsin reservoirs, the lower Wisconsin River and Green Bay.

### Regulation Evaluations

During the course of the study, several dramatic angling regulation changes were adopted and evaluated (Table 27.1). A minimum size limit for walleye of 381 mm (15 inches) was adopted in 1988, 2 years before a

**Table 27-1.** Comparison of Lake Mendota angling regulations and statewide angling regulations during the study period.

Species	Year	Minimum size limit		Daily bag limit	
		Statewide	Mendota	Statewide	Mendota
Walleye	1987	None	None	5	5
	1988–89	None	381 mm (15 inches)	5	3
	1990	381 mm (15 inches)	381 mm (15 inches)	5	3
	1991	381 mm (15 inches)	457 mm (18 inches)	5	3
Northern pike	1987	None	None	5	5
	1988–91	None	813 mm (32 inches)	5	1
Largemouth bass	1987–88	None	None	5	5
Smallmouth bass	1989–91	356 mm (14 inches)	356 mm (14 inches)	5	5
	1987–88	None	None	5	5
	1989–91	356 mm (14 inches)	356 mm (14 inches)	5	5

similar size limit was adopted statewide. Although size limits for walleyes have been regarded as “off-the-shelf” technology elsewhere (Brousseau and Armstrong 1987), managers in Wisconsin were reluctant to use them after mixed results from two earlier evaluations (Serns 1978, 1981). Modeling done to determine optimum size limits for Lake Mendota and early results from the limit (Johnson et al. 1992a) contributed to the institution of the statewide limit. Preliminary findings on Lake Mendota that the targeted walleye fishing effort and the exploitation rate of vulnerable-sized fish increased dramatically (Johnson and Staggs, Ch. 17) alerted the WDNR to the need for careful evaluation of the statewide limit and static-fishery modeling assumptions.

Statewide minimum size limits of 356 mm (14 inches) for largemouth and smallmouth bass went into effect in 1989. Information collected during the Lake Mendota project will provide the only comprehensive evaluation of the regulation in the state.

Lake Mendota has also been a proving ground for highly restrictive regulations designed to provide virtually complete protection for a species undergoing population rehabilitation. A “trophy-only” 813-mm (32 inches) minimum size limit (one daily bag limit) for northern pike was implemented when early surveys showed there were too few adult northern pike even to estimate. The success of the size limit in Lake Mendota, in part, prompted the WDNR to propose “trophy” northern pike regulations on 10–12 lakes throughout the state. The 351-mm (15 inches) walleye minimum size limit was raised to 457 mm (18 inches) in 1991 after growth, harvest, and exploitation results in 1989 showed females were not adequately protected. Stockings have increased the number of smaller fish, which are now protected pending determination of the capability for natural reproduction.

**Table 27-2.** Total angler harvest from Lake Mendota and percent of harvest that was smaller than the legal minimum size limit.

Species	1988		1989	
	Harvest	Sublegal	Harvest	Sublegal
Walleye	1,471	17%	3,989	10%
Northern pike	95	0%	203	33%
Largemouth bass	624	No min. size	628	42%
Smallmouth bass	2,041	No min. size	594	33%

An analysis of the creel survey data gave our first statistically accurate look at regulation compliance. Results were generally discouraging (Johnson et al. 1992c). In 1989, sub-legal-sized fish comprised from 10% to 42% of the total harvest of bass, walleye, and northern pike (Table 27.2). Compliance with the walleye size limit did improve slightly in the second year of the regulation, lending hope that overall compliance will improve as anglers become more familiar with the regulations.

## Stocking

Stocking is universally viewed by anglers as a “cure-all” for any fisheries management problem. However, evidence is mounting that much stocking—particularly in naturally reproducing populations—may be ineffective (e.g., Mraz 1968; Kempinger 1977) or actually harmful (e.g., Gresswell and Varley 1988). The Lake Mendota project provided a detailed multiyear examination of the success and impacts of walleye and northern pike stocking. Preliminary results from the northern pike fingerling stocking were encouraging. Survival was relatively high and the population of spawning fish rose dramatically by 1990 (Johnson and Staggs, Ch. 17). Stocking of northern pike fry, in contrast, produced few fingerlings.

Results of walleye stocking have been mixed. Fry stocking has generally been unsuccessful (Johnson et al. 1992b, 1992c), while some fingerling stockings have been successful. Estimation of survival was hampered by the difficulty in accurately sampling walleye young; however, adult walleye numbers have been steadily rising (Johnson and Staggs, Ch. 17).

Lake Mendota stocking results, however, underscore the high cost of stocking. Although not even meeting requested stocking quotas in some years, walleye and northern pike fingerling stockings into Lake Mendota have been 14% and 58%, respectively, of the total WDNR hatchery statewide production during 1987–89 (Table 27.3). These numbers alone would suggest that Lake Mendota today should be overflowing with game fish; however, the population densities observed are still only average.

**Table 27-3.** Comparison of statewide hatchery fry and fingerling production and number of fish stocked in Lake Mendota during the study years. Numbers in parentheses are percent of statewide production.

Year	Size	Northern pike		Walleye	
		Statewide	Mendota	Statewide	Mendota
1987	Fry	14,583,482	10,760,000 (74%)	46,124,000	20,100,000 (44%)
	Fingerling	37,794	23,434 (62%)	2,881,524	550,000 (19%)
1988	Fry	26,675,400	9,923,400 (37%)	80,088,711	26,865,000 (34%)
	Fingerling	2,583	2,520 (98%)	2,974,603	500,986 (17%)
1989	Fry	20,579,388	10,000,000 (49%)	49,085,972	20,000,000 (41%)
	Fingerling	43,970	22,732 (52%)	5,369,546	510,038 (9%)
Sum	Fry	61,838,270	30,683,400 (50%)	175,298,683	66,965,000 (38%)
	Fingerling	84,347	48,686 (58%)	11,125,673	1,561,024 (14%)

Survival of stocked fish to adult stage was variable and often low; survival to angler creel was lower still. Lower-than-expected returns have raised significant questions about existing WDNR stocking procedures and what can actually be expected from stocking.

This project has demonstrated that a high-density population is most cost-effectively produced by natural reproduction. Unless the department can find funds to establish a hatchery operation on the shores of Lake Mendota such as has been done on Oneida Lake, New York (Forney 1980), the current fishery cannot be sustained. More modest stocking levels, such as those from the 1970s, will produce only a lower-level "background" fishery—although current regulations should ensure a better fishery than was achieved in earlier years. Modeling techniques developed as part of the project (Johnson et al. 1992a) can be used to better predict the results from maintenance stocking plans.

Analysis of the Lake Mendota stockings has been our best look at the use of walleye stocking both to generate a fishery and for rehabilitation. The results are being extensively used in the development of a WDNR walleye management plan which recognizes that WDNR hatcheries cannot sustain high stocking levels on more than a relative handful of lakes statewide. Consequently, waters selected for intensive stocking must have

potential for restoration or establishment of natural reproduction if long-term fishery improvements are expected.

### **Importance of Habitat Protection and Natural Reproduction**

The finding that intensive stocking is not an economically practical way to perpetuate a high-density game fish population forced fisheries managers to concentrate on ways to ensure and improve natural reproduction. In addition to building an adequate spawning population through stocking and harvest control, steps were taken to optimize available spawning and nursery habitat. Lake Mendota wetlands are a prime northern pike spawning area. During 1987–89, WDNR fisheries managers worked with local municipalities to open access channels to previously inaccessible wetlands, raise and stabilize spring water levels, build a controlled rearing pond, and protect critical macrophyte habitat.

### **Research–Management Cooperation**

When the Lake Mendota project started, working relationships between aquatic research programs at the WDNR and the University of Wisconsin, and WDNR fisheries management programs were at an ebb. Similar problems have been documented in the water resources programs of other agencies (Cullen 1990). One of the objectives of the project was to improve these relationships to mutual benefit, and much has been accomplished toward this objective.

From the management agency perspective, design and execution of a large-scale management-oriented research project such as that on Lake Mendota has many benefits. The technical competence of managers is improved through exposure to current research methods and interaction with top scientists in the field. The research product is ultimately more valuable to management, since management input is continuously incorporated into project design and activities. Such projects can also bring state-of-the-art science to bear on management problems of special importance. The long-term working relationships developed also provide managers with better routine access to scientific expertise for future projects.

From the research agency perspective, collaborative projects can mean more than simply research support dollars. Researchers gain a better understanding of the immediate problems and limits that management agencies face. This ultimately translates into project proposals more attractive to management agencies. For example, the original Lake Mendota proposal called for study of a one-year hyperstocking of walleyes. It soon became apparent, however, that existing hatchery capacity

and competing stocking priorities elsewhere in the state made such stocking levels impractical both for this project and for any similar future management applications. The project had to be redesigned to examine the impacts of walleye stocking levels more in line with state production capacities. The project then became much more attractive to the WDNR management program.

Lake Mendota project researchers were also able to take advantage of technical expertise and data existing within the management agency that otherwise might be unavailable in more typical research projects. Management strengths in game fish sampling, creel surveys, and dealing with local angler groups as well as long-term fisheries and limnological data sets were all used to advantage during the Lake Mendota project.

The benefits of successful collaborative research–management projects nurtured on the Lake Mendota project have spread via migrations of graduate students and postdoctoral fellows to many other areas. Lake Mendota project alumni are now actively working in Utah, British Columbia, Ohio, Alberta, Idaho, and even Australia. In many cases, these researchers have developed similar collaborative projects with the same range of benefits for local management and research programs.

## Water Quality Management

One of the initial objectives of this study was to see if high-density predator stocking could reduce the average levels of phytoplankton in Lake Mendota, thereby improving a local water quality problem (Kitchell, Ch. 1). Skeptics concluded before the study began that phytoplankton growth was nutrient driven and food web manipulation was doomed to failure. In fact, the results of this project demonstrate conclusively that food web manipulations can have profound impacts on phytoplankton densities—if not always the ones we prefer. Through 1989, large zooplankton densities increased and average phytoplankton levels declined (Vanni et al., Ch. 13). In 1990 blue-green algae levels reached near-record levels despite high zooplankton abundance, suggesting that the effects of food web manipulation on blue-green algae are highly variable (Lathrop and Carpenter, Ch. 7; Carpenter et al., Ch. 22; Carpenter, Ch. 23).

The challenge to the water quality biologists, then, is to determine whether these interactions are predictable and whether there are realistic goals for species composition within the fish community that fisheries managers can strive for. Modeling and experimental enclosure results suggest that, if we are willing to tolerate some system variability, improved average water quality may in fact be achievable. This concept has already been implemented by the WDNR in a 1990 whole-lake restoration project on highly eutrophic 839-ha (2,072 acres) Lake Delevan

in southeastern Wisconsin. Clean-up efforts included watershed non-point pollution controls, upstream wetland restoration, alum treatments, and diverting nutrient-rich tributary inflows downstream. The fishery—formerly dominated by planktivorous bigmouth buffalo (*Ictiobus cyprinellus*)—was chemically treated and restocked with piscivores specifically to increase phytoplankton predation.

Other practical spin-offs of the Lake Mendota project for water quality specialists within the WDNR are more difficult to describe because the WDNR water resources management personnel who would benefit most from these advances were not involved in the project. High performance liquid chromatography (HPLC), described by Hurley et al. (Ch. 5), has tremendous potential for reducing the time needed to adequately identify and quantify phytoplankton abundance and zooplankton diet samples. Paleolimnological techniques described by Kitchell and Sanford (Ch. 4) have benefits in determining the historical productivity of disturbed lake systems. Certainly the aquatic community system models developed during the project have potential for understanding and developing management plans for other large waters similar to Lake Mendota. This volume is a major step in describing and making available potential water quality management benefits.

### **System Management Models**

Another critical objective of the Lake Mendota project was to develop aquatic community system models which could be used to help develop management plans. The ultimate usefulness of these models remains to be seen, since most are only now being calibrated and reported. However, these models are being actively used to explain and understand the Lake Mendota ecosystem. In the future, management plans may contain target predator and forage species abundances, nutrient loading limits, or desirable lake level ranges. It may be necessary to use a system model to “correct” for foodweb effects when analyzing the impacts and effectiveness of current municipal and WDNR watershed pollution control programs.

### **Summary: Showcase Management**

The WDNR Fisheries Management Strategic Plan, “FISH 2,000,” adopted in 1987, specifies that showcase management and increased public participation in management activities are two strategic directions for the twenty-first century. Showcase management allows concentration of management effort on large, high-visibility waters. Positive results not

only create locally enhanced fishing and economic opportunities but demonstrate the benefits (and limits) of management efforts, building support for similar efforts on other waters. Higher public awareness and enthusiasm also result in increased public participation in cooperative management programs.

The Lake Mendota project is the best example of showcase management that has been initiated by the WDNR fisheries program since the strategic plan was developed. A critical stated goal of the project was to produce an outstanding game fishery, and that goal has been met. Gamefish populations have been increased substantially from the 2 fish/ha (all species combined) present at project start (Johnson et al. 1992b), and angling effort and harvest have dramatically increased (Johnson and Staggs, Ch. 17). A recent outdoors article listed Lake Mendota as the top new walleye fishing lake in Wisconsin (Small 1990).

Success of angling regulations usually rests on acceptance by the fishing public, for law enforcement presence is often minimal and noncompliance can quickly eliminate the benefits of any regulation (Gigliotti and Taylor 1990). The success of new, more restrictive regulations in Wisconsin has been mixed. A 1984 walleye slot-size limit on Pine Lake in northern Wisconsin was abandoned after local support waned. Public pressure has led to widespread and sometimes unwarranted exemptions of individual lakes from a recent statewide walleye minimum size limit. At public hearings in 1990, proposals for more restrictive statewide northern pike regulations were soundly rejected.

In contrast, Lake Mendota is the most strictly regulated sport fishery in the state and acceptance of these regulations has been positive and widespread. Local anglers and sportsmen's groups have repeatedly supported efforts to protect rebuilding game fish stocks with higher size limits, and a recent popular article hails fisheries work on Lake Mendota as producing a "fisheries management model" for Wisconsin (Peck 1990). The positive correlation between the improving fishery and the presence of restrictive harvest regulations will help to build public support for such needed regulations on other waters.

Although stocking is not a cure-all for overfishing and habitat degradation, it is a valuable tool for rehabilitation of fisheries and selected development of put-grow-and-take fisheries. Unlike most previous WDNR efforts in Lake Mendota and other lakes statewide, heavy game fish stocking was coupled with habitat improvement efforts and harvest regulation to restore high levels of natural reproduction in the lake. At the time of publication of this chapter, it is too early to tell if significant natural reproduction will occur, but high-density stockings and harvest regulations will ensure that adequate adults are present at maturity. Success in natural reproduction of walleye or northern pike will yield a long-term, low-cost fishery, while failure of natural reproduction will

allow the WDNR to design a fishery around species more suited to the Lake Mendota environment.

In the meantime, the perception that the WDNR is “doing something” to dramatically improve fishing has developed widespread support for programs in the area and encouraged angler cooperation in programs with true long-term benefits such as catch-and-release, water level control, and protection of important macrophyte beds. The project provided valuable data and an excellent case study of the costs and benefits of stocking as a management tool, rather than the usual public perception of stocking as a “cure-all.”

Even within the scientific community, the Lake Mendota project can be viewed as a showcase management project. The project has generated numerous scientific publications (as can be seen from this book) and participation by the WDNR has enhanced our reputation as a national leader in fisheries management. This has direct program benefits in attracting talented employees, improving the general level of technical competence within the WDNR, and ultimately improving our management of the resource.

## References

- Brousseau CS, Armstrong ER (1987) The role of size limits in walleye management. *Fisheries* 12:2–5
- Cullen P (1990) The turbulent boundary between water science and water management. *Freshwat. Biol.* 24:201–209
- Forney JL (1980) Evolution of a management strategy for the walleye in Oneida Lake, New York. N.Y. *Fish Game J.* 27:105–141
- Gigliotti LM, Taylor WW (1990) The effect of illegal harvest on recreational fisheries. *No. Am. J. Fish. Mngt.* 10:106–110
- Gilbert SJ, Johnson BM (1992) An efficient, easy-to-use stomach sampling device for live fishes. Wisconsin Department of Natural Resources Administrative Report No. 33
- Gresswell RE, Varley JD (1988) Effects of a century of human influence on the cutthroat trout of Yellowstone Lake. *Am. Fish. Soc. Symp.* 4:45–52
- Hamley JM, Regier HA (1973) Direct estimates of gillnet selectivity to walleye (*Stizostedion vitreum vitreum*). *Can. J. Fish. Aquat. Sci.* 30:817–830
- Hansen MJ (1989) A walleye population model for setting harvest quotas. Wisconsin Department of Natural Resources Fish Management Report No. 143
- Hauber AB (1983) Two methods for evaluating fingerling walleye stocking success and natural year-class densities in Seven Island Lake, Wisconsin, 1977–1981. *No. Am. J. Fish. Manage.* 3:152–155
- Johnson BM, Luecke C, Stewart RS, Staggs MD, Gilbert SJ, Kitchell JF (1992a) Forecasting effects of harvest regulations and stocking on prey fish communities in a eutrophic lake. *No. Am. J. Fish. Manage.* (in press)
- Johnson BM, Stewart RS, Gilbert SJ (1992b) Ecology of fishes in the Madison Lakes—1987. Wisconsin Department of Natural Resources Fish Management Report No. 147

- Johnson BM, Stewart RS, Gilbert SJ (1992c) Ecology of fishes in the Madison Lakes—1988–1989. Wisconsin Department of Natural Resources Fish Management Report No. 148
- Kempinger JJ (1977) Cost of stocked walleyes caught by anglers in Escanaba Lake. Wisconsin Department of Natural Resources Research Report No. 91
- Lyons J (1986) Capture efficiency of a beach seine for seven freshwater fishes in a north-temperate lake. *No. Am. J. Fish. Manage.* 6:288–289
- Marz D (1968) Recruitment, growth, exploitation and management of walleyes in a southeastern Wisconsin lake. Wisconsin Department of Natural Resources Technical Bulletin No. 40
- Peck T (1990) Lake Mendota: A Wisconsin fisheries management model. *Wisc. Sportsman* 1990:28–53
- Robson D, Jones CM (1989) The theoretical basis of an access site angler survey design. *Biometrics* 45:83–98
- Serns SL (1978) Effects of a minimum size limit on the walleye population of a northern Wisconsin lake. *Am. Fish. Soc. Spec. Publ.* 11:390–397
- Serns SL (1981) Effects of a minimum length limit on the walleye population of Wolf Lake, Vilas County, Wisconsin. Wisconsin Department of Natural Resources Fish Management Report No. 106
- Serns SL (1982) Relationship of walleye fingerling density and electrofishing catch per effort in northern Wisconsin lakes. *No. Am. J. Fish. Manage.* 2:38–44
- Serns SL (1985) Proportional stock density index—is it a useful tool for assessing fish populations in northern latitudes. Wisconsin Department of Natural Resources Research Report No. 132
- Small D (1990) Wisconsin's winning walleye waters. *Wisc. Sportsman* 1990:20
- Staggs MD (1989) Walleye angling in the ceded territory, Wisconsin, 1980–87. Wisconsin Department of Natural Resources Fish Management Report No. 144

# **28**

## **Summary: Accomplishments and New Directions of Food Web Management in Lake Mendota**

**James F. Kitchell and Stephen R. Carpenter**

### **Accomplishments**

An experienced reviewer pointed out that many readers will gauge their interest in a book by initially examining its first and last chapters. This chapter is intended to assure that those readers get the main elements of our message. It identifies and restates the general as well as some of the specific conclusions derived from this work. It also offers some updating of the limnological events that have transpired since the manuscripts were written and offers a forecast of what we expect will occur over the next few years.

As nearly as we can tell, 1987 was as close to a typical year as any for the recent past of Lake Mendota. In a more pragmatic sense, we employed the full suite of our standard methods in that year and have logically used it as the basis for many of the detailed comparisons. The major cisco mortality late that summer initiated food web changes most dramatically evident in the summer of 1988 and sustained to the present. The stocked populations of northern pike and walleye are having an increasing effect as predators. Although perch and cisco have spawned each year, the resultant year classes have been relatively weak. In short, piscivory has increased regularly since 1987, predation by zooplanktivores has decreased, and large *Daphnia* have dominated the zooplankton each summer for the period of 1988–91.

If food web interactions were the sole or predominant regulator of water quality in Lake Mendota, then the miracle of the summer of 1988 should have been sustained. Obviously it was not, and therefore we reject

the hypothesis that food web interactions are the sole regulator of algal community structure. One alternative hypothesis, that nutrients are the sole regulator of phytoplankton production and species composition, is also unsupported. The paleolimnological record, statistical analysis of the long-term neolimnological records, the results of experimental studies, and the events of 1988 all force rejection of the nutrients-alone hypothesis.

In fact, forcing the choice between food web effects and nutrient effects is a simple-minded and debilitating exercise. Nutrient and food web effects interact, they alternate in importance, and they operate with different time frames and spatial scales. They are not independent of the weather nor of the physical factors that regulate the volume and mixing of water masses where they interact.

Contrary to the wishes of statisticians, there is only one Lake Mendota. There are analogues and homologues, but the probability of finding a true replicate is exceptionally small. Lake Mendota has been and will be managed as a unique entity if for no other reason than that the social and political context of doing fishery and water quality work there is unique. As we have demonstrated, that fact is a very important one. That is one of the major lessons learned as a result of this effort.

We learned that certain differences among species can matter. In an ecological context, some are very different. In a management context, some are more desirable. For example, *Daphnia galeata* and *D. pulicaria* can be of similar size in Lake Mendota, but the latter has a severalfold greater effect on the phytoplankton. Shifting the balance of these two species is the key component to this biomanipulation effort. When the exotic *Myriophyllum* replaced the native *Vallisneria* and *Potamogeton*, total macrophyte biomass did not change dramatically, but Eurasian milfoil makes itself visible to the public and they reacted with a major harvesting and chemical control program. That becomes an important issue for food web management because the littoral zone is a habitat critical to the life histories of many fishes.

Other lessons at the species level included the evidence that Lake Mendota is not an optimal habitat for the walleye and that northern pike may become the predator of choice. We stocked 30 times more walleye fingerlings than pike, yet fully 50% of the total piscivory was due to the latter. We also learned that the State's hatchery system cannot produce enough walleyes to meet the ecological demand of complete piscivore dominance and that the political demand for walleyes elsewhere makes that even less likely.

We learned that size at stocking has a huge effect on survival. One unfortunate reality is that most of the hatcheries are generally located in the northern parts of the state. Shipping those fish into southern waters is the equivalent of putting them 2–3 weeks behind the ontogeny of predator-prey interactions that so strongly influence their early survivorship. The good press that preceded their arrival caused higher expecta-

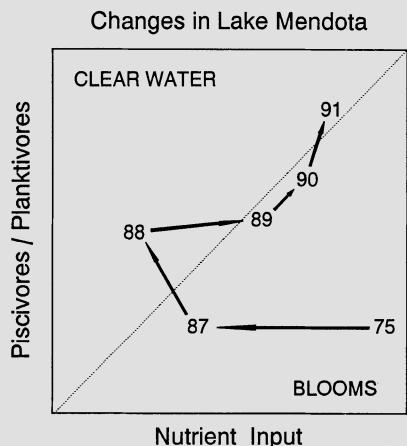
tions. The ecological realities that followed caused a reconsideration of fisheries management activities and, surprisingly, an even stronger commitment of public support to the goals of the program. Lake Mendota now has among the most restrictive trophy fishery regulations in the state.

Since 1988, we have been praying for a spring of average runoff and its consequent nutrient load so that we could witness food web effects less confounded by exceptional nutrient conditions. That hasn't happened. The local agricultural practices involve a winter of spreading manure on fields which were plowed the previous autumn. Urban development within the drainage basin continues its exponential rise. Runoff and nutrients were generally higher in 1989, and blue-green blooms reappeared during the summer.

The spring of 1990 brought intense rains on still-frozen soils. A massive runoff resulted and nutrient loadings increased yet again. Instead of the expected spring bloom of diatoms, we witnessed an intense bloom of blue-green algae, dominated by *Aphanizomenon flos-aquae*. Periodic strong winds delayed stratification. The continuous mixing that resulted kept those nutrients from being sequestered in the hypolimnion and the blooms persisted. Feedback through the food web probably contributed to the maintenance of blooms. Grazing was intense but selective for small edible forms and, of course, offered recycled nutrients to the ungrazed blue-greens and fostered their growth. At one point in the early summer of 1990, algal biomass was 99.6% blue-greens. Incredible abstract forms appeared in the resulting surface scums, although the average citizen did not find them aesthetically pleasing. On the positive side, shading by the blooms produced a poor year for littoral macrophytes and complaints about weeds were minimal.

While preparing the final draft of this volume we are witnessing the spring and early summer of 1991, which has brought yet another unexpected result. Although piscivory continues to increase and predation on *Daphnia* continues to decline, total phosphorus levels this spring were among the highest ever recorded. We expected more algal art. Instead, we had a spring bloom of diatoms, the lake stratified on schedule, large *Daphnia* flourished, and we are seeing one of the longest clear-water phases we've witnessed. Based on these events, we have updated the diagram that relates food web structure and nutrient loading (Figure 28.1). We will restate the lesson emphasized earlier: there is strong need for insightful studies of the interactions between nutrient loading and food web structure. Those studies could best be done on whole lakes because the physics of mixing and the mobility of fishes require that scale.

We started this project with the idea that managing fish was a way to manage water quality. We learned that managing people has to come first. That reality is among the conventional wisdom of experienced fisheries folk, but even they were surprised by the strong response of the angling public. Remarkable administrative and political effort was



**Figure 28-1.** Simplified conceptual diagram of the interactions of food web structure and nutrient loading as regulators of blue-green algal blooms. This extends the description of Carpenter (Ch. 23) to include the observations for 1990 and 1991.

required to allocate the large number of stocked fish to the waters of one lake. Equally remarkable was the rate at which their predator responded. This predator learns rapidly. It communicates quickly. A modest number of those most experienced and skilled can quickly undo a carefully planned food web manipulation. At the ecosystem scale for lakes, this role of humans is insufficiently appreciated and poorly anticipated.

### New Directions

While the interannual variability of Lake Mendota will probably continue to fascinate and surprise its observers, we can forecast a series of changes that are both highly likely and most desirable. These are:

1. Nutrient abatement must continue. Agricultural practices remain the major source. Pointing the finger at beleaguered farmers should be replaced by action programs that fully subsidize the cost of controlling non-point sources. The people who sail, ski, fish, or gaze on Lake Mendota should be expected to cover the cost of its maintenance and improvement.
2. Prepare for a major recruitment event **or** a substantial and continuing change in fish community structure. All our analyses lead to the conclusion that an ecological vacuum exists at the zooplanktivore level. If the perch and/or cisco are to sustain their dominance in the face of growing piscivory, then there must be a strong year class within the next few years. Alternatively, the gradual change to a fish community dominated by littoral zone species will continue. In either case, a continuing research effort must record the outcome and fisheries managers must work to redirect public expectations.

3. Efforts to protect and foster the large predators—northern pike, in particular—should increase through restoration and protection of spawning marshes, development of a local hatchery operated in cooperation with angling clubs, and maintenance of fishery regulations. Lake shore property is valuable real estate but its development typically includes disturbed soils, green lawns, greater runoff, and the increased nutrient loading that results. A better view of the lake will make the lake less desirable to look at. Stronger constraints on shoreline and riparian development should be a primary goal for the institutions that regulate urban growth. Scientists need to offer the best of informed advice to that process.
4. The role of the littoral zone must be added to the whole-system view. Interactions with the pelagic food web derive from the life histories and behaviors of fishes. They also derive from the diversity of public interests that alternately demand more or less littoral vegetation. Attention to an ecologically sensible compromise is an obvious need.
5. Managing the human component of this ecosystem is a significant challenge. The kinds of regulatory constraint now employed to reduce the effect of the angling predator may prove insufficient. A proper scientific understanding may prove elusive, but we need to encourage the pursuit of that prospect. This predator is ecologically potent and it can vote.

Perhaps the most enduring benefit of this program will derive from the experiences of the people who participated in it. The graduate students and postdocs learned both the scientific and the political components of a large-scale and complex project. They knew that doing good research usually requires some extramural funding. They learned that the intensity of competition at the centroids of basic or applied funding agencies tends to reinforce conformity and restrict freedom of inquiry. They learned that working the interface of research and management requires some special skills and offers some unique opportunities. They learned that the world of management decisions is importantly different but not independent from that of the researcher. Based on the several examples seen since our first generation of program participants left Madison, the lessons have been worthwhile. Analogous projects are now initiated in states and provinces far distant from Lake Mendota.

The state agency participants—including researchers, managers, and administrators—learned that creating a partnership rather than a rivalry with the university can lead to substantial gains. They learned that tools designed in the ivory tower can be forged to make them of practical value. Academics have the freedom to have lots of ideas. Being around and involved when those are developing can yield tremendous benefits.

Perhaps the most important lesson for other scientists and managers is that fisheries management can readily become food web management,

which can improve both water quality and angling. That causes researchers, resource managers, and the public to gain a greater perspective because it allies the sometimes disparate interests of various constituencies. It also encourages adoption of an ecosystem approach, which is widely advocated but usually difficult to accomplish. Although development of similar programs elsewhere will undoubtedly have many idiosyncratic elements, the lessons from our experience can help promote more effective planning, reduce the undesirable surprises, and minimize mistakes.

We have probably been insufficiently modest and not fully objective in describing this program. The accidents of history and geography play a large part in its development because they are the reasons that Madison is sited on the shores of Lake Mendota, thereby juxtaposing a research institution and the administrative center of the state resource agency. Further, we've been able to employ nearly a full array of methods in this project. Few institutions could afford that. It's also not likely that many places have the benefit of a century-long string of limnological observations. Given all that, we are only barely emerging from the twilight of uncertainty about what will happen in 1992.

The Lake Mendota program will continue well into this decade. We will have some major surprises along the way, but the commitment to large-scale and sustained food web manipulation will probably enhance our learning rate. We are reminded of another, local interaction: when younger scientists discuss their work with Art Hasler, they often point out that every year is different and that they are frustrated by the unpredictability of algal blooms. Based on observations made while walking the lake path to work for more than four decades, he typically responds with an observation such as "That's right, but it's better than it used to be." We hope his judgment will be that our work produced both a more rapid improvement in the average condition and some increase in the things we understand.

# Index

**Acanthocyclops vernalis**, 138, 234  
acoustic, 284–286, 511–519  
adaptive management, 3, 377  
**Addis**, J., 1–2, 7, 32, 428, 520, 525  
age-structured model, 502  
agriculture, 1, 17–19, 32–38, 43, 45, 78, 89, 240, 315, 520, 541–542  
aldrin, 187–188  
algal growth rate, 472  
algal succession, 483  
*Ambloplites*, *see* bass, rock  
*Ambrosia*, *see* ragweed  
*Amia*, *see* bowfin  
ammonia nitrogen, *see* nitrogen, ammonia  
ammonium excretion, 71, 103, 244, 249, 263  
amphipods (*Hyalella*), 177–178, 190  
*Anabaena*, 98–100, 115–116, 120–121, 234, 255  
angler, 7–9, 12–14, 235, 357, 362–374, 383, 419, 529–531, 533, 536  
antennules, 34–35  
*Aphanizomenon*, 98–100, 116–117, 120–122, 147, 234, 254–255, 269, 541  
*Aplodinotus*, *see* freshwater drum  
Aquatic Resources Trust Fund, 10  
autocorrelation, 98, 104–106, 136–137

banded killifish (*Fundulus*), 204, 207, 209, 220–221, 228  
bass, 319, 326, 225–343  
black, 208, 215–216, 218–219, 221, 330, 335–338, 341–343  
largemouth (*Micropterus salmoides*), 8–9, 201, 204, 207–208, 216, 228, 305, 324, 326, 329, 330, 337–338, 341–342, 355–358, 360–364, 494–495, 527  
rock (*Ambloplites*), 201–204, 207, 209, 228, 305  
smallmouth (*Micropterus dolomieu*), 194, 201, 204, 207–208, 216, 228, 239, 325–326, 330, 337–338, 341–342, 360, 364  
white (*Morone chrysops*), 41, 199, 201, 204, 207, 209, 215, 221, 228, 234, 236, 239, 283, 287, 305, 319, 321, 332–334, 358–362, 515–517  
yellow (*Morone mississippiensis*), 194, 202, 204, 207, 209, 218–219, 224  
benthivores, 198, 200–203, 206–207, 209–211, 220, 223–224, 231  
benthos, 174–176, 181, 183, 185–187, 189–190, 217  
benthic macroinvertebrates, 173, 176–177, 186, 234, 286, 468, 487

- bioenergetics, 12, 275, 288, 290–291, 294, 297, 320, 322, 323, 326, 332, 338, 340–343, 346, 348, 355–356, 366, 370, 377, 380, 389, 445, 451, 497, 507–509, 519
- biomanipulation, 1, 10, 168, 237, 353–354, 370, 373, 457, 493, 503, 507, 540
- bioturbation, 36
- Black Earth Creek, 70, 78, 239
- blue-green algae, 1–3, 53, 56–57, 64–65, 69, 74, 97–103, 105, 107–108, 110–113, 116–117, 119–123, 142–144, 146–148, 255, 378–379, 428, 437, 440, 455–457, 458, 461–466, 468–470, 476–477, 483, 486–488, 533, 542
- bluegill (*Lepomis*), 199, 201–205, 207, 209, 222, 224, 228, 234, 305–310, 312, 321, 332–335, 339, 357–359, 361–363, 420, 495, 496, 498
- boaters, 8
- Bosmina*, 31, 34–35, 40, 42–43, 139–140, 248, 276
- bowfin (*Amia*), 202–204, 207–208, 222, 224, 228
- brook silverside (*Labidesthes*), 305, 336–337
- Ca**, *see* calcium
- caddisflies (*Leptocella*), 177–178
- calcium, 24–27, 33–36, 53, 103, 133, 245, 464–465
- cannibalism, 314–315, 325, 335–336, 348, 391–392, 453, 458
- carotenoid, 50, 52–59, 62, 64, 228
- carp (*Cyprinus*), 187, 193, 198, 200, 204–207, 209, 211, 215, 217–219, 222, 224, 305
- catch per unit effort, 239, 321, 323, 328, 330, 332, 356, 363, 398–399, 517, 518
- Centrarchidae, *see* bluegill
- Ceratium hirundinella*, 98–103, 107–108, 112, 115–117, 121–122, 234–235, 254–255, 267, 269, 279, 408
- Ceratophyllum*, 152, 154, 164–165, 178
- Ceriodaphnia*, 34, 42
- cesium-137, 35, 51–52, 59
- Chaoborus*, 176, 185–187, 189
- Chaoborus punctipennis*, 181, 183, 186
- Chara*, 152–155, 160–161, 166–168, 178
- chloride, 27, 71
- chlorophyll-a, 49–50, 52–61, 101–102, 107–109, 117–119, 248–249, 261–263, 432, 462, 465–466, 468–469, 475, 484–485
- chromatography, *see* High Performance Liquid Chromatography (HPLC)
- Chroococcus*, 115–116
- Chroomonas*, 98, 100, 113–116, 253
- Chydorus*, 34–35, 37–39, 128–129, 139
- cisco (*Coregonus*), 2, 40–43, 45, 87, 90–92, 135, 141–142, 145–146, 193–194, 198–201, 203–204, 207, 209, 215, 221–224, 228, 234–240, 244, 256, 263, 266–269, 275, 280, 283, 286–294, 296–298, 306, 308–310, 314, 361, 408–409, 411–413, 415–421, 434–435, 437, 446, 476, 490, 511, 515, 517, 539, 542
- cisco kill, 91–92, 142, 145–146, 237, 238
- clear-water phase, 57, 66, 83, 86, 107, 112, 122, 144, 146–147, 234, 249, 253–256, 258, 261–263, 266–269, 296, 432, 435, 443–447, 468, 474, 483–484
- clearance rate, 245–246, 257, 263–265, 267–268, 270, 280–281, 283
- climate, 20
- Coelosphaerium*, 99, 115, 121
- compared sampling methods, 25, 53, 61, 71–72, 76, 90, 102, 110, 133–134, 141, 153, 161, 255–256, 266–267, 270–271, 275, 280, 307, 361, 372, 416–417, 420, 441, 443, 446, 484, 496, 509, 512, 526
- electrofishing, 526
- fyke netting, 526
- seining, 526
- Sern's index, 526
- competition, 9, 33, 282, 303, 373, 390–393, 400–401, 473–474, 543
- coolwater fishes, 198, 203, 205, 213, 222–224, 231
- Copepoda, 33, 235
- Coregonus*, *see* cisco

- coring, 32–33, 35–42, 44, 50–52, 61–63, 65–66, 91, 145, 519  
cost/benefits, 525  
habitat protection, 525, 532–533, 535, 536  
CPUE, *see* catch per unit effort  
crappie, 199, 207, 209, 228  
  black (*Pomoxis nigromaculatus*), 201, 203–204, 222, 234, 239, 283, 287, 305–310, 357  
  white (*Pomoxis annularis*), 201, 203–204, 209, 218–219  
creel survey, 353–355, 359–360, 366, 370, 508, 518, 526, 528, 530  
“bus-route,” 528  
crossed correlation, 106, 117–118, 120  
cryptomonads, 100, 250–251, 253  
*Cryptomonas*, 98, 113, 115–116, 253  
cultural eutrophication, 1, 10, 32, 38, 40–41, 44, 58–59, 62–63, 65, 420  
*Cyanophyta*, 50, 113, 279, 408  
*Cyclotella*, 98, 114, 116, 252, 268  
*Cyprinus*, *see* carp
- Dane County, 17, 78, 156  
*Daphnia*, 31–34, 40–44, 69, 76, 83, 90–92, 94, 108, 110, 122, 127, 129, 130, 132–135, 137, 139–148, 234–235, 239, 240, 246, 248–249, 256–258, 260–264, 266–269, 271, 277–280, 283, 287–288, 291, 293, 295–297, 310, 312, 314, 409–410, 412, 419, 428–430, 432, 435, 437, 439–441, 443, 445–447, 455, 457–458, 474, 483–490, 539–541  
*Daphnia galeata mendotae*, 34–35, 40–44, 90–92, 94, 128–132, 136–137, 140, 144–146, 234, 239, 256, 267–269, 276–280, 282, 287, 296–297, 416, 430  
*Daphnia pulicaria*, 34–35, 40–44, 90–92, 94, 110, 128–132, 135–137, 140–141, 144–146, 234, 239, 256, 262, 267, 269, 276–280, 282, 287, 294, 296, 416, 419  
*Daphnia retrocurva*, 34, 128–132, 137, 145, 278  
darter (*Etheostoma*), 305–306, 308–310  
  fantail, 221, 229  
  Iowa, 207–208, 220, 229  
  johnny, 207, 209, 220, 229  
DDT, 188  
depth distribution, 22, 320, 322–323, 327–330, 516  
destabilization, 147, 458, 461, 468, 472–475  
*Diacyclops*, 137, 140, 144, 234, 277  
diagenesis, 49–50, 58–59, 61–66  
*Diaphana soma birgei*, 128–129, 139, 276  
die-off, 41, 87, 199, 209, 212–214, 222–224, 238–239, 275, 290, 297, 446  
diel distribution, 511  
dieldrin, 188  
Dingel-Johnson, 10  
dissolved oxygen, 23–24, 73, 134, 190, 268, 510  
dissolved reactive phosphorus, *see* phosphorus, dissolved reactive  
dissolved reactive silica, 104, 111, 122  
DO, *see* dissolved oxygen  
drainage basin, 17–19, 37, 78, 80, 541  
DRP, *see* phosphorus, dissolved reactive  
  phosphorus, dissolved reactive  
ecosystem approach, 451, 544  
edible algae, 94, 101–103, 107–108, 118, 142–144, 146–148, 235, 458, 474, 483, 486, 489  
edible phytoplankton, 246, 248–249, 271, 279–281, 408, 462, 490  
egg ratio, 278–280  
environmentalists, 10  
*Esox*, *see* northern pike  
*Etheostoma*, *see* darter  
*Eubosmina*, 35, 40, 42, 139, 144  
*Eucalyptus*, 33–34  
eutrophication, 1–2, 8, 32, 44–45, 58, 62–65, 69, 121–122, 146–147, 233–234, 243, 249, 255, 266–267, 269, 271, 434, 453, 464, 466, 474, 483, 489, 490, 512, 533

- exoskeleton, 33–34  
 exotic species, 1, 9, 33, 42, 155, 215, 218, 540  
 exploitation, 41, 44, 355, 361, 363–366, 372–373, 393, 474, 529  
 extirpation, 193, 205–206, 208–209, 213, 219–221
- filamentous algae, 151, 152, 162–166, 280  
*Filinia*, 34  
 fingerling, 8, 323–326, 328, 330, 341–342, 344, 348, 356–357, 366, 368, 496–498, 500, 502–503, 530–531  
 fish diet, 290, 495  
 fish movement, 322  
 fish predation, 186–187, 190, 411, 428, 430–431, 443, 445, 453, 470, 474  
 fish rescue, 205–206, 209, 215, 217, 219, 223  
 fisheries management, 4, 9, 11–14, 32, 45, 353, 358, 365, 369, 373, 381–382, 389, 392–394, 397, 400–403, 452, 478, 503, 507–508, 519, 525, 527, 530, 532, 534–536, 541, 543  
 fishery regulations, 528–530, 534  
 fishing effort, 359, 361, 363–364, 366–367, 372, 529  
 food habits, 319  
 food web description, 1–3, 8, 12, 22, 27, 31–32, 37, 40–41, 43–45, 69–70, 81, 83, 97, 99, 127, 145, 233–234, 236–237, 239–240, 243, 266, 268–269, 271, 298, 303, 354, 358, 362, 370, 373–374, 378, 407, 411, 419, 421, 428–429, 435, 445–447, 453, 457–458, 461, 478, 489, 527, 533, 539–544  
 food web management, 1–4  
 forecast, 123, 148, 168, 355–356, 377, 427, 458, 500, 539, 542  
 fossil, 32–39, 42, 44  
*Fragilaria*, 100, 114, 252  
 freshwater drum (*Aplodinotus*), 187, 201, 204, 207, 209, 218–219, 224, 228, 234, 239, 283, 286–287, 305–311, 515, 517  
*Fundulus*, *see* banded killifish
- geology, 19  
 GIFSIM, 355–356, 366–367, 370  
 gill net, 239, 286–287, 290, 334, 514, 517  
*Gleotrichia*, 100, 234  
 global change, 4  
 golden shiner (*Notemigonus*), 202, 204, 207, 209, 228  
 grazing, 2, 31, 44, 53, 57, 59, 61, 64–66, 69, 83, 108, 123, 127, 146–148, 244–246, 248, 249, 256–257, 261–264, 266, 268–270, 377, 427–429, 431, 432, 443, 445–447, 455, 461, 468–475, 477, 484–486, 488–490, 541  
 growth rate, 268, 297, 431, 445, 463–464, 472, 502, 508
- harvest regulation, 318, 328, 340, 342, 344–345, 348–349, 530, 535  
 Hasler, Arthur D., 9, 74–75, 87, 130, 145, 152, 236, 515, 544  
 hatchery, 366–367, 503, 510, 530–532, 540, 543  
 herbivory, 31, 43, 69–70, 89, 91–94, 97, 127, 145, 243, 245–246, 255–256, 258, 263, 266, 269–271, 378, 407, 451–453, 461, 474, 484–486, 488–490  
 High Performance Liquid Chromatography (HPLC), 51, 534  
 HPLC, *see* High Performance Liquid Chromatography  
*Hyalella*, *see* amphipods  
 hydroacoustic, 321, 333, 507, 511, 519  
 hydrogen sulfide, 26, 189  
 hydrographic map, 161
- individual-based model, 494, 497, 502  
 intervention analysis, 105, 135, 136, 141, 146  
 invasion, 39, 152, 155–156, 161, 166–167  
 invertebrate planktivore, 419–420  
 iron sulfide, 25  
 ivory tower, 543

- Labidesthes*, *see* brook silverside  
Lake Kegonsa, 17, 19  
Lake Mendota Fisherman's Association, 8–9  
Lake Monona, 17, 19, 42, 103  
Lake Waubesa, 17, 19, 42  
larval fishes, 303, 313, 379, 507, 510  
*Lepisosteus*, *see* longnose gar  
*Leptocella*, *see* caddisflies  
*Leptodiaptomus sicilis*, 138  
*Leptodiaptomus siculooides*, 234, 277  
*Leptodora*, 34, 42, 129–130, 140, 144, 234–235, 275, 277–278, 280–283, 286–288, 293–294, 297, 379, 408–420, 451, 474  
littoral zone, 8, 14, 20, 22, 38–39, 151, 153, 159, 162, 166–169, 226, 234, 307, 333, 335, 339, 340, 348, 457, 464, 511, 517, 540–543  
fishes, 332, 338  
planktivores, 339  
longnose gar (*Lepisosteus*), 202, 204, 207–208, 221–222, 224, 228  
*Lyngbya*, 99, 120, 255
- macrophytes, 8, 13, 39, 151–153, 155–156, 158–160, 163–164, 166–169, 457, 511, 532, 536, 540  
manure, 541  
marl, 32, 35–36, 41, 58, 167  
media, 358–359, 365  
*Melosira*, 100, 114  
*Mesocyclops*, 138, 234, 275, 277, 280–283, 293–294, 297  
methane bubble, 515  
*Microcystis aeruginosa*, 98, 100, 116, 120, 122, 254–255  
*Micropterus dolomieu*, *see* bass, small-mouth  
*Micropterus salmoides*, *see* bass, large-mouth  
milfoil, 152, 155–157, 159, 161, 164, 166–168, 540  
decline, 156–157, 159, 161, 166–167  
eurasian water, 152, 157, 176–178, 186, 193, 217–218, 220–221, 224, 540
- Myriophyllum spicatum*, 39, 152–157, 163–166, 169, 178, 540  
minnow, 197  
blackstripe topminnow, 204, 207, 221, 229  
bluntnose (*Pimephales*), 201, 204, 207, 209, 220, 228, 305  
central mudminnow, 202, 204, 207, 229  
fathead, 202, 204, 207, 228  
molluscs, 177  
*Morone chrysops*, *see* bass, white  
*Morone mississippiensis*, *see* bass, yellow  
morphometry, 20  
*Myriophyllum spicatum*, *see* milfoil
- N, *see* nitrogen  
nanoplankton, 428–429, 431–432, 435, 439, 440, 445, 455–456, 458, 462–466, 468  
net efficiency, 133  
 $\text{NH}_4\text{-N}$ , *see* nitrogen, ammonia  
nitrogen, 17, 24, 69–71, 73–74, 78, 80–81, 83, 89, 91, 99, 102–104, 106, 109–111, 117–119, 122–123, 151, 158–159, 243–244, 247–249, 258–263, 267–271, 290, 310, 427, 431–432, 434, 461, 465, 488, 515, 517, 531  
ammonia, 70, 73–74, 83, 103–104, 109–110, 243–244  
loadings, 70, 80–81, 437, 456, 542  
non-point pollution, 7–8, 534  
northern pike (*Esox*), 2, 9–10, 75, 194, 197, 201, 203–204, 207–208, 215–216, 218–219, 221, 228, 233–234, 240, 319, 324–325, 328–331, 337–338, 341–349, 353, 355–358, 360–361, 363, 368, 370, 435, 464, 497, 503, 508, 511, 526–530, 532, 535, 539–540, 543  
*Notemigonus*, *see* golden shiner  
*Notropis*, *see* shiner  
*Noturus*, *see* tadpole madtom  
nuisance plant growth, 7–8, 13, 120, 153, 155, 166, 168, 461  
numerical response, 236, 364, 372

- nutrient, 1–2, 8, 20, 32–33, 37–40, 44–45, 65–66, 69–70, 73, 77–78, 89–92, 94, 97, 99–100, 103, 105, 111, 121–123, 146, 148, 164–165, 167–168, 233, 239, 240, 243, 244, 246, 248–249, 258, 260–261, 263–264, 267–271, 298, 377–378, 419, 427–428, 431, 435, 437–438, 440, 445, 447, 451–453, 455, 457, 462, 468, 473–474, 476–478, 484, 486–490, 533–534, 540–543
- nutrient loading, 8
- Oligochaetes*, 176–180, 182, 184–187, 189
- organic nitrogen, 73
- Oscillatoria*, 100, 116, 121
- paleolimnology, 3, 49, 58
- panfish, 7–9, 357, 373, 526–527
- paradox of enhancement, 369
- Paul Lake, 8, 466–467
- PEG, *see* Plankton Ecology Group
- pelagic, 20, 22, 31–32, 37–44, 137, 153, 198, 200, 210–211, 231, 275–276, 283–284, 286, 303–310, 313–314, 428, 543
- Perca*, *see* perch, yellow perch
- log (*Percina*), 202, 204, 207–209, 220, 229, 305–310
  - yellow (*Perca*), 2, 41, 43, 90–92, 145, 193, 199, 201, 203–204, 207, 209, 212–214, 222–224, 228, 234–239, 275, 280, 283, 286–294, 297–298, 305–315, 319, 322, 333–334, 337–339, 343, 345–347, 349, 353, 355, 357–363, 371–372, 383, 386, 408–409, 411–412, 415, 417–421, 453, 458, 495–496, 498, 502–503, 508, 510, 515, 517–518, 539, 542
- Percina*, *see* perch, log
- Peter Lake, 8
- Pheasant Branch Creek, 17, 70
- pheophorbide, 44, 49–50, 52, 56–57, 59–61, 66
- pheophytin, 49, 52, 56, 57, 59, 61
- phorbin, 49, 56, 59–61, 64–65
- phosphorus
- biologically available, 70, 80
  - dissolved reactive, 71–74, 77–78, 81, 83, 89, 103–110, 117–120, 122–123
  - loadings, 70, 77, 80–81, 89–91, 434, 437, 443
  - total, 70, 72–74, 83, 103–104, 106–110, 117–120, 123, 244, 260–261, 434, 439, 484, 487–488, 541
- physical characteristics, 20, 50, 117–118, 148, 483–484, 540
- phytoplankton, 22, 24, 31, 49–50, 53, 55, 57, 64–65, 76, 91–92, 97–103, 107–108, 112–113, 120–122, 124, 127, 130, 134, 147–148, 234, 240, 243–253, 255, 256, 258, 260–264, 266–271, 279, 280, 314, 378, 407, 408, 411–412, 427–429, 431–435, 440, 443, 446–447, 458, 462, 465, 468, 470, 475, 484–486, 488, 490, 533–534, 540
- pigment, 35, 49–53, 55–57, 61, 63–66
- Pimephales*, *see* minnow, bluntnose
- piscivore, 32, 298, 319–325, 328, 330–333, 338–349, 354–356, 358, 360, 370, 372–374, 419, 421, 451, 453, 455, 476–477, 490, 503, 508, 510, 540
- assemblage, 323, 331, 335
  - planktivore, 348–349
  - utility, 340
- piscivory, 31, 43, 44, 193, 198, 200, 203, 206–208, 210, 215, 222, 224, 231, 298, 355–356, 372, 377–379, 451–458, 477, 539, 541–542
- Pisidium*, 177, 182, 184–187, 189–190
- planktivorous fish, 8, 94, 233, 236, 244, 256, 281, 283, 286, 291–292, 294, 296–298, 407–408, 415–421, 428, 434–435, 437
- planktivory, 43, 45, 70, 90–94, 141, 145–146, 239, 275, 290, 294, 296, 298, 303, 314, 315, 378, 407, 409, 411, 427–428, 435, 437–438, 440–441, 443, 445–447, 451, 453, 455, 458, 471, 476

- Plankton Ecology Group (PEG), 8, 32, 34, 36–37, 41, 57–58, 66, 70, 99–100, 112–113, 117, 121–122, 129–130, 137, 139–140, 145–146, 243–244, 246, 269, 411, 416, 427, 434–435, 439, 445, 447, 453, 462, 471, 483–484, 488–490
- pollen, 33–35, 38, 51
- population dynamics, 3, 45, 275–276, 294, 314, 355, 381–383, 387, 389, 390–394, 397, 400–402, 458, 577
- Potamogeton*, 152–155, 164–167, 178, 540
- Pomoxis annularis*, *see* crappie, white
- Pomoxis nigromaculatus*, *see* crappie, black
- predation inertia, 2, 8, 12, 144, 147–148, 151, 236, 282–283, 341, 343, 345, 348, 356, 370, 374, 408, 411, 427, 458, 474, 494, 503, 527, 533–534, 540, 542–543
- predator-prey interaction, 295, 386, 409, 411
- prey assemblage, 39, 321, 331
- Procladius*, 182–183, 185–187, 189
- profundal, 173–176, 180–183, 185–187, 189–190
- Project Wild, 11
- purse seine, 304–307, 315, 495, 507
- radio
- tagging, 322, 327
  - telemetry, 322, 327, 339
  - tracking, 327
- radiocarbon, 35–36
- ragweed (*Ambrosia*), 35–36, 38, 51
- recruitment, 41, 92, 94, 236, 238, 298, 303, 314, 321, 326, 328, 332, 335–337, 343–349, 355–373, 378–379, 390–397, 400–402, 407, 411, 421, 432, 458, 502, 503, 517–518, 526, 542
- regulation evaluations, *see* fishery regulations and trophy fishery
- return time, 451
- richness, 193–194, 203, 205, 211, 223
- rostra, 34
- Rotifera, 33–34
- sampling design, 12, 35, 42, 44, 51, 73–77, 94, 98–104, 116, 120–123, 129–134, 139–140, 153–154, 157, 159, 163, 167, 244–245, 255, 257, 263, 279, 283–286, 304–309, 313, 355–356, 359, 379, 495–496, 500, 507–512, 520, 526–527, 530, 533
- Schmidt stability, 104, 106, 111–112, 119–123
- seasonal succession, 76–78, 90, 92, 97, 104–107, 110–111, 117–122, 130, 134–147, 243–246, 249, 255–263, 266, 269–270, 275, 277, 279, 290, 292, 294, 296, 306–307, 408, 413, 415–416, 419, 434, 447, 453, 458, 475, 477, 486, 510
- Secchi disk, 74–77, 83–92, 94, 102, 133
- sensitivity analysis, 412, 435, 467, 471–473, 508
- sewage effluent, 70–72
- Shapiro, J., 1–2, 97, 127, 147, 461, 490
- shiner (*Notropis*)
- blackchin, 204, 207, 209, 220–221, 228
  - blacknose, 204, 207, 209, 221, 229
  - common, 204, 207, 229
  - emerald, 202, 204, 207, 221, 229
  - pugnose, 204, 207, 221, 229
  - spotfin, 202, 204, 207–208, 228
  - spottail, 202, 204, 207–209, 218–221, 228
- shoreline electrofishing, *see* compared sampling methods, electrofishing
- showcase management, 353–354, 358, 369–370, 374, 534–536
- silica, 24, 53, 56, 58–59, 62–65, 103–104, 264
- simulation model, 407, 416, 421, 427, 445–446, 494
- Sixmile Creek, 17, 77–78, 368
- size at stocking, 494, 498–499, 540
- size-selective predation, 33, 41, 43, 427, 470
- Skistodiaptomus oregonensis*, 277
- small bodied fishes, 194, 198, 200, 204, 206, 208, 211, 218–221, 223–224, 230
- soil disturbance, 43, 45

- spawners  
 pelagic, 198, 200, 210–211, 231  
 substrate, 198, 210–211, 219–220,  
 223, 231  
 vegetation, 198, 210–211, 220, 223,  
 231
- spawning marshes, 238, 307–309, 356–  
 357, 366–368, 370, 495, 503, 526,  
 530, 532, 543
- Sport Fish Restoration Act, 10, 45, 124,  
 148, 240, 315, 374, 504, 520
- spring runoff, 70, 80–81, 109–110, 239,  
 268
- stability, 92, 104–106, 111, 119–123,  
 378–379, 457–458, 462, 466–467,  
 470–472, 474, 477, 502, 514
- standing crop, 51, 151, 159–162, 166–  
 168, 483–486, 489, 528
- Stephanodiscus*, 98, 100, 112, 114
- Stizostedion*, *see*, walleye
- stocking, 8–10, 12–13, 319, 323–326,  
 328, 330, 332, 338, 340, 344, 348–  
 349, 353, 355–357, 360, 365–368,  
 371–372, 377, 379, 395, 407, 419–  
 420, 458, 493–504, 508, 510–511,  
 525, 530–533, 535–536, 540
- sulfate, 25, 27
- sulfide, 25–27
- swimmers, 8, 166
- tadpole madtom (*Noturus*), 204, 207,  
 209, 221, 229
- technology transfer, 3, 507, 519
- temporal distribution, 98, 303, 306–309,  
 412, 413, 416, 419, 433, 447, 511,  
 519
- theory, 2, 31, 369, 378, 419, 472, 489,  
 519
- time series analysis, 103–105, 117, 124,  
 134–135, 141, 147–148, 458
- Token Creek, 17, 77
- total phosphorus, *see* phosphorus, total
- toxic insecticides, 187–190
- TP, *see* phosphorus, total
- transfer function, 3, 13, 57, 106, 118–  
 119, 123, 127, 135–137, 144, 359,  
 457, 507–508, 519
- trophy fishery, 367–368, 370, 529, 541
- University Bay, 32, 152–157, 159–165,  
 167, 249, 304, 310
- urbanization, 45
- urban runoff, 80
- Vallisneria*, 152–154, 161, 164–165, 167,  
 178, 540
- vegetation, 8, 31, 39, 151–152, 155, 162,  
 168, 457, 543
- walleye (*Stizostedion*), 2, 7–9, 12–13,  
 197, 201, 203–204, 207–208, 215–  
 216, 218–222, 224, 228, 233–235,  
 239, 305, 314, 319, 321–330, 333,  
 335–339, 341–349, 353, 355–358,  
 360–368, 371–373, 379, 386, 435,  
 453, 458, 493–504, 508, 510, 519,  
 526–531, 533, 535, 539–540
- Wallop-Breaux, 10–11, 373
- warm water fishes, 198, 203, 211, 223–  
 224, 231
- water  
 chemistry constituents, 24  
 clarity, 12, 69, 74–77, 83, 85–94, 112,  
 121, 148, 158, 168, 419, 457, 489–  
 490  
 level, 19, 536  
 mites, 177–178, 181  
 quality, 1–2, 8–9, 11–13, 45, 69, 89,  
 99, 123, 148, 151, 168, 248, 373–  
 374, 377, 452, 455, 461, 478,  
 489–490, 525, 533–534, 539–541,  
 544  
 temperature, 22, 238, 495–496
- weeds, 7–9, 155–156, 236  
 harvesting, 8
- wetlands, 17, 19, 193, 215, 217–220,  
 357, 368, 532
- Wisconsin Idea, 7
- workshop, 452, 509–510, 527
- Yahara Lakes, 12, 17–20, 72, 75–76,  
 132
- Yahara River, 17, 19, 22, 39, 70, 76–78,  
 101
- year class failure, 346–348

- zooplankton, 2, 8, 31–33, 35, 37, 39–45, 49, 53, 55, 57, 64–65, 69, 94, 97, 99–100, 122, 127–130, 132–134, 137, 140–141, 144–145, 148, 233–234, 236, 239–240, 243–249, 255–257, 261–264, 266, 268–271, 275–277, 280, 283, 286, 288, 291–293, 296–298, 303–304, 314–315, 361, 379, 407–408, 412, 417, 420–421, 427–435, 445–447, 458, 462–464, 468, 474–475, 484, 486–490, 533–534, 539

**Springer Series on  
Environmental Management**  
Robert S. DeSanto, Series Editor

---

**Disaster Planning: The  
Preservation of Life and Property**  
*Harold D. Foster*  
1980/275 pp./48 illus./cloth  
ISBN 0-387-90498-0

**Air Pollution and Forests:  
Interactions between Air  
Contaminants  
and Forest Ecosystems**  
*William H. Smith*  
1981/379 pp./60 illus./cloth  
ISBN 0-387-90501-4

**Natural Hazard Risk Assessment  
and Public Policy:  
Anticipating the Unexpected**  
*William J. Petak*  
*Arthur A. Atkisson*  
1982/489 pp./89 illus./cloth  
ISBN 0-387-90645-2

**Environmental Effects of Off-Road  
Vehicles: Impacts and Management  
in Arid Regions**  
*R. H. Webb*  
*H. G. Wilshire (Editors)*  
1983/560 pp./149 illus./cloth  
ISBN 0-387-90737-8

**Global Fisheries:  
Perspectives for the 1980s**  
*B. J. Rothschild (Editor)*  
1983/224 pp./11 illus./cloth  
ISBN 0-387-90772-6

**Heavy Metals in Natural Waters:  
Applied Monitoring and Impact  
Assessment**  
*James W. Moore*  
*S. Ramamoorthy*  
1984/256 pp./48 illus./cloth  
ISBN 0-387-90885-4

**Organic Chemicals in Natural  
Waters:  
Applied Monitoring and Impact  
Assessment**  
*James W. Moore*  
*S. Ramamoorthy*  
1984/282 pp./81 illus./cloth  
ISBN 0-387-96034-1

**The Hudson River Ecosystem**  
*Karin E. Limburg*  
*Mary Ann Moran*  
*William H. McDowell*  
1986/344 pp./44 illus./cloth  
ISBN 0-387-96220-4

**Human System Responses to  
Disaster:  
An Inventory of Sociological  
Findings**  
*Thomas E. Drabek*  
1986/512 pp./cloth  
ISBN 0-387-96323-5

**The Changing Environment**  
*James W. Moore*  
1986/256 pp./40 illus./cloth  
ISBN 0-387-96314-6

**Balancing the Needs of  
Water Use**  
*James W. Moore*  
1988/280 pp./39 illus./cloth  
ISBN 0-387-96709-5

**The Professional Practice of  
Environmental Management**  
*Robert S. Dorney*  
*Lindsay Dorney (Editors)*  
1989/248 pp./23 illus./cloth  
ISBN 0-387-96907-1

*(continued on next page)*

**Springer Series on  
Environmental Management**  
Robert S. DeSanto, Series Editor

---

(continued)

**Chemicals in the Aquatic Environment:**  
**Advanced Hazard Assessment**  
*Lars Landner (Editor)*  
1989/415 pp./102 illus./cloth  
ISBN 3-504-50863-5

**Landscape Ecology:**  
**Theory and Applications**  
(Student edition)  
*Zev Naveh*  
*Arthur S. Lieberman*  
1990/384 pp./78 illus./pbk  
ISBN 0-387-97169-6

**Inorganic Contaminants of Surface Water:**  
**Research and Monitoring Priorities**  
*James W. Moore*  
1991/360 pp./13 illus./cloth  
ISBN 0-387-97281-1

**Chernobyl:**  
**A Policy Response Study**  
*Boris Segerstål (Editor)*  
1991/180 pp./cloth  
ISBN 3-540-53465-2

**Long-Term Consequences of Disasters:**  
**The Reconstruction of Friuli, Italy, in Its International Context, 1976-1988**  
*Robert Geipel*  
1991/192 pp./81 illus./cloth  
ISBN 0-387-97419-9

**Food Web Management: A Case Study of Lake Mendota**  
*James F. Kitchell (Editor)*  
1992/576 pp./177 illus./cloth  
ISBN 0-387-97742-2