

**ECOLOGY AND WATER QUALITY DYNAMICS OF A SHALLOW
HYPEREUTROPHIC LAKE DOMINATED BY CYANOBACTERIA**

(Aphanizomenon flos-aquae)

by

Jacob Kann

A dissertation submitted to the faculty of the University of North Carolina at Chapel Hill in
partial fulfillment of the requirements for the degree of Doctor of Philosophy in the
Curriculum in Ecology.

Chapel Hill

1997

Chapter 1

**Effects of Nutrients, Consumers, and Physical Factors on Phytoplankton Biomass and
Succession in a Shallow Hypereutrophic Lake**

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ABSTRACT

JACOB KANN: Ecology and Water Quality Dynamics of a Shallow Hypereutrophic Lake Dominated by Cyanobacteria (*Aphanizomenon flos-aquae*).

This dissertation consists of two distinct chapters relating to ecological and water quality dynamics in Upper Klamath Lake, Oregon. In the first chapter, entitled: *Effects of Nutrients, Consumers, and Physical Factors on Phytoplankton Biomass and Succession in a Shallow Hypereutrophic Lake*, I present an examination of the seasonal and interannual patterns leading to dominance of large blooms of blue-green algae (*Aphanizomenon flos-aquae*) and their relationship with *Daphnia* (*D. pulicaria*) in shallow, hypereutrophic Upper Klamath Lake, Oregon. Contrary to trophic cascade theory, which predicts that systems dominated by large *Daphnia* should have low phytoplankton biomass, Upper Klamath Lake experiences extremely high biomass levels of both large-bodied *Daphnia* and algae. While light and temperature play a large role in initiation of the spring bloom, it also appears that continued seasonal succession toward *Aphanizomenon* dominance in Upper Klamath Lake depends not only upon low TIN:SRP ratios, but also on high SRP concentrations, and adequate levels of TIN during periods when SRP is low and/or reduced light conditions retard nitrogen fixation. Although periods of *Aphanizomenon* dominance in Upper Klamath Lake occurred at both high and low levels of *D. pulicaria*, *Daphnia*'s clear suppression of more edible algal competitors, regeneration of TIN and SRP, and apparent enhancement of low TIN:SRP ratios, may contribute to both dominance and biomass of *Aphanizomenon*.

In the second chapter, entitled: *Chlorophyll as a Predictor of Elevated pH in a Hypereutrophic Lake: Estimating the Probability of Exceeding Critical Values for Fish Success Using Parametric and Nonparametric Models*, I present two empirical models which predict the frequency or probability of exceedence of critical values of photosynthetically elevated pH from algal biomass (as estimated by concentrations of chlorophyll *a*), in Upper Klamath and Agency Lakes, Oregon. The first model relies on the linear regression model and associated parametric

assumptions as its base, and the second is based on a nonparametric cross-tabulation of paired values of chlorophyll α and pH. As opposed to models which only predict the mean response of the dependent variable, these probabilistic models reexpress the inherent spatial and temporal variance in the independent and dependent variables as the probability or frequency of conditions likely to be experienced by fish. In the specific case of Upper Klamath Lake, extensive algal blooms dominated by the blue-green alga *Aphanizomenon flos-aquae* significantly degrade water quality by photosynthetically elevating water column pH. Lake-wide pH typically remains above suitable levels (> 9.50) for two endangered fish species during the summer, and a strong linear relationship was observed between pH and concentrations of chlorophyll α ($r^2=0.71$; $P<0.0001$). Both parametric and nonparametric models performed similarly, showing that a 45% reduction in the probability of exceeding pH 9.5 (a likely sublethal limit) could be realized by reducing chlorophyll α from 200 to 100 $\mu\text{g L}^{-1}$. This suggests that significant benefits to fisheries could be attained through restoration efforts that do not require a complete eutrophication reversal. Model validation using independent data indicated the predictive ability of both models was excellent, and I present a framework to assess the assumptions inherent in the development of both models.

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I especially wish to thank my primary advisor, Dr. Val Smith, who, despite his transition to Associate Professor at the University of Kansas, continued to provide guidance and support throughout my doctoral tenure. I would also like to thank the current members of my graduate committee, Drs. Robert Peet, Hans Paerl, Seth Reice, and Peter White for their help and support; and the earlier members of my committee, Drs. Edward Kuenzler and Ken Reckhow, who, along with Dr. Nelson Hairston, Sr., participated in my doctoral oral examination; and Cottie Pasternak of the Curriculum in Ecology for her great help, especially for facilitating my doctoral defense when I was on the opposite side of the country.

I also especially want to thank the Klamath Tribes for their willingness to support my decision to return to school, as well as for their foresight in realizing that data collection and scientific research are key to understanding and management of the aquatic systems in the Klamath Basin. Specifically I would like to thank my colleagues at the Tribes, Craig Bienz and Larry Duns Moor, for their support and valued insight on the ecology of the Klamath Basin. Others who provided help along the way include Bill Ehinger, Rick Barbiero, Emily Dyke, and Mark Osburn. Without the invaluable field and laboratory assistance of Ken Knight, much of the data collection effort would not have been possible. Financial support for Upper Klamath Lake research and monitoring was provided by the Klamath Tribes and the U.S. Bureau of Reclamation, Klamath Falls and Denver Offices. I especially thank Sharon Campbell and Mark Buettner of the U. S. Bureau of Reclamation for their supportive roles in this research effort.

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INTRODUCTION

Upper Klamath and Agency Lakes are a large, shallow hypereutrophic lake system located in south-central Oregon (Fig. 1). Extensive land-use and hydrologic alterations have resulted in cultural eutrophication (defined here as an acceleration of the eutrophication process due to human-caused nutrient enrichment) of most of the lakes and rivers of the Klamath Basin. As a result, these aquatic systems exhibit many water quality problems typically associated with excessive enrichment and excessive algal biomass production. These water quality problems are of great concern because of their potential impact on diversity and viability of native fish populations and other aquatic life. In particular, the historically abundant shortnose (*Chasmistes brevirostris*) and Lost River suckers (*Deltistes luxatus*) which are endemic to the Upper Klamath River Basin, are now in jeopardy of extinction. These species were listed as endangered under the Endangered Species Act in 1988, and water quality degradation resulting from algal blooms has been identified as a probable major factor in their declines (Williams 1988). Both endangered catostomid species are predominantly adfluvial (spawning takes place in tributaries with rapid emigration of larvae to the lake upon hatching) and long-lived (>25 years), and therefore depend heavily upon satisfactory lake water quality conditions for long term population viability. Adverse effects of degraded water quality on native fishes in Upper Klamath Lake include summer fish-kills (Scoppettone and Vinyard 1991; BRD 1996), as well as pronounced horizontal re-distribution of fish in response to changes in water quality (Vincent 1968; Hazel 1969; Buettner and Scoppettone 1990).

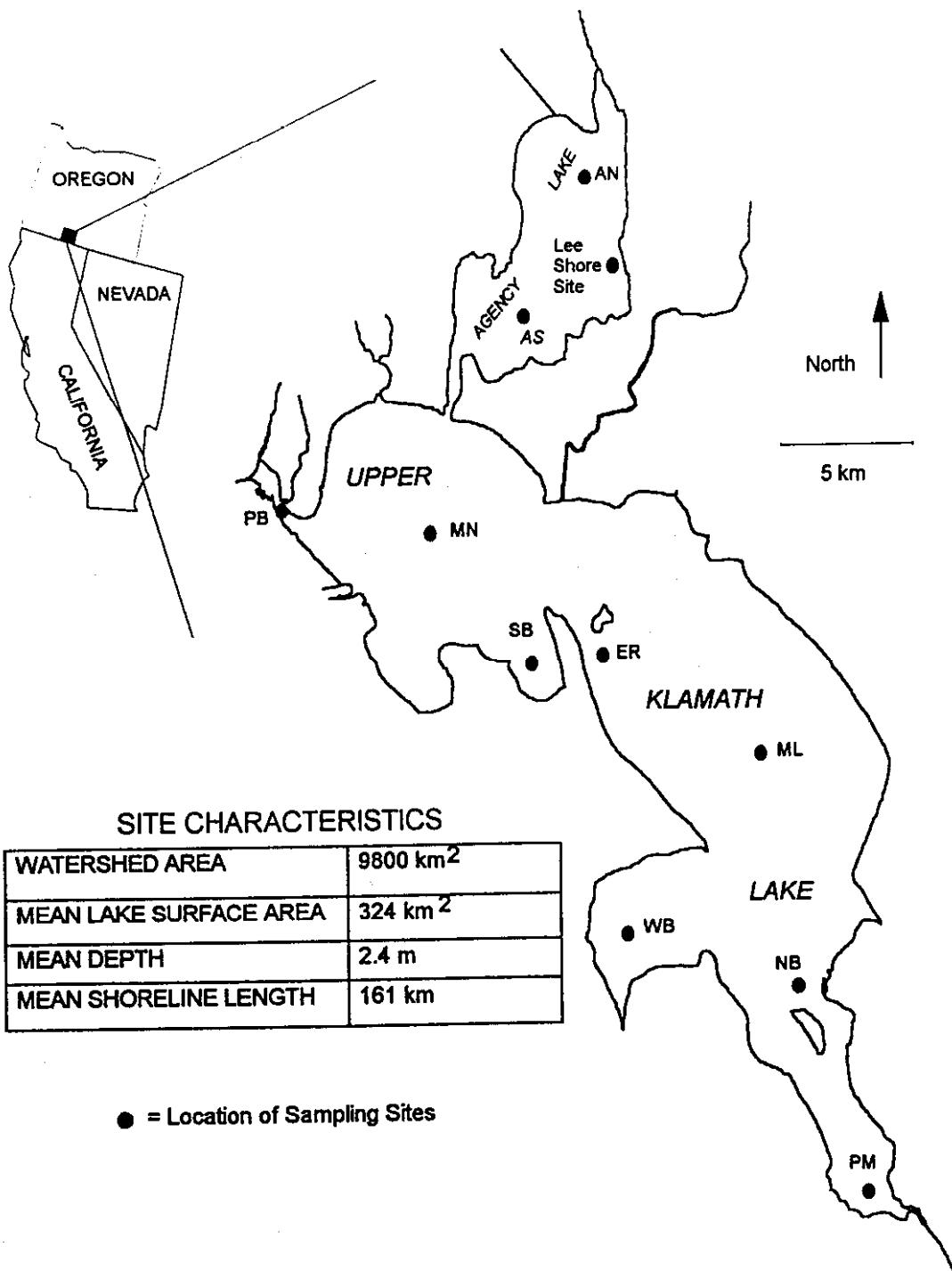


Fig. 1. Location and characteristics of Upper Klamath and Agency Lakes, Oregon, USA.

Although historic accounts indicate the lake would have been considered eutrophic even 100 years ago, in-lake habitat loss and degraded water quality are now widespread. The hydrology of the lake has been profoundly changed by water diversions and by the construction of a dam at the lake's outlet in 1921. As a result, both the timing and quantity of lake flushing flows essential for nutrient export from the lake have been greatly altered, and lake level has been reduced below pre-1921 levels. In addition, historic shorelines in Upper Klamath Lake consisted of uninterrupted edges of rooted vegetation, but now consist of either very narrow bands of vegetation or bare expanses of sand or riprap. These shoreline alterations have reduced both the quantity of available structural habitat for native fishes, and the algal inhibitory effect of humic substances flowing from interior wetlands.

There have also been major changes in the watershed including forest clear-cutting, grazing of >75,000 head of cattle in upstream flood plains, the degradation of riparian corridors, and the conversion of 35,000 acres of wetlands to pasture and agriculture on the lake periphery itself (Klamath Tribes 1994). The Environmental Protection Agency (USEPA 1997) indicates that at least 110,000 acres of the watershed have been converted to irrigated pasture or other agricultural activities, with the majority being flood-irrigated. Due to the proximity to water sources and the ability to gravity convey water, most of these 110,000 acres occur in riparian and flood plain areas. These land use changes have altered the watershed hydrology, and have increased nutrient loading both to the lake and to its tributaries. The enormous extent of floodplain wetland (including riparian areas), upland wetland (Klamath and Sycan Marshes), and lake peripheral wetland degradation and loss alone are indicative of major structural and functional watershed alteration. Such riparian and wetland areas provide fish and wildlife habitat, water storage, nutrient and sediment retention

(filtering), and provide for late season base flows essential for in-stream habitat and lake flushing flows. Under current management these areas contribute greatly to the export of nutrients (particularly phosphorus, which in large quantities contributes to dense growth of aquatic plants and algae in the tributaries and in Upper Klamath Lake), and to severely diminished base flows.

Despite high background phosphorus (P) levels in Upper Klamath Basin tributaries ($\sim 65 \mu\text{g L}^{-1}$), P loading is elevated substantially above these levels (Klamath Tribes 1994). One of the earliest nutrient loading studies (Miller and Tash 1967; updated by USACE 1982) indicates that direct agricultural input from pumps and canals account for 31% of the annual external total phosphorus (TP) budget. Furthermore, drained and diked wetlands consistently pump effluent containing 3-10X the phosphorus (P) concentration of tributary inflows (Klamath Tribes 1994), and nitrogen and phosphorus liberated from drained wetland areas are leached into adjacent ditches, and subsequently pumped to the lake or its tributaries (Snyder and Morace 1997). Coupled with the additional non-point loadings from wetland loss, flood plain grazing, flood irrigation, and channel degradation, the total anthropogenic TP input accounts for a far greater percentage than that indicated by the 31% contributed due to direct pumping alone.

As a result of these changes to the lake and its watershed, massive algal blooms of the blue-green alga *Aphanizomenon flos-aquae* now occur nearly continuously from June through October (Fig. 2). The respiration, decay, and high photosynthetic rate of these algal blooms result in marked minima ($< 2 \text{ mg L}^{-1}$) and maxima ($> 150\%$ saturation) of dissolved oxygen in the water column (Fig. 3). These dissolved oxygen minima are lower than the 96 hr LC_{50} for the various sucker species (Bellerud and Saiki 1995), and the oxygen commonly found in

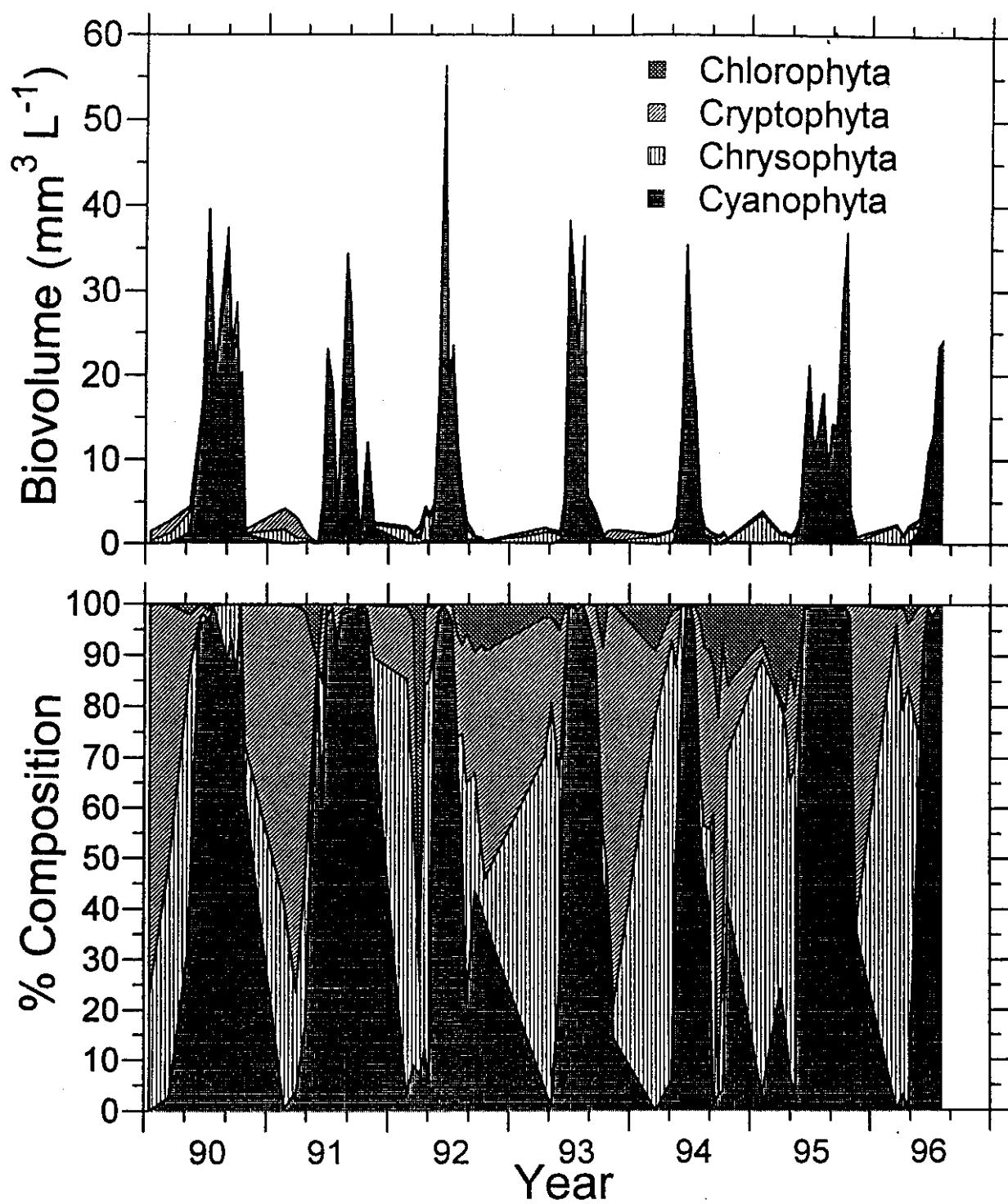


Fig. 2. Lake-wide mean total biovolume ($\text{mm}^3 \text{L}^{-1}$) and percent composition of major phytoplankton taxa in Upper Klamath Lake, Oregon, 1990-1996. *Aphanizomenon flos-aquae* generally represents 90-99% of the Cyanophyta (blue-green) biovolume present during the summer growing season. Species composition and biovolume were measured using sedimentation chamber/inverted microscope methodology on integrated water column samples preserved in Lugol's solution (Lund et al. 1958).

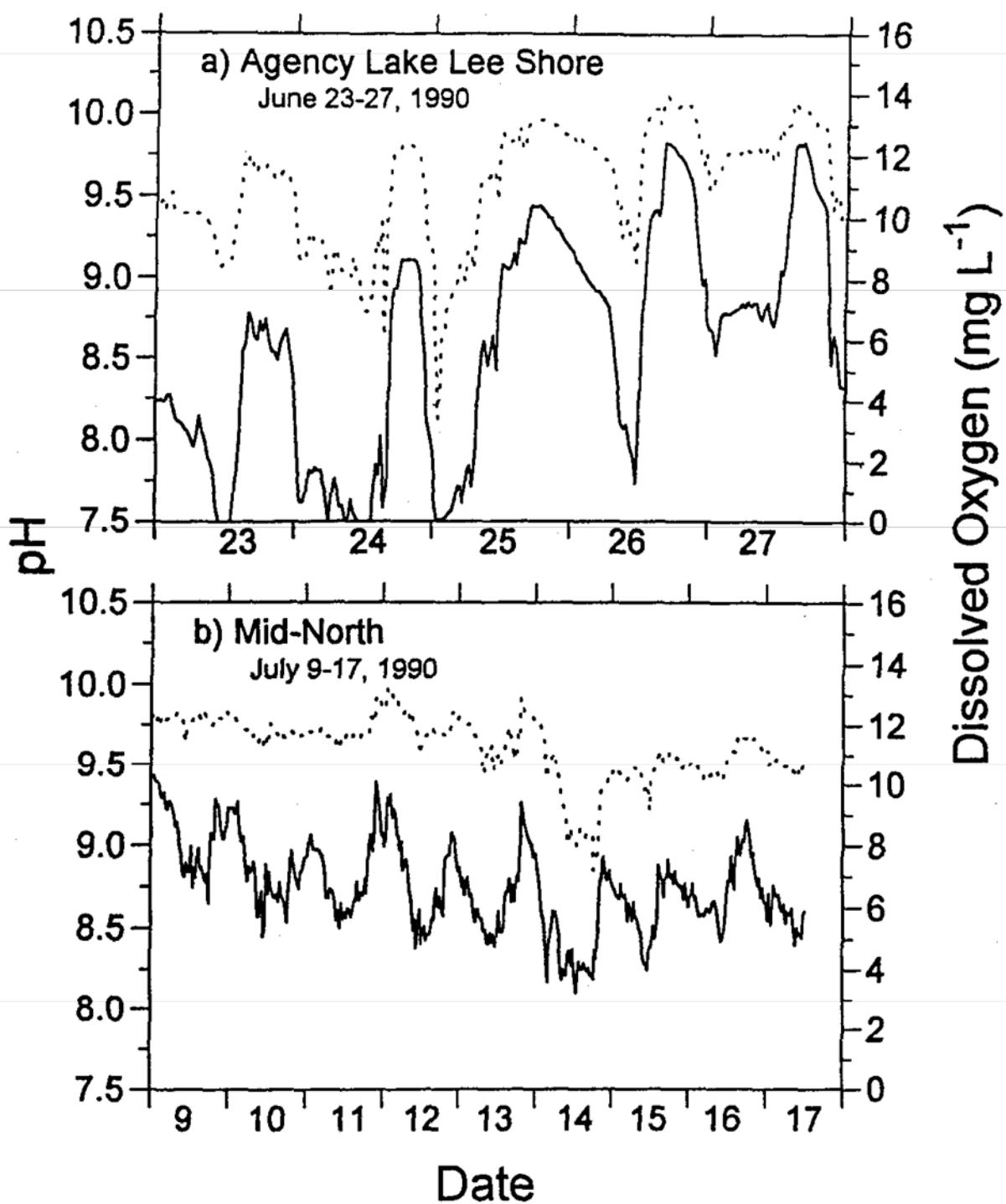


Fig. 3. Diel variations in pH (dashed line) and dissolved oxygen (mg L^{-1} ; solid line) at a near-shore site (a), and an open water site (b) in Upper Klamath and Agency Lakes, Oregon. Data were collected at half hour intervals using remote Hydrolab DataSonde instrumentation deployed at the mid-point of the water column.

Upper Klamath Lake can also cause chronic stress ($2\text{-}5 \text{ mg L}^{-1}$). In addition, the buffering capacity of the water is relatively low, and photosynthetically-elevated pH values commonly exceed 9.50 (Fig. 3).

Bioassays have shown that pH values >9.55 caused a loss of equilibrium in native *Chasmistes brevirostris* (Falter and Cech 1991), and short-term acute lethality tests (96 hr LC50's) indicate that mortality of juvenile *Chasmistes brevirostris* occurs when pH values >9.76 are reached (Bellerud and Saiki 1995). Photosynthetically-elevated pH is thus an important component of water quality that has likely had profound effects on fish growth and survival in Upper Klamath Lake (see Chapter 2). Other factors associated with excessive algal blooms in Upper Klamath Lake that may limit fish survival include *high concentrations* of unionized ammonia and the presence of algal toxins.

Given the bloom-induced water quality problems and subsequent effects on fishes described above, an understanding of both the controlling factors of algal bloom dynamics, and the linkages between algal biomass and water quality, is essential for scientifically-based management of Upper Klamath Lake. In the following two chapters, I evaluate the factors leading to *Aphanizomenon flos-aquae* biomass and dominance, and I present a series of models utilizing algal biomass to predict the probability of exceeding critical values of photosynthetically-elevated pH in Upper Klamath Lake.

Introduction

Summer algal blooms dominated by cyanobacteria are a consistent feature of eutrophic and hypereutrophic lakes worldwide (Reynolds 1987; Smith 1990). Such cyanobacterial blooms not only result in impaired human use of lake systems (Cooke et al. 1986; Ryding and Rast 1989), but also alter the intrinsic ecological dynamics of these lakes through fish kills (Barica 1975a,b, 1978; McQueen et al. 1989; Vanni et al. 1990). As a result, much attention has been focused on the factors leading to cyanobacterial dominance (e.g., Smith 1983; Reynolds et al. 1987; Paerl 1988; Shapiro 1990, 1997). Alterations of algal community structure and biomass may be brought about by physical factors (e.g., temperature and light, cf. Reynolds 1984; Robarts and Zohary 1987; Tilzer 1987); by changes in the loading and relative supply rates of the macro-nutrients nitrogen (N) and phosphorus (P) (cf. Dillon and Rigler 1964; Vollenweider 1976; Tilman et al. 1986; Smith 1983, 1990, 1995); and by changes in food web structure which cascade down to algal communities (e.g., Hrbáček et al. 1961; Shapiro et al. 1975; Shapiro and Wright, 1984; Carpenter et al. 1985; Carpenter and Kitchell 1988, McQueen et al. 1989). Differential recycling of N and P by fish (Vanni 1996; Vanni et al. 1997) and zooplankton (Lehman 1980; Elser et al. 1988; Sterner 1990; Andersen and Hesssen 1991; Urabe 1993; Wen and Peters 1994) has also been advanced to explain differences in algal community structure and biomass. The above mechanisms work in concert through a set of complex interactions and reciprocity between trophic levels (see recent review by Reynolds, 1994).

One of the most consistent features of the classic trophic cascade in lakes is that when zooplanktivorous fish are either absent or are reduced in abundance, large *Daphnia* spp. dominate due to release of size-selective predation on larger individuals (Brooks and Dodson 1965). Communities dominated by large *Daphnia* tend to be associated with reduced algal biomass yields per unit concentrations of nitrogen and phosphorus as these large herbivores effectively reduce phytoplankton biomass in the water column (Sarnelle 1992; Mazumder 1994a; Mazumder and Lean 1994). In a series of experimental and empirical studies Mazumder and Lean (1994) and Mazumder (1994a,b) found this relationship to be quite robust across a wide range of lake enrichment, and proposed that contrasting herbivory among lakes can explain much of the variability in observed phosphorus-chlorophyll relationships (also see Pace 1984). However, numerous other studies have suggested a trend of increasing phytoplankton density with increasing *Daphnia* density (e.g., McCauley et al. 1988; Pechar 1992; Diehl et al. 1993). The main reason for this discrepancy is the failure to account for the size structure of both the herbivores and their algal prey (Diehl et al. 1993). These size structure relationships are particularly relevant when considering the interaction between large *Daphnia* and large colonial cyanobacteria, where large inedible filaments or colonies are not effectively grazed by *Daphnia*, and both *Daphnia* and cyanobacterial populations can be enhanced at the expense of more edible algal species (Porter 1977; Haney 1987; Liebold 1989; Sterner 1989a; Vanni and Tempte 1990).

Alternatively, filaments or colonies of varying size may interfere with *Daphnia* feeding and suppress *Daphnia* population viability (Webster and Peters 1978; Haney 1987; Kerfoot et al. 1988; Gliwicz and Lampert 1990). It is clear from these studies that not all inedible or grazing resistant species have an equal effect on the outcome of zooplankton/phytoplankton

interactions, and either positive or negative associations can occur between herbivorous zooplankton and their algal prey. Nevertheless, it is clear that in enriched aquatic systems large *Daphnia* have the potential to contribute to the dominance of grazing-resistant filamentous cyanobacteria through suppression of smaller, faster growing competitors (Porter 1977; Sterner 1989a,b, Vanni and Tempte 1990; Elser and Goldman 1991).

Despite this alternative outcome from the expected relationship between large *Daphnia* and phytoplankton biomass (i.e., high density of large-bodied herbivores leading to high instead of low phytoplankton biomass), there has been relatively little literature dealing with the role of zooplankton in promoting either long-term or seasonal succession towards cyanobacterial dominance relative to nitrogen and phosphorus dynamics (but see Horne and Commins 1987; Sterner 1989a,b and Sarnelle 1992, 1993).

One of the best demonstrated examples of this association between high abundance of large-bodied *Daphnia* and high algal biomass (but that is largely omitted from the trophic cascade literature), occurs between large-bodied *Daphnia* (e.g., *D. pulex*, *D. pulicaria*, or *D. magna*) and the filamentous cyanophyte *Aphanizomenon flos-aquae* in systems where zooplanktivorous fish are absent or restricted (Hrbáček 1964; Lynch 1980; Lynch and Shapiro 1981; Ganf 1983; Andersson and Cronberg 1984; Pechar and Fott 1991; Pechar 1992). This association appears to be restricted to *Aphanizomenon flos-aquae* varieties forming large flake-like colonies, generally ranging in size from 2-20mm, that consist of a series of intertwined filaments (Pechar 1992). Holm et al. (1983) concluded that grazing on *Aphanizomenon flos-aquae* colonies is restricted to colonies less than 1.5 mm, indicating superior grazing resistance by large flakes to even the largest *Daphnia*.

Superior grazing resistance along with *Aphanizomenon flos-aquae*'s nitrogen fixing

ability should make it a superior competitor over non-fixing and smaller more edible species (Sterner 1989a), especially in systems with low nitrogen to phosphorus ratios (Smith 1983). Consistent with resource-based competition theory (Tilman 1982), Smith (1983) found greater dominance by cyanobacteria under conditions of low loading or water column TN:TP ratios. Such increased competitive ability allows *Aphanizomenon* to easily replace and exceed algal biomass lost to efficient grazing by large-bodied *Daphnia*. Most of the research on this fairly ubiquitous relationship has been performed in small enclosures and over short time scales (Lynch 1980, Ganf 1983, Ehinger 1992), and while results show promotion of *Aphanizomenon* dominance in the presence of large *Daphnia*, overall *Aphanizomenon* biomass has been observed to either increase or decrease (reviewed in Ehinger 1992). This does not appear to be the case in whole lake systems, where both *Aphanizomenon* and overall algal biomass is typically greatest during periods of *Daphnia-Aphanizomenon* association (Andersson and Cronberg 1984; Pechar 1992; this study, pers. observation).

The discrepancy in the relative increase or decrease in *Aphanizomenon* biomass in the presence of *Daphnia* may be due in part to the short time scale of the experiments or to container effects which do not truly mimic whole lake systems (Reynolds 1994; Vanni et al. 1997). Furthermore, most in-lake studies following seasonal progression of phytoplankton and zooplankton communities have been limited to 1-3 years, limiting the ability to examine interannual and seasonal variability.

The continuous seven-year study reported here of the nutrient and plankton dynamics in shallow, hypereutrophic Upper Klamath and Agency Lakes, Oregon, has provided the opportunity to examine seasonal and interannual patterns of development of massive blooms of *Aphanizomenon flos-aquae*. The goal of this research was to examine seasonal and

interannual patterns of nutrient and herbivorous zooplankton dynamics relative to *Aphanizomenon* dominance and biomass. Specifically, I wished to evaluate the following two hypotheses in this non-experimentally altered lake ecosystem: 1) low levels of inorganic nitrogen and high levels of soluble reactive phosphorus (and subsequent low N:P ratios) promote *Aphanizomenon flos-aquae* dominance; and 2) through both suppression of more edible algal competitors and regeneration of nitrogen and phosphorus, high levels of large *Daphnia* can promote *Aphanizomenon flos-aquae* dominance and biomass in Upper Klamath Lake.

Study site

Upper Klamath and Agency Lakes are a large (324 km^2), shallow (mean depth = 2.4 m), hypereutrophic lake system located in south-central Oregon (Fig. 1 introduction). They exhibit consistent water quality problems (e.g., elevated pH, and widely fluctuating dissolved oxygen) typically associated with excessive algal production (see introduction and Chapter 2). These water quality problems, combined with decreases in available pelagic and shoreline habitat due to lake draw-down, limit both the numbers and distribution of zooplanktivorous fish during periods of summer dominance by *Aphanizomenon*. In addition, the foraging ability of the remaining fish may be reduced due to visual impairment by large *Aphanizomenon* flakes. As a result of these water quality and algal-induced habitat and foraging restrictions, fish are unable to effectively suppress large-bodied *Daphnia pulicaria* (previously identified as *D. shodderi*), which are often found in high numbers throughout the period of *Aphanizomenon* dominance (Kann 1993).

Methods

Physical Chemical Parameters

Regular limnological measurements were made in Upper Klamath and Agency Lakes from January 1990 through September 1996 in order to monitor seasonal water quality, nutrient, phytoplankton, and zooplankton dynamics. Samples were taken biweekly or occasionally weekly during the June-September growing period, and were taken approximately monthly during the winter-early spring period except when prevented by ice cover or dangerous storms. In general, 10 sites were sampled on each date, 2 in Agency Lake, and 8 in Upper Klamath Lake (Fig. 1 introduction). The exceptions to this were in 1990 when a subset of sites (ER, SB, MN, PB, and AS) in the northern portion of the lakes were sampled on some dates, and in 1996 when only 6 (PM, ML, ER, SB, MN, and AS) of the 10 sites were regularly sampled.

Daily minimum and maximum air temperature data from two stations (Klamath Falls and Chiloquin; Western Regional Climate Center, Reno, NV) were averaged to obtain a daily mean air temperature over the period of sampling. Depth profiles of temperature, pH, dissolved oxygen, and conductivity were measured using a Hydrolab Surveyor® multi-parameter probe at each sample site and date. The relative thermal resistance to mixing (RTRM, a dimensionless index of water column mixis) was computed from density gradients taken from temperature profiles using the formula:

$$RTRM = \frac{ABS(\rho_s - \rho_b)}{\rho_{4-5}}$$

where ρ_s is the density of water at surface temperature, ρ_b is the density of water at off-bottom temperature, and $\rho_{4,5}$ is the density difference between 4 and 5 °C (Jones and Welch 1990). Weak density gradients result in low RTRM values and indicate less resistance to wind-induced mixing (Reynolds 1984). Likewise, high RTRM values indicate increased water column stability. The underwater light climate was evaluated from both 20 cm Secchi disc transparency and from depth profiles of photosynthetically active radiation (PAR $\mu\text{Em}^2\text{s}^{-1}$, Li-Cor® Model LI-1000 Data Logger fitted with a spherical quantum sensor). Vertical extinction coefficients for PAR were computed according to Wetzel (1983):

$$k = \frac{\ln I_0 - \ln I_z}{z}$$

where k is the vertical extinction coefficient (m^{-1}), I_0 is irradiance at the lake surface ($\mu\text{Em}^2\text{s}^{-1}$), I_z is irradiance at depth z ($\mu\text{Em}^2\text{s}^{-1}$), and z is the light path (m) over which extinction is being computed.

Because the lake is polymictic and only undergoes weak and intermittent stratification, a depth-integrated water sample of the entire water column was taken coincidentally with the water quality profiles. This was accomplished by combining a minimum of three replicate hauls from a weighted 5 cm diameter plastic tube at each site. This composite sample was then mixed and portioned off to appropriate collection bottles for the analysis of chlorophyll a (Chl) and phaeophytin, total phosphorus (TP), soluble reactive phosphorus (SRP), nitrate+nitrite nitrogen ($\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$), ammonia nitrogen ($\text{NH}_4\text{-N}$), and total nitrogen (TN). APHA (1985) was followed for all analyses except CHL and phaeophytin (Nusch

1980), and TN which followed D'Elia et al. (1977). Total inorganic nitrogen (TIN) was taken as the sum of $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$ and $\text{NH}_4\text{-N}$. All sampling trips included field duplicates and blanks, and laboratory analysis included split samples as well as samples spiked with a known concentration of the parameter to be analyzed.

Phytoplankton Composition and Biomass

A final subsample from the depth-integrated sample was placed in 500 ml opaque polyethylene bottles and preserved with 5 ml Acid-Lugol's solution (APHA 1985). Algal species abundance was then determined using the inverted microscope/settling chamber technique (Lund et al. 1958). Depending on algal density, from 5-50 ml were settled for a minimum of 10 h per cm of chamber height. After settling, the slide was scanned at 100x and 320x magnification to ensure random distribution of organisms. Enough cells were then counted in haphazardly chosen fields until the standard error as a percent of the mean was $\leq 10\%$ for dominant species. Cell volume was then determined by measuring cell dimensions of 10 individuals per species in each sample (generally 6-10 samples per date), and averaging among the samples to obtain an average size per species per date. Volumetric equations for shapes most resembling species form were used to determine total cell volume (e.g., Willén 1970). The total biovolume of each species was then computed as cell abundance (individuals L^{-1}) multiplied by average individual volume (μm^3). Final biovolume estimates are reported as $\text{mm}^3 \text{ L}^{-1}$, which approximates wet weight biomass in mg L^{-1} . Due to high variability in flake size of *Aphanizomenon flos-aquae*, all counts and volume measurements were made on individual cells within a filament (flakes tended to break apart into filaments during preservation and transport). Heterocysts and akinetes were enumerated separately.

Zooplankton Composition and Biomass

Crustacean zooplankton and rotifers were sampled at each location using a 12 L Schindler-Patalas trap with 64 μm mesh. A depth-integrated sample was collected by taking one sample from between the surface to 1 m depth interval, one from between the 1 m above bottom to bottom interval, and then combining the two samples for a total of 24 L filtered. The exception to this was the deeper Eagle Ridge site (ER) where a third collection was made from the midpoint of the water column (approximately 3 m) for a total of 36 L filtered. Due to very shallow nature of Upper Klamath and Agency Lakes (mean depth = ~2.4 m), the collection method provided a representative water column sample. Zooplankton samples were narcotized with carbonated water prior to preservation in an ethanol-glycerin solution (Pennak 1989). Individual species abundance was determined (at 100x) from the average of three subsamples taken from the depth-integrated sample at each site and date. Measurements of individual species (at least 10% of the total count) were made on a site-composited sample for each date, and dry weight biomass conversions were made according to Dumont et al. (1975), McCauley (1984), Culver et al. (1985), and Lawrence et al. (1987). Both phytoplankton and zooplankton data are available only through August 1996.

Data Analysis

Although individual sites were evaluated to ensure conformity to lake-wide trends (data not shown), the analyses reported here were generally performed on the lake-wide mean of a given sample date. Further data reduction consisted of both monthly and growing season (June-September) means. Because of bloom timing differences between Upper Klamath and Agency Lake (see Chapter 2), lake-wide means reported here were computed from open-

water sites in Upper Klamath Lake only. The Pelican Bay site PB (Fig. 1 introduction) was also not included in computation of the lake-wide mean due to the unique influence of cold spring-water and wetland vegetation on the plankton dynamics at this site.

All data collected tended to be either normally or lognormally distributed both within a date and seasonally. Based on a comparison of both log transformed (\log_{10} or $\log_{10}(x+1)$) and non-transformed data with the normal distribution using Kolmogorov-Smirnov one-sample tests (cf. Wilkinson 1996; Zar 1984), either a mean or geometric mean provided the best estimate of lake-wide or seasonal central tendency. For percent composition data (phytoplankton and zooplankton), an arcsin square root transformation (Zar 1984) was performed prior to taking means.

Sensitivity of seasonal trends and parameter estimates to utilizing a subset of sample sites in the computation of sample date means (hereafter referred to as lake-wide means) was negligible based on a comparison of means computed from a reduced number of sample sites on a given date to means computed using all sites on that same date (data not shown).

Seasonal and interannual associations among variables were assessed both graphically and with linear regressions. The assumptions of linear regression were evaluated using residual and normal probability plots, autocorrelation of residuals, estimates of skewness and kurtosis, and Kolmogorov-Smirnov tests of fit (Kleinbaum et al. 1988; Wilkinson 1996).

Results

Interannual and seasonal phytoplankton dynamics

Approximately 80 different phytoplankton species were found in Upper Klamath Lake, 15% of which showed occasional local or site-specific importance. However, on a lake-wide

mean basis, dominance was limited to only a few species. Despite the presence of high biomass levels of non-Cyanophyte taxonomic groups relative to other productive lake ecosystems, the biomass levels attained by Cyanophyta (blue-green algae) far exceeded levels of any other taxa in Upper Klamath Lake (Fig. 1.1). The Cyanophyta were comprised almost entirely of the colonial heterocyst-producing *Aphanizomenon flos-aquae* (Fig. 1.2). From initial dominance in late-May or early-June through the bloom decline in October or November (with the exception of 1992 and 1994, when bloom crashes occurred in late July) (Fig. 1.1), *Aph. flos-aquae* comprised between 90-100% of the total phytoplankton biomass (Fig. 1.3). It is generally not until *Aph. flos-aquae* enters its final seasonal decline that other taxa comprise a majority of the composition (Fig. 1.3).

Aside from interannual differences in the magnitude (Fig. 1.1) and timing of the initial *Aph. flos-aquae* bloom, early season successional patterns and appearance of particular species guilds were quite consistent among years. For example, late-winter and spring periods were typically dominated by both members of the Cryptophyta (mainly *Cryptomonas ovata*, *Cryptomonas reflexa*, with minor contributions from *Rhodomonas minuta*) and Chrysophyta (mainly of the family Bacillariophyceae or Diatoms, and consisting of small *Stephanodiscus* spp., *Asterionella formosa*, and *Melosira granulata*) (Fig. 1.3). Occasional minor dominance by Chlorophyta (*Chlamydomonas* sp. and *Sphaerocystis schroeteri*) also occurred during the late-winter and spring period (Fig. 1.3). A very small peak of the Cyanophyte *Anabaena flos-aquae* (< 0.7 mg L⁻¹) consistently occurred in late-May or Early June, just prior to the onset of the *Aphanizomenon flos-aquae* bloom. During the summer period of *Aphanizomenon flos-aquae* dominance, *Cryptomonas ovata* and *Rhodomonas minuta* remained at low levels of abundance, but in comparison to *Aph. flos-aquae* generally represented less than 1% of the

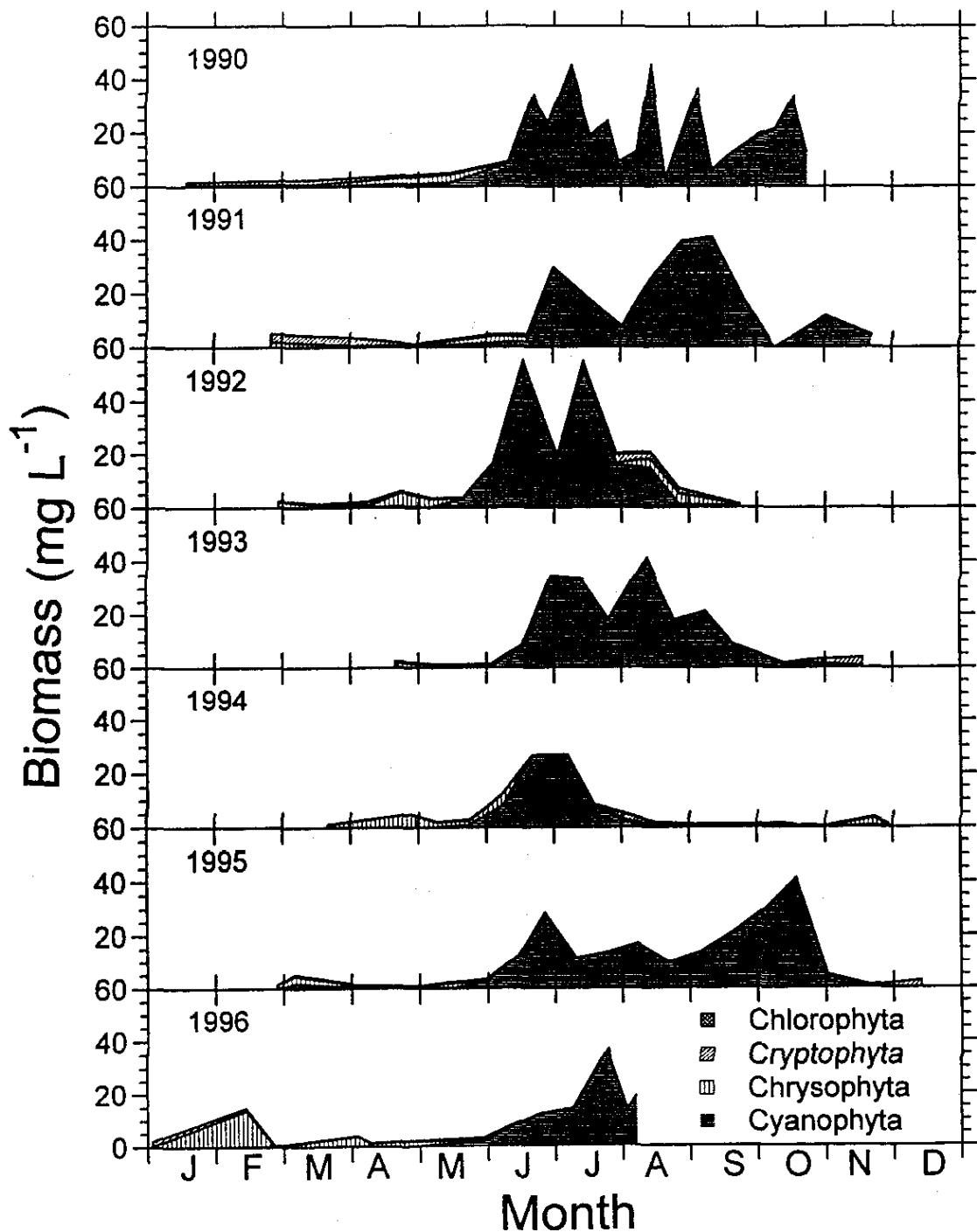


Fig. 1.1. Lake-wide mean total biomass (mg L^{-1} wet wt.) of major phytoplankton taxa in Upper Klamath Lake, Oregon, 1990-1996.

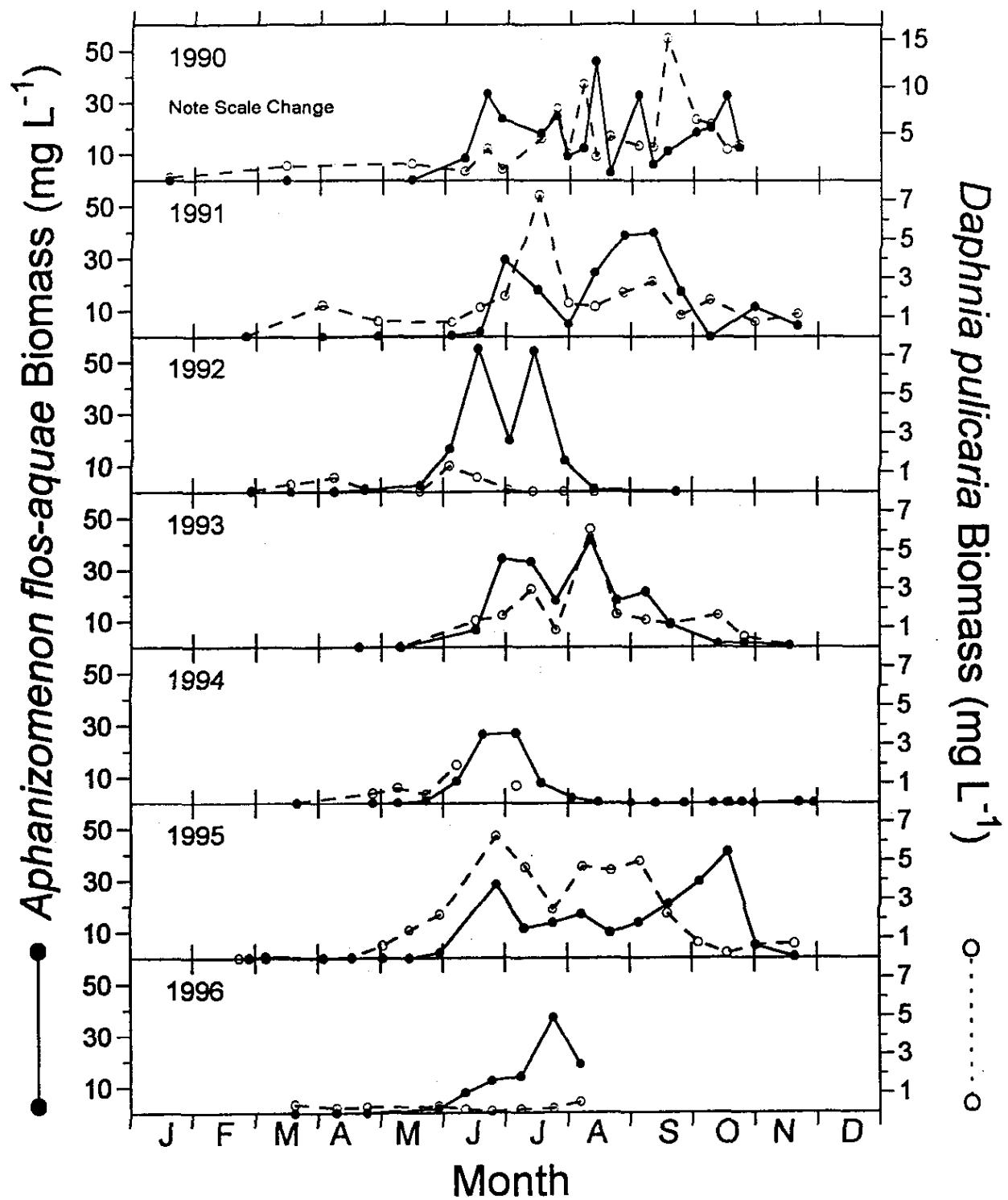


Fig. 1.2. Lake-wide mean total biomass of *Aphanizomenon flos-aquae* (mg L^{-1} wet wt.; solid line) and *Daphnia pulicaria* (mg L^{-1} dry wt.; dashed line) in Upper Klamath Lake, Oregon, 1990-1996.

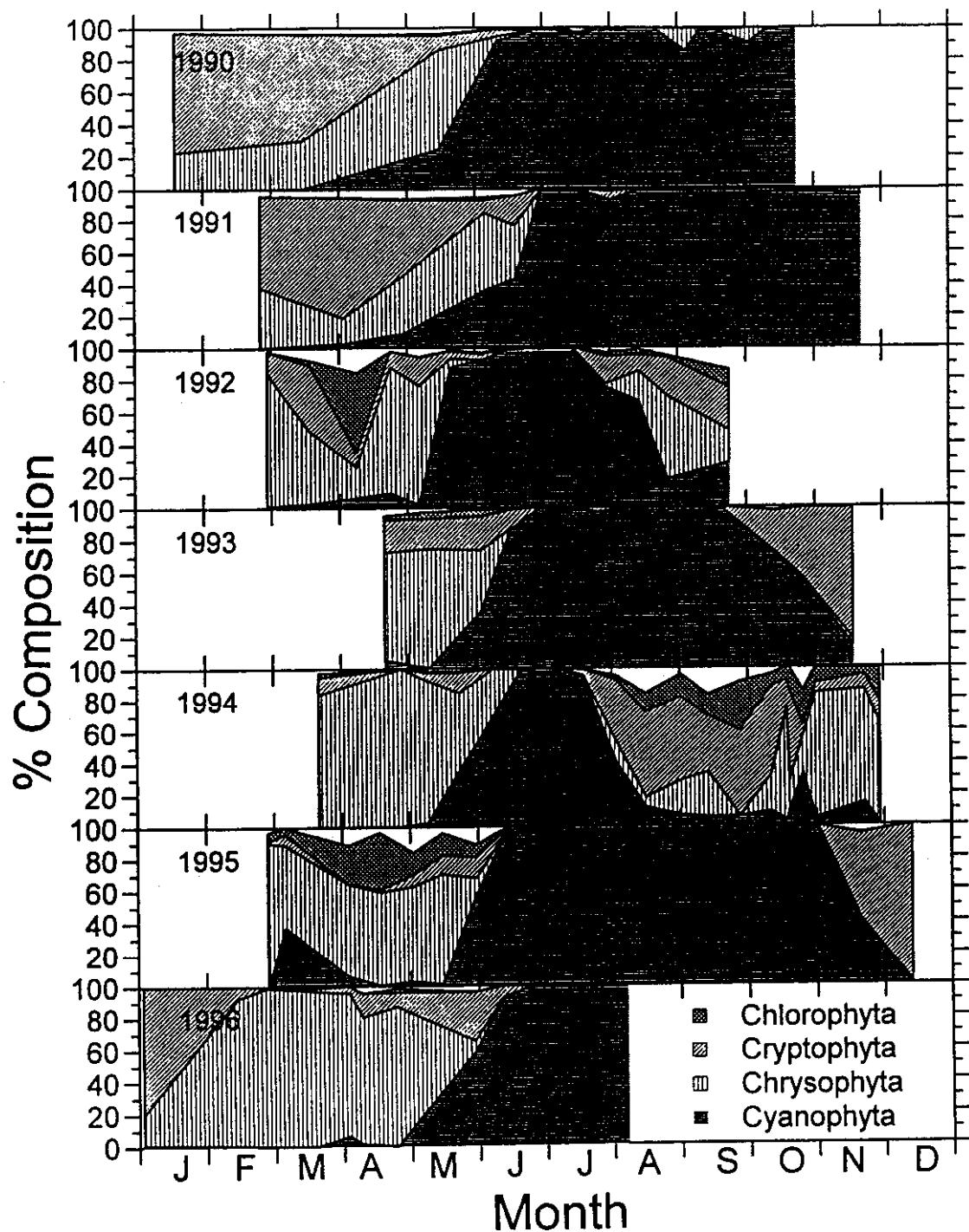


Fig. 1.3. Lake-wide mean percent composition (by biomass) of major phytoplankton taxa in Upper Klamath Lake, Oregon, 1990-1996.

total phytoplankton biomass. A toxic strain of the large, non-heterocystous colonial cyanophyte, *Microcystis aeruginosa*, also occasionally appeared during mid-summer and early-fall, forming a visible thin film at the lake surface. However, on a water column mean basis *Microcystis* generally represented a minor portion of the total biomass, with the exception of leeward shore accumulations during daily summer wind events. The predominant fall through mid-winter assemblage consists of *Cryptomonas ovata* along with occasional diatoms (e.g., *Stephanodiscus niagarae*). The above seasonal succession pattern then repeats as diatoms increase in importance in late-winter, particularly after ice-out.

The greatest inconsistencies in the above successional pattern among the 7 years occurred in 1992 and 1994. Subsequent to the late-July *Aphanizomenon* decline, the Cryptophytes *Cryptomonas ovata* and *Rhodomonas minuta* increased in dominance, as did the Chrysophyte *Synedra ulna* (pennate diatom). In addition, members of the Chlorophyta (*Chlamydomonas* spp. and *Ankistrodesmus* spp.) and small colonial Cyanophyta (*Coelosphaerium* and *Gloeothecace* spp.) also increased in importance (Fig. 1.3).

Interannual and seasonal zooplankton dynamics

Due to its very large size in comparison to other zooplankton taxa (range 1-5 mm, mean ~2 mm), *Daphnia pulicaria* biomass far exceeded that of all other zooplankton groups on an annual basis (Figs. 1.2 and 1.4), and also represented almost the entire Cladoceran biomass. The only other prevalent Cladoceran was *Chydorus sphaericus*, which remained at levels several orders of magnitude lower than *D. pulicaria* during periods of *D. pulicaria* dominance. Despite overall *D. pulicaria* dominance within a given year, its biomass varied considerably between years; for example 1992, 1994 and 1996 (through early-August)

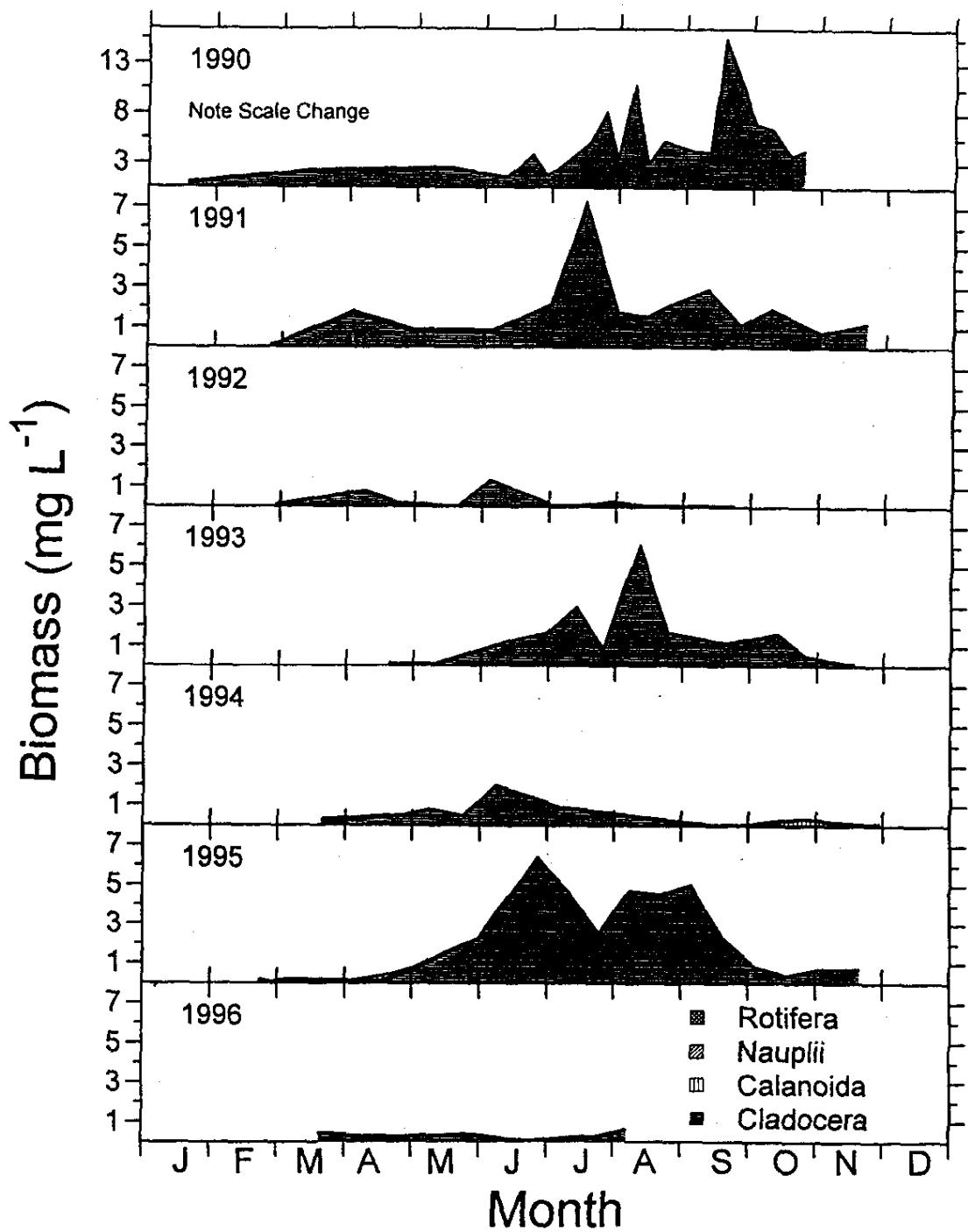


Fig. 1.4. Lake-wide mean total biomass (mg L^{-1} dry wt.) of major zooplankton taxa in Upper Klamath Lake, Oregon, 1990-1996.

showed considerably lower *D. pulicaria* biomass than other years (Fig. 1.4). *D. pulicaria* was present at low levels ($<1 \text{ mg L}^{-1}$) during the spring period of cryptophyte and diatom dominance, but generally increased during the initial *Aphanizomenon flos-aquae* bloom (Fig. 1.2), although the magnitude of the initial *D. pulicaria* increase was highly variable.

During certain periods of low *D. pulicaria* biomass (e.g., late winter and early spring, and late July through fall 1992 and 1994) the biomass of other zooplankton taxa increased in importance (Fig. 1.5). These included the calanoid copepods *Epishura nevadensis* and *Leptodiaptomus ashlandi*, the cyclopoid copepod *Diacyclops thomasi*, copepod nauplii, and rotifers (numerous species, but chiefly *Asplanchna sieboldi*, *Euchlanis dialata*, and *Kertella quadrata*) (Fig. 1.5). It is evident from Fig. 1.4, however, that absolute biomass of these taxa was insignificant relative to that of *D. pulicaria* (maximum biomass of non-*Daphnia* groups may reach 0.3 mg L^{-1} compared to $1\text{-}7 \text{ mg L}^{-1}$ for *D. pulicaria*). Based on abundance alone these secondary taxa (particularly rotifers and nauplii) frequently exhibited numerical dominance (Figs. 1.6 and 1.7), and it is evident that they were present in large numbers even when *D. pulicaria* dominated.

Relative effects of nutrients and zooplankton on initial bloom development

The transition from spring dominance by cryptophytes and diatoms to dominance by *Aph. flos-aquae* is characterized by increasing water temperatures and water column stability (Fig. 1.8), and a decreasing light climate (Fig. 1.9). Initiation of *Aph. flos-aquae* blooms in many lakes occurs in the range of $15\text{-}20^\circ\text{C}$ (reviewed in Pechar et al. 1992), and 15°C appeared to be a consistent threshold temperature for Upper Klamath Lake. However, because spring water temperature measurements were widely spaced (Fig. 1.8), it is difficult

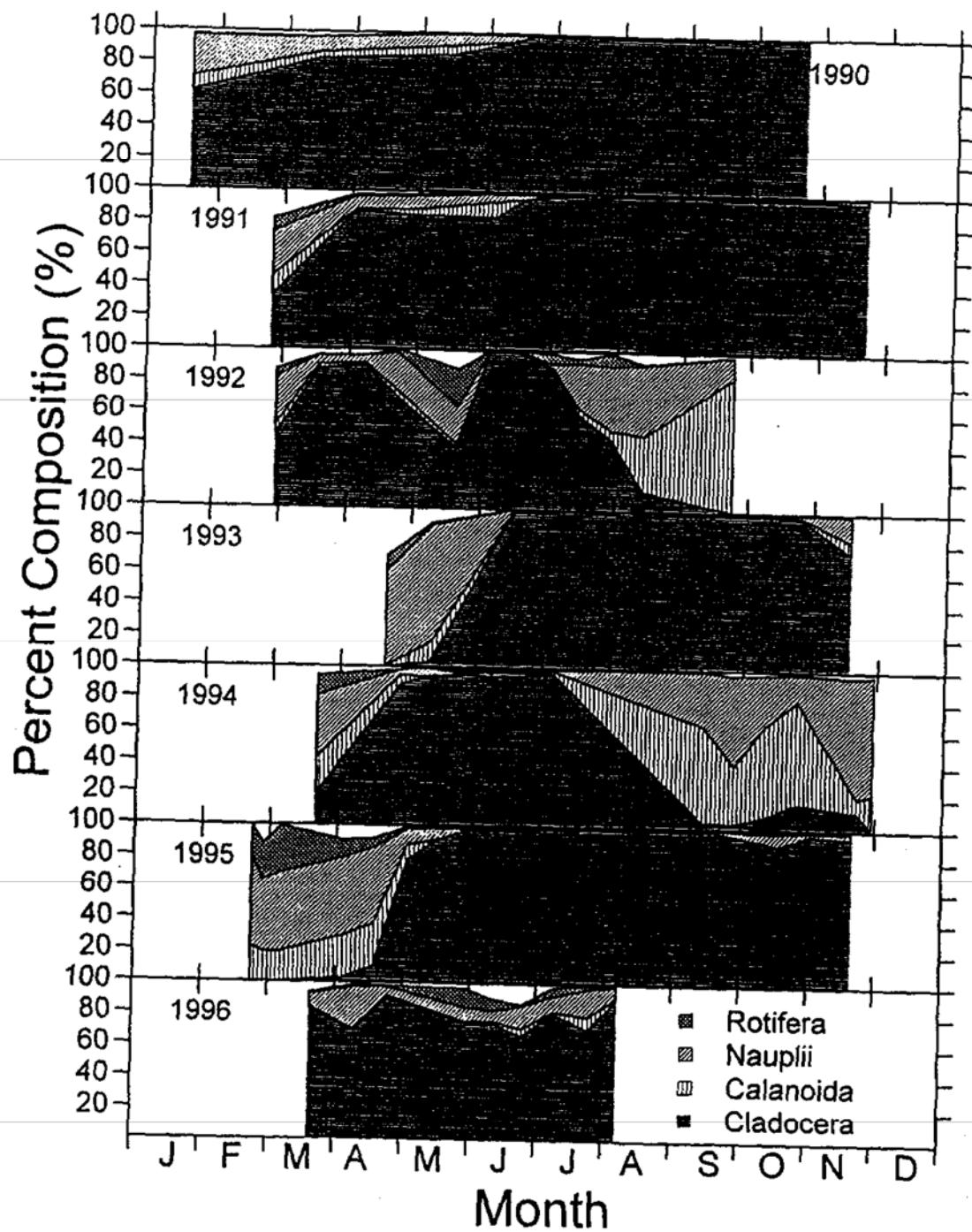


Fig. 1.5. Lake-wide mean percent composition (by biomass) of major zooplankton taxa in Upper Klamath Lake, Oregon, 1990-1996.

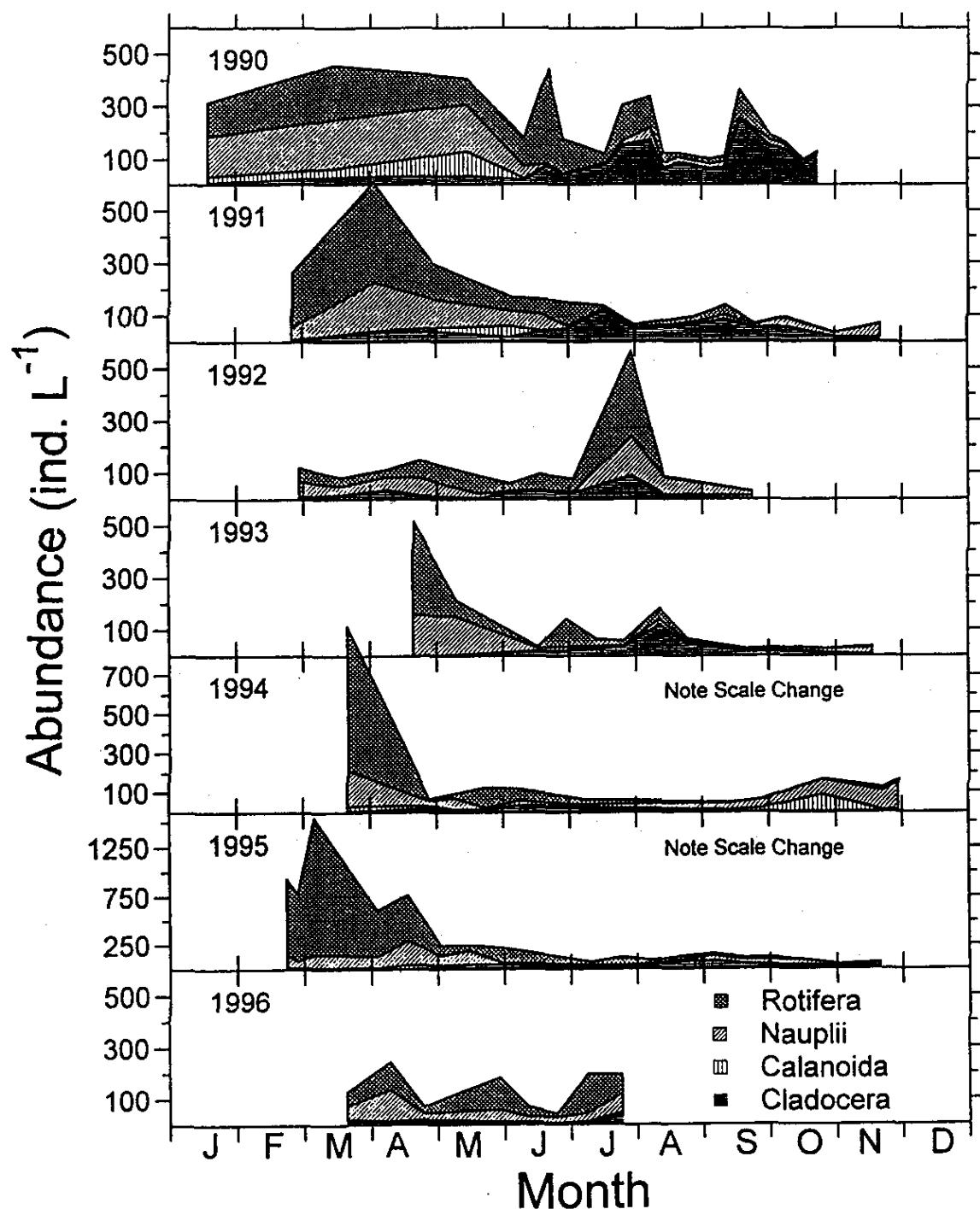


Fig. 1.6. Lake-wide mean total abundance (individuals L^{-1}) of major zooplankton taxa in Upper Klamath Lake, Oregon, 1990-1996.

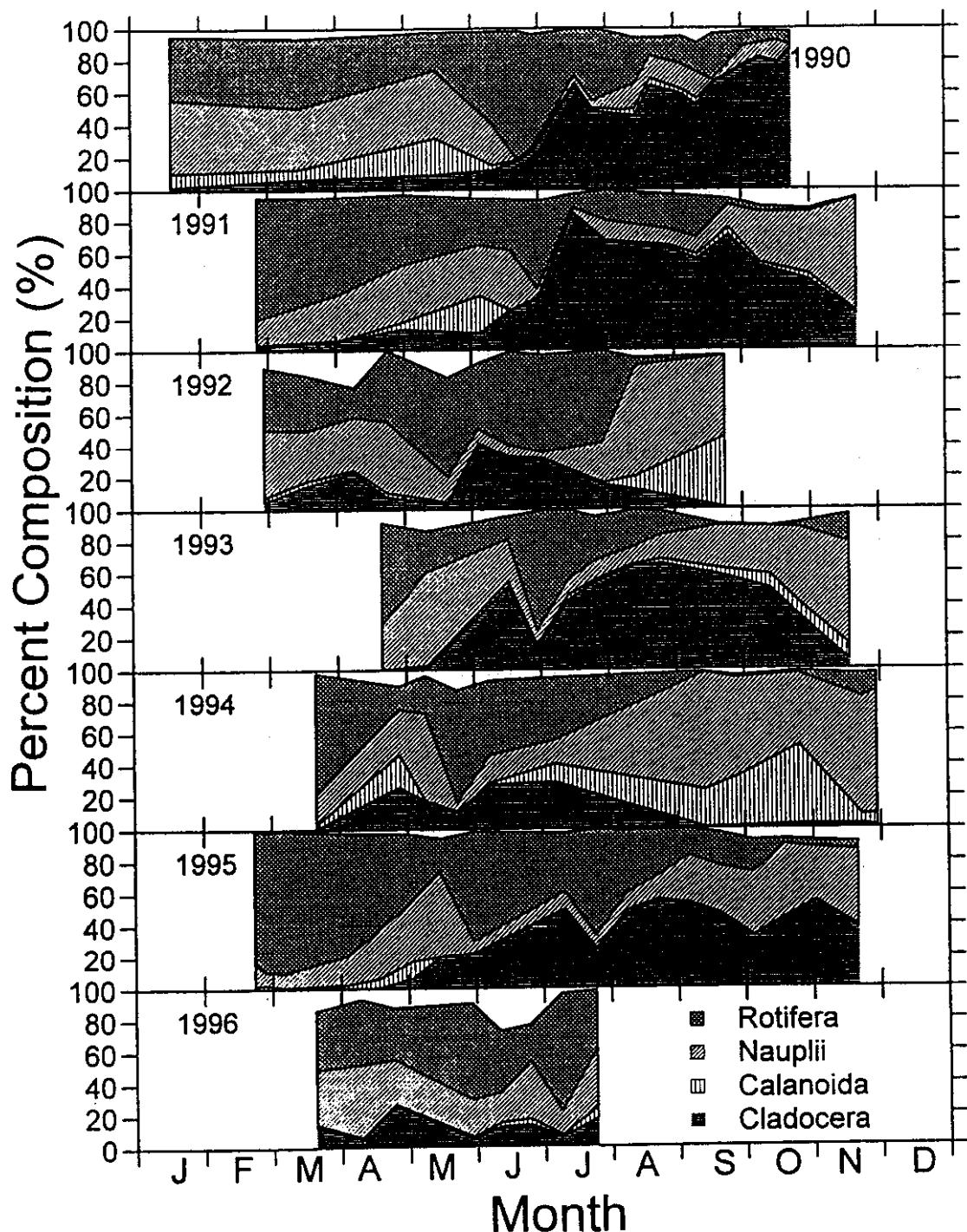


Fig. 1.7. Lake-wide mean percent composition (by abundance) of major zooplankton taxa in Upper Klamath Lake, Oregon, 1990-1996.

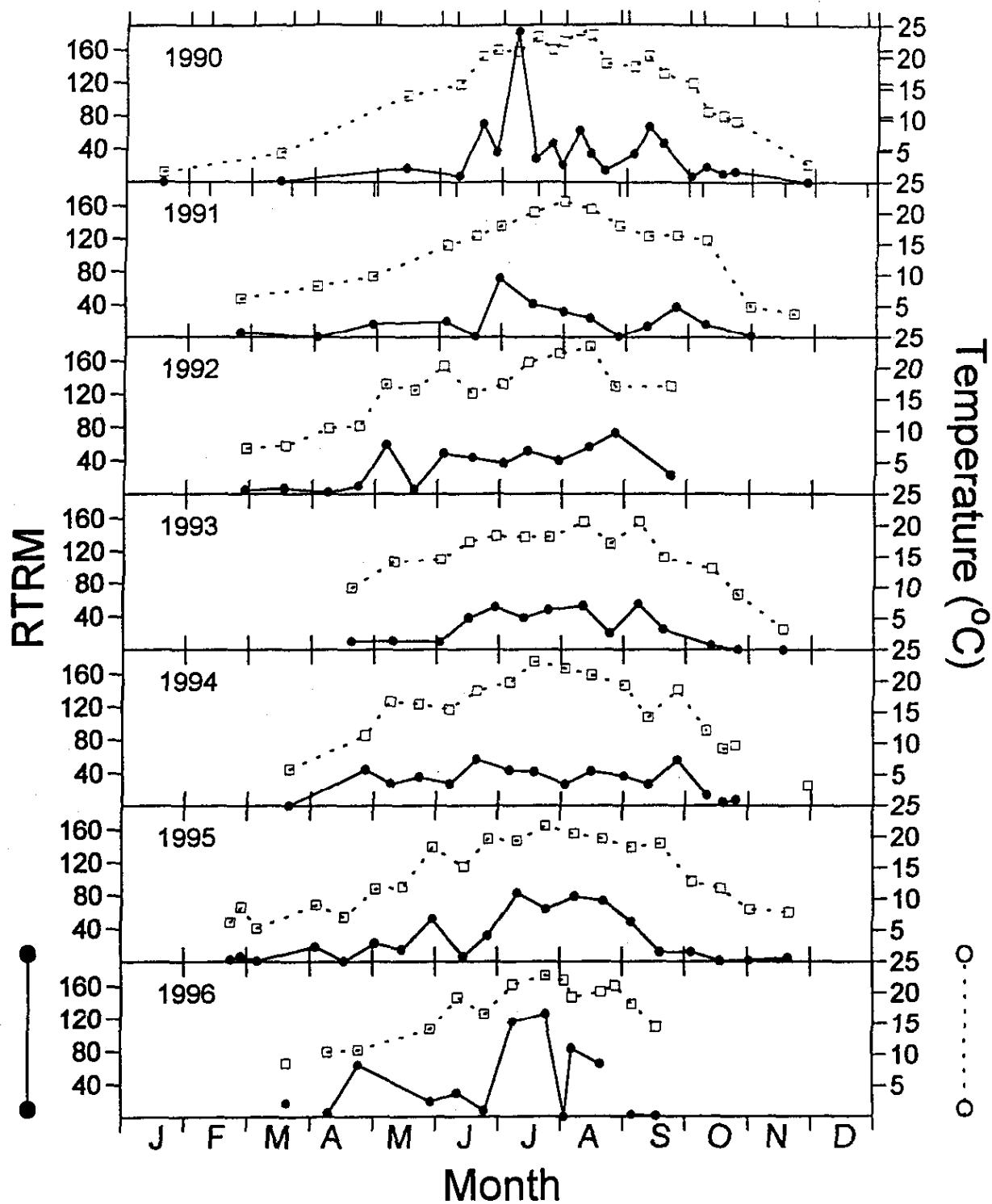


Fig. 1.8. Seasonal trends in relative thermal resistance to mixing (RTRM - solid line) and water temperature (dashed line) in Upper Klamath Lake, Oregon, 1990-1996.

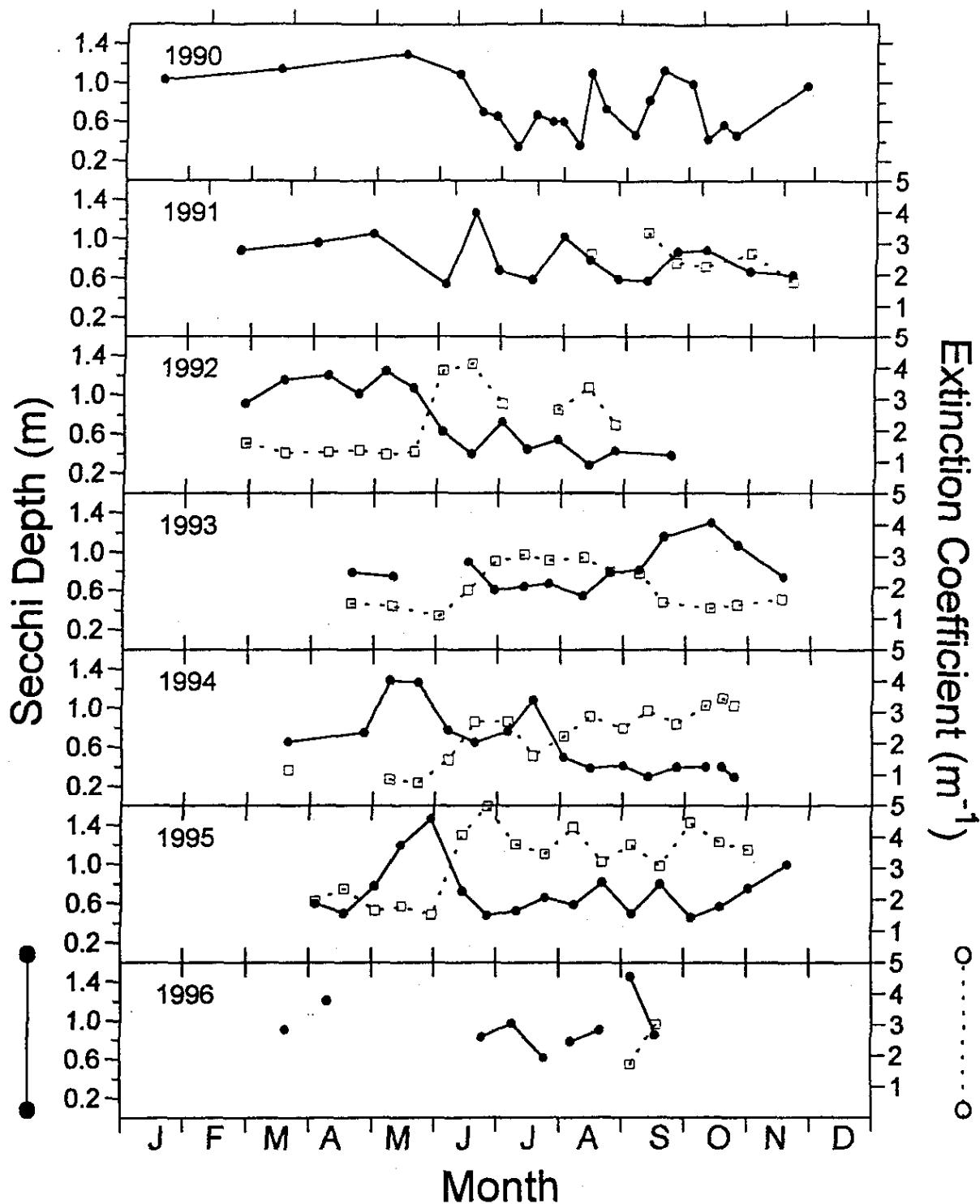


Fig. 1.9. Seasonal trends in Secchi depth (solid line) and extinction coefficient (m^{-1} , dashed line) in Upper Klamath Lake, Oregon, 1990-1996.

to relate bloom onset directly to water temperature. However, in a shallow system such as Upper Klamath Lake, the expected lag time between air and water temperatures should be small. Accordingly, a regression analysis (data not shown) between consecutive daily mean air temperatures and water temperature indicated that a 7-day consecutive mean (i.e., a mean of air temperature for the 7 day period prior to the date at which water temperature was measured) provided the best fit ($r^2 = 0.82$, slope=1.06, $P < 0.001$) to measured water temperature during the spring period. To determine the effect of lake warming on bloom initiation, both the date when this 7-day consecutive mean equaled 15 °C and the number of degree days between April 1 and May 15 (chosen as another index of lake warming) were regressed against the date when the initial bloom began to clearly increase (defined here as 10 mg L⁻¹ *Aph. flos-aquae* biomass). Both indices show significant ($P < 0.02$) relationships, indicating later bloom onset when the lake took longer to reach 15 °C, or the higher the integrated air temperature (i.e., degree days) during the late spring period, the earlier the bloom onset (Fig. 1.10a,b).

Further effects on bloom timing could be caused by variable lake volume among years, where high volume would 1) be expected to delay lake warming (through influences on the heat budget), and 2) greater mean depth would be expected to decrease the overall amount of light available to algal cells in a mixed water column. A plot of lake volume in May versus the number of days to bloom initiation indeed does show a significant positive relationship (Fig. 1.10c), but to the extent that annual lake volume and air temperature are correlated it is not possible to tease apart the relative effects.

The effect of lake volume on the underwater light climate is further evidenced by the fact that mean water column light as a percent of the surface is inversely related to lake

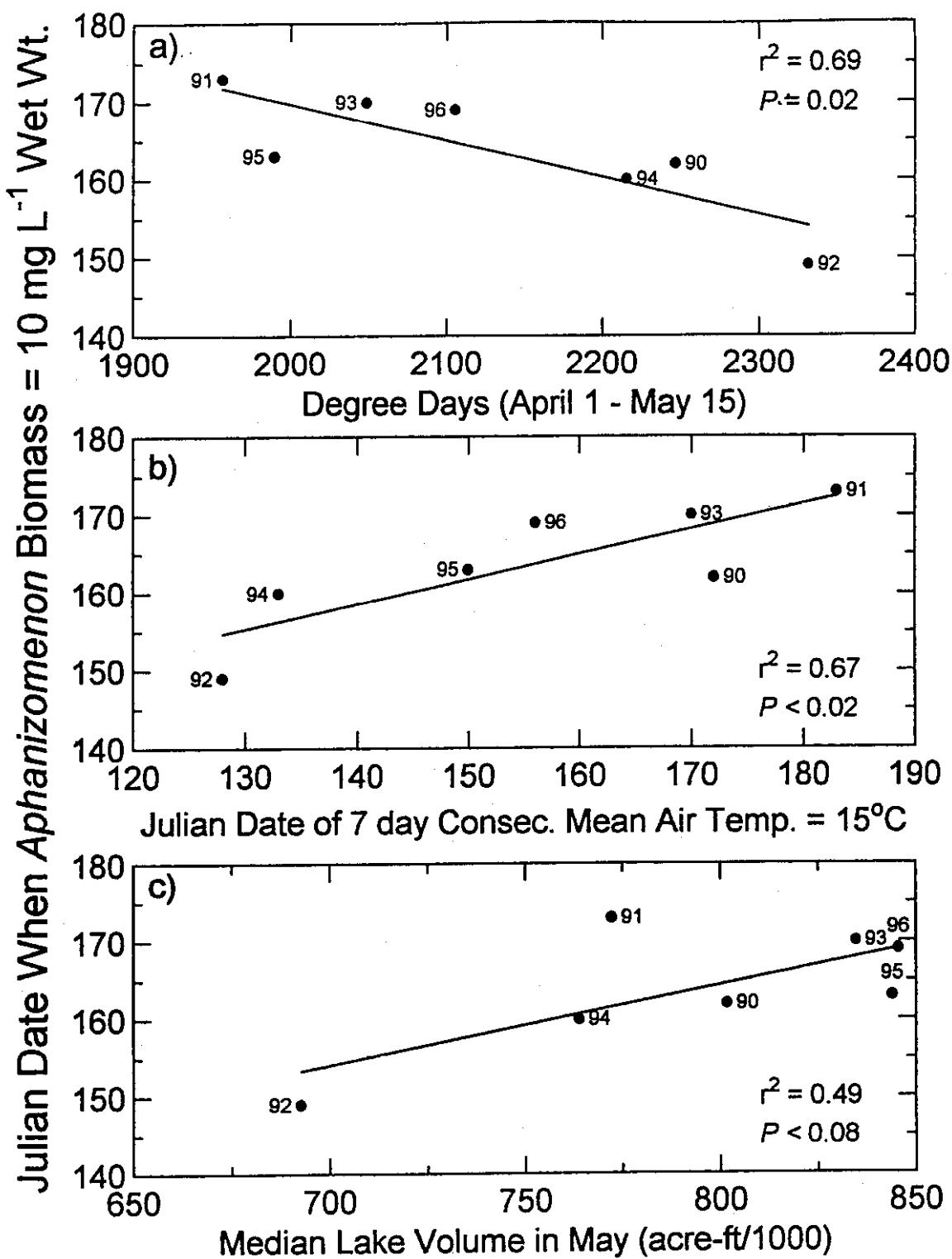


Fig. 1.10. Scatter plots of bloom initiation (defined as the Julian day at which *Aph. flos-aquae* biomass reached 10 mg L⁻¹) versus April 1-May 15 degree days (a), Julian date when 7-day mean consecutive air temperature reached 15 °C (b), and median May lake volume (c). Symbol labels refer to years.

elevation (Fig. 1.11). As phytoplankton cells are circulated throughout the water column (particularly during the spring period of low water column stability), they will on the average experience less light at deeper depths, thus delaying both the onset of the bloom and the time until the bloom peaks.

It is clear that physical factors influence the initiation of the bloom in Upper Klamath Lake. However, transition to dominance by *Aph. flos-aquae* was also accompanied by increasing *D. pulicaria* (Fig. 1.2), increasing TP and TN concentrations (Figs. 1.12 and 1.13), decreasing TIN (Fig. 1.14), and increasing heterocyst abundance and frequency (expressed as percent of vegetative cells) (Figs. 1.13 and 1.14). Three major conclusions can be drawn from the seasonal pattern of these variables. First, the increase in water column TP does not occur until after the bloom has begun, and internal (sediment) phosphorus loading data show that as pH increases due to photosynthetic activity of increasing biomass of algae (beginning in June; Chapter 2), the loading rate of TP from the sediments also increases (Fig. 1.15; methods described in figure caption). This is a common mechanism in shallow, high pH lakes, whereby high pH increases phosphorus flux to the water column by solubilizing iron-bound phosphorus from sediment or resuspended material (Welch 1992; Sondergaard 1988; Jacoby et al. 1982). While this source of phosphorus is extremely important for supplying phosphorus to *Aph. flos-aquae* once the bloom has initiated (discussed below), it does not appear to be responsible for the transition to *Aph. flos-aquae* dominance.

Second, *D. pulicaria* generally remained at a steady population density throughout the spring (implying a consistent grazing rate on small phytoplankton species), and did not increase in biomass until *Aph. flos-aquae* increased (Fig. 1.2). Further, in 1996 *D. pulicaria* remained low through the period of *Aph. flos-aquae* increase (Fig. 1.2), and in 1992

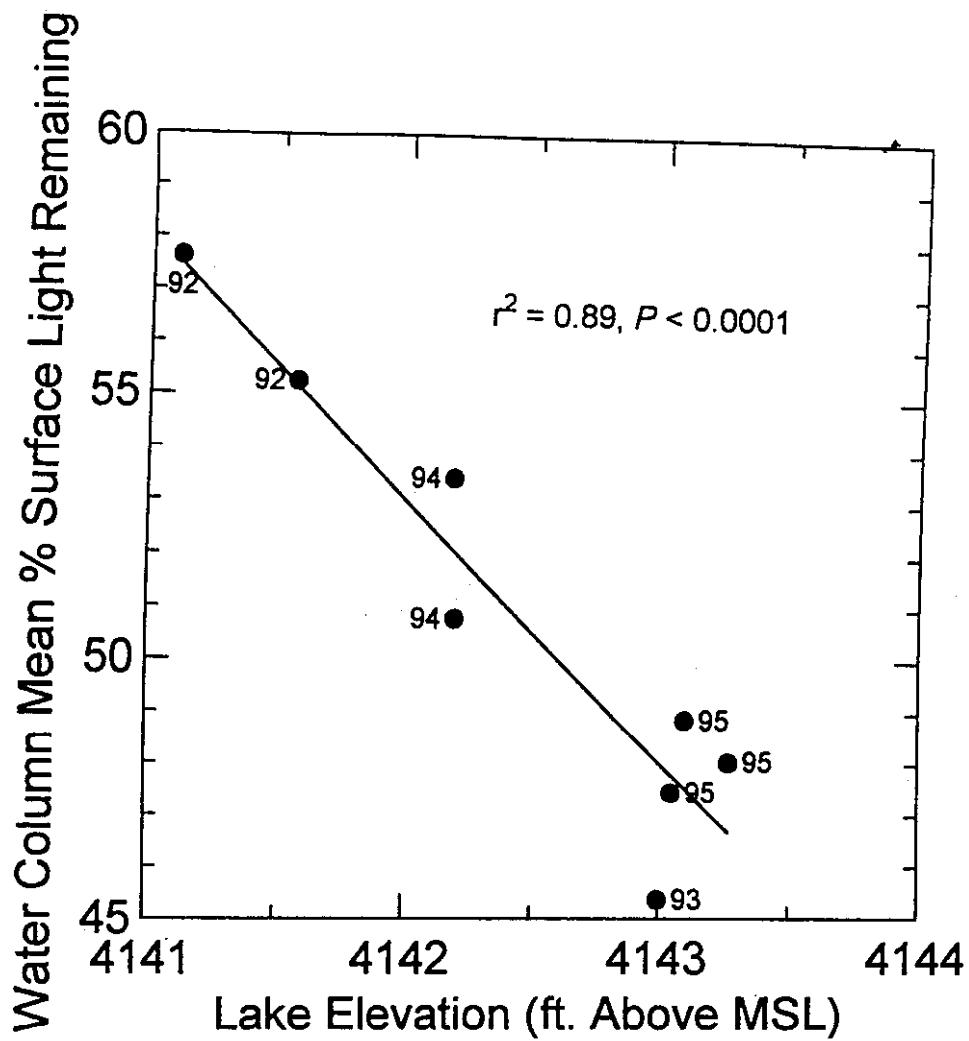


Fig. 1.11. Scatter plot of water column mean incident light intensity expressed as a percent of surface light intensity (mean % surface light remaining in water column) versus lake elevation in May (in ft. above mean sea level, which indicates mean depth). Symbol labels refer to years (multiple points per year reflect biweekly sampling, data not available for all years).

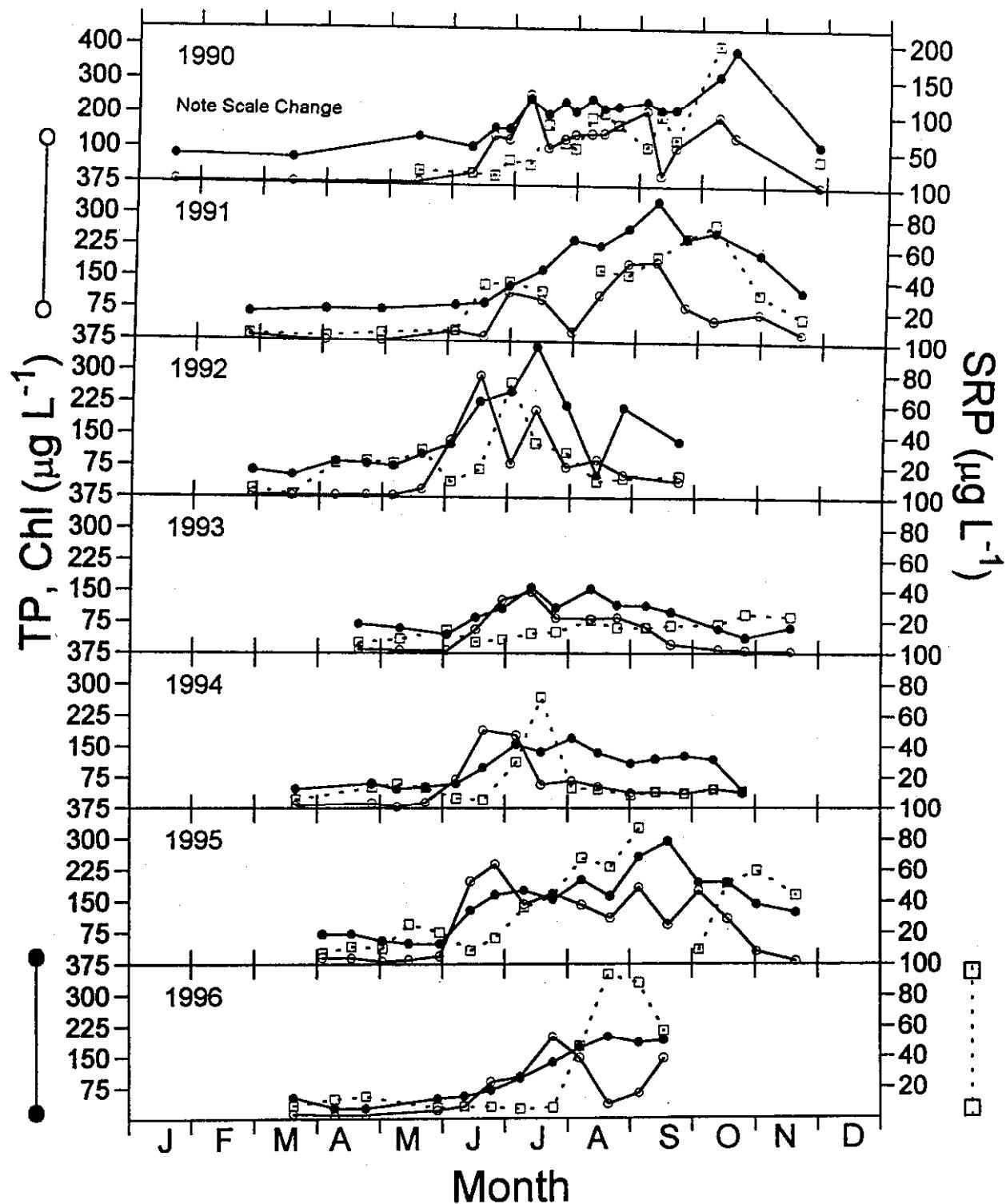


Fig. 1.12. Seasonal trends in TP (closed circle), Chl (open circle) and SRP (open square) in Upper Klamath Lake, Oregon, 1990-1996.

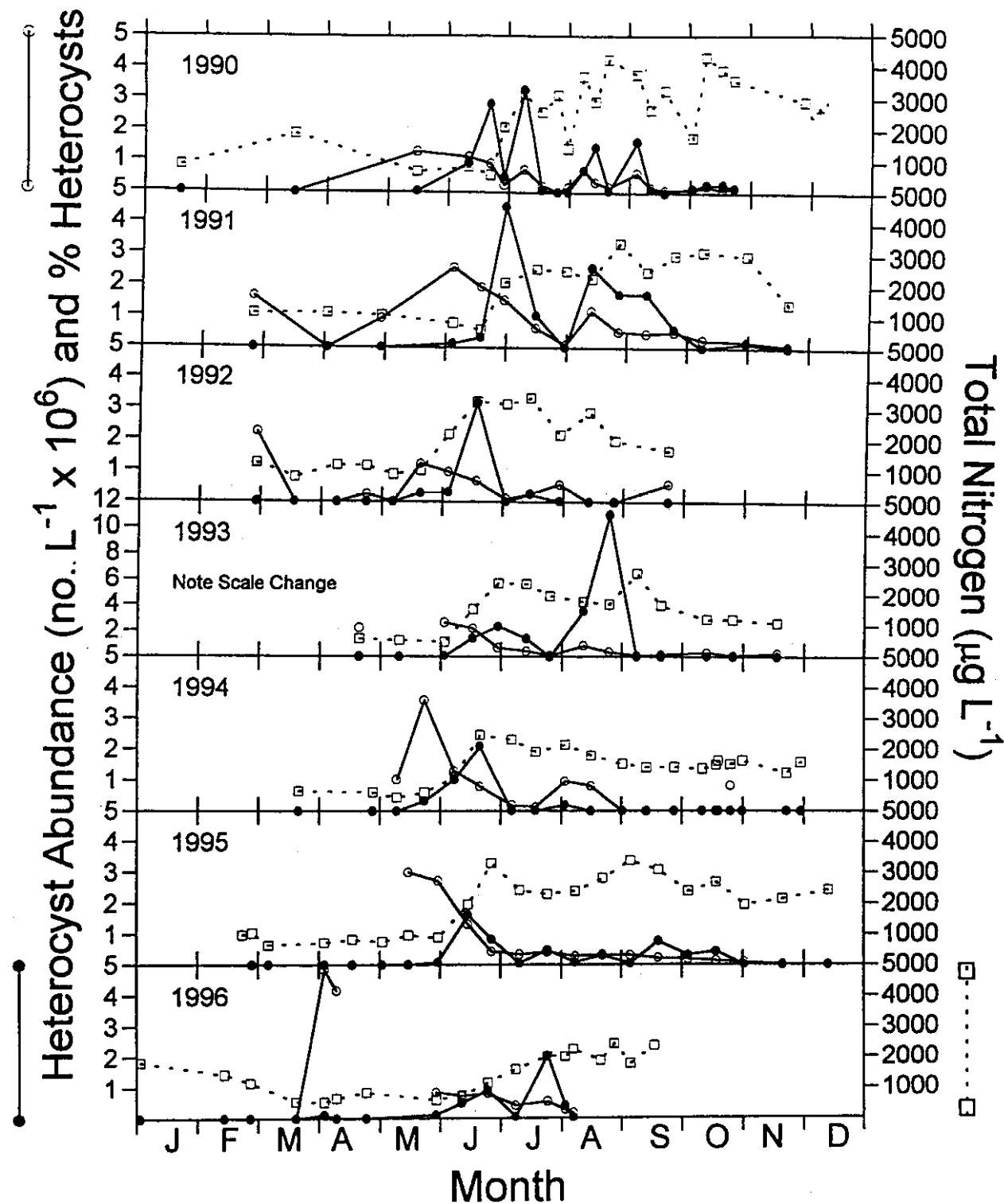


Fig. 1.13. Seasonal trends in heterocyst abundance (closed circle), heterocyst ratio (open circle) and TN (open square) in Upper Klamath Lake, Oregon, 1990-1996.

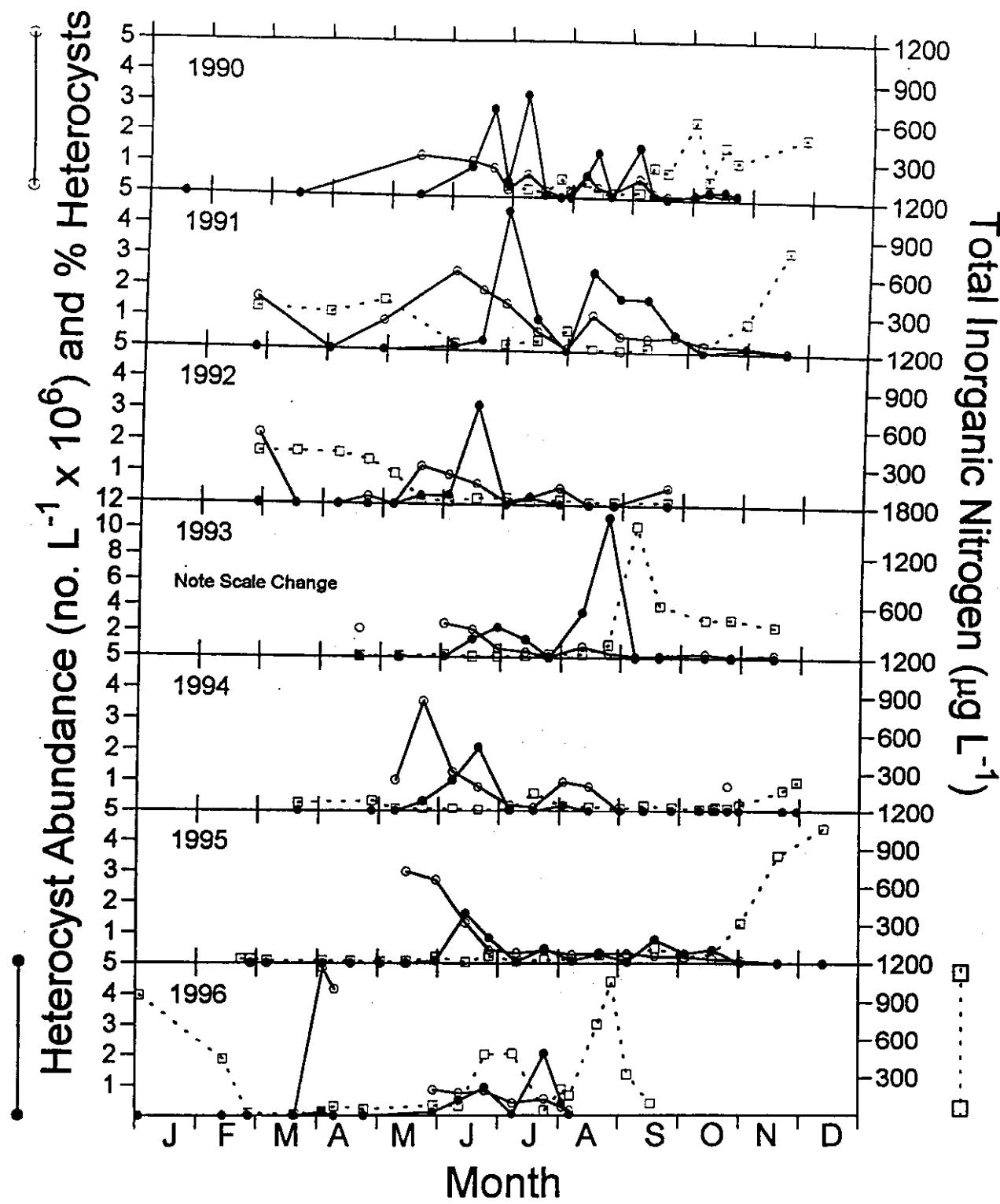


Fig. 1.14. Seasonal trends in heterocyst abundance (closed circle), heterocyst ratio (open circle) and TIN (open square) in Upper Klamath Lake, Oregon, 1990-1996.

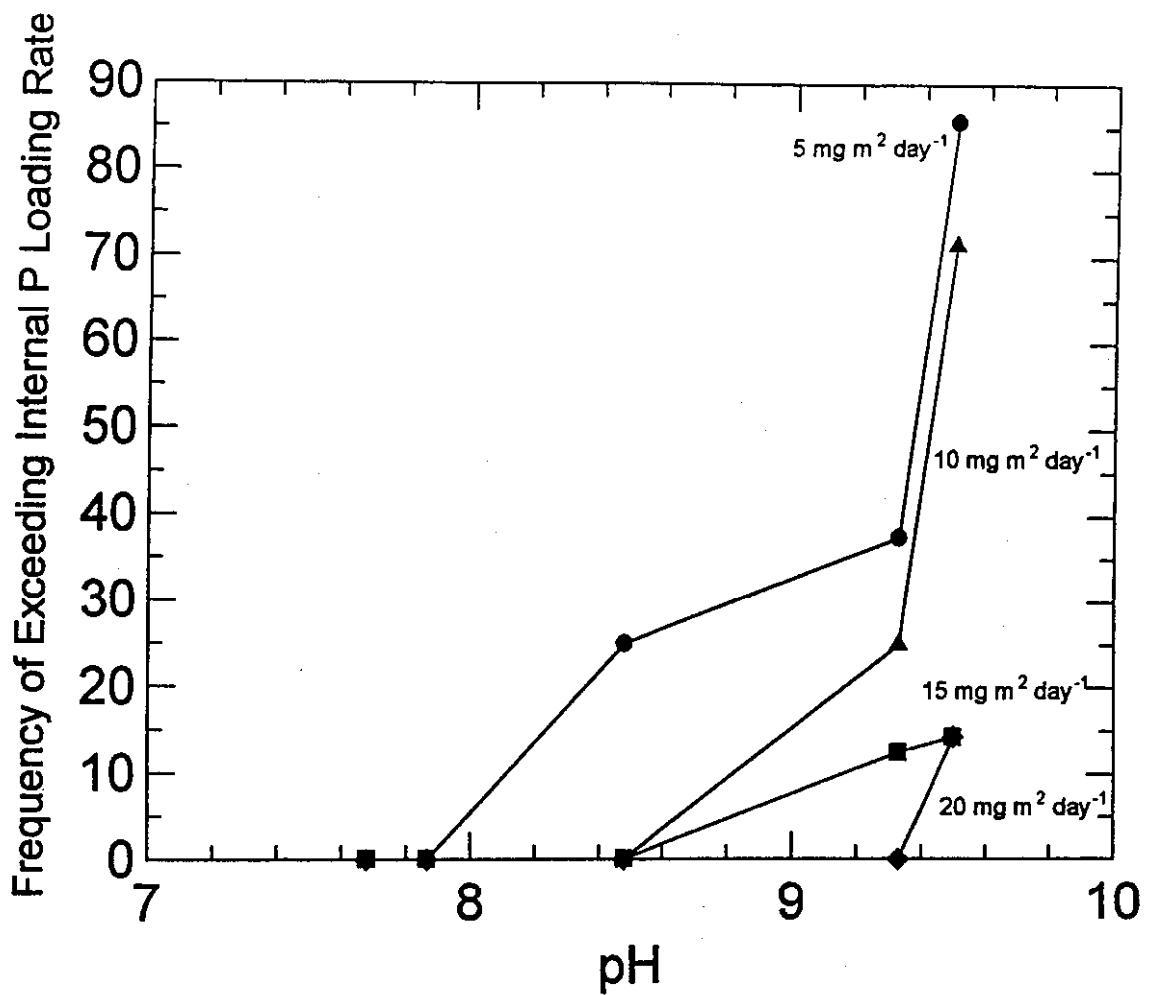


Fig. 1.15. Plot of the frequency of exceeding various internal phosphorus loading rates as a function of pH in Upper Klamath Lake. Data represent lake-wide biweekly mean pH and internal P loading estimates for the 1991-1992 growing seasons. Internal loading was estimated from a lake-wide P budget computed during 1991 and 1992. The plot represents a non-parametric cross tabulation method (see Chapter 2) where the frequency of exceeding chosen internal loading rates is computed within ordered (ascending) pH intervals and plotted against the median pH in each interval. For example, at a median pH value of 8.5 a loading rate of $10 \text{ mg m}^{-2} \text{ d}^{-1}$ was exceeded in 0% of the observations, while at pH 9.5 it was exceeded in 70% of the observations.

D. pulicaria increased only slightly, yet *Aph. flos aquae* reached its highest peak of any of the years. High numbers of *Daphnia* do not appear to be needed for transition to *Aph. flos-aquae* dominance.

Third, the data suggest that the decreasing or low levels of TIN prior to *Aph. flos-aquae* dominance is very likely creating favorable conditions for dominance by *Aph. flos-aquae* (discussed below); however, examination of the seasonal trends reveals that heterocyst abundance and frequency increase whether TIN started high and then decreased (e.g., 1991 and 1992; Fig. 1.14), or whether TIN was already depressed for a period of time prior to bloom initiation (e.g., 1994-1996; Fig. 1.14). While there is a clear increase in heterocyst frequency and abundance preceding the increase in *Aph. flos-aquae* biomass (Fig. 1.14), these increases do not appear to be linked to observable trends in TIN.

It is evident from these data that the transition from spring cryptophytes and chrysophytes to *Aph. flos-aquae* can not be explained solely by observable trends in SRP, *Daphnia*, or heterocyst/TIN dynamics. Although these variables are likely important for continued dominance and biomass development of *Aph. flos-aquae* (see below), the temperature and light environment appear to play a stronger role in bloom initiation than either grazing pressure or the nutrient environment. This may be especially true considering that germination of *Aph. flos-aquae* akinetes (resting cells) occurs in the sediments in response to light and temperature, and that benthic recruitment of *Aph. flos-aquae* to the plankton occurs as small (but still grazing-resistant) flakes (Barbiero and Kann 1994). The role of grazers in maintaining a high light environment could potentially affect this process, but extinction coefficients remained fairly constant during the spring transition period (as did *D. pulicaria* level) until *Aph. flos-aquae* increased, and only then did light decrease in

response to higher algal biomass levels (Fig. 1.9).

Relative effects of nitrogen and phosphorus on bloom dominance

In late spring of each year, an increase in the frequency of heterocysts (open circles; Fig. 1.13) preceded increases in total heterocyst abundance (solid circles; Fig. 1.13) and TN indicating that nitrogen fixation was occurring (*cf.* Horne and Goldman 1972; Horne et al. 1979). Following an initial increase in TN, heterocyst frequency decreased and generally remained low throughout the remainder of the bloom period, although occasional peaks in heterocyst abundance occurred (Fig. 1.13). Even though heterocyst frequency and abundance tended to decrease, TN remained elevated through the growing season indicating the importance of the early season nitrogen fixation for input of nitrogen to the system. With the exception of 1996, TIN was generally low (ranging between 15 and 85 $\mu\text{g L}^{-1}$) during the initial period of high heterocyst frequency (Fig. 1.14), and then tended to remain low except for occasional large pulses of $\text{NH}_4\text{-N}$. Based on inorganic N and P criteria suggested by Horne and Commins (1987), Smith et al. (1995) concluded that ideal SRP and TIN concentrations for nitrogen fixation are attained when conditions of $\leq 100 \mu\text{g L}^{-1}$ TIN and $\geq 10 \mu\text{g L}^{-1}$ SRP occur simultaneously in the water column. A plot of lake-wide means for all years indicated that the majority (~60 %) of sample dates in Upper Klamath Lake either were close to or met this criterion, and furthermore that those dates exhibiting the greatest frequency of heterocysts also occurred within or very close to the $\leq 100 \mu\text{g L}^{-1}$ TIN and $\geq 10 \mu\text{g L}^{-1}$ SRP thresholds (larger diameter circles; Fig. 1.16a). It should be noted, however, that these high heterocyst frequencies correspond to early season bloom development, and that *Aph. flos-aquae* continued to dominate July-September when heterocyst frequency was low and TIN

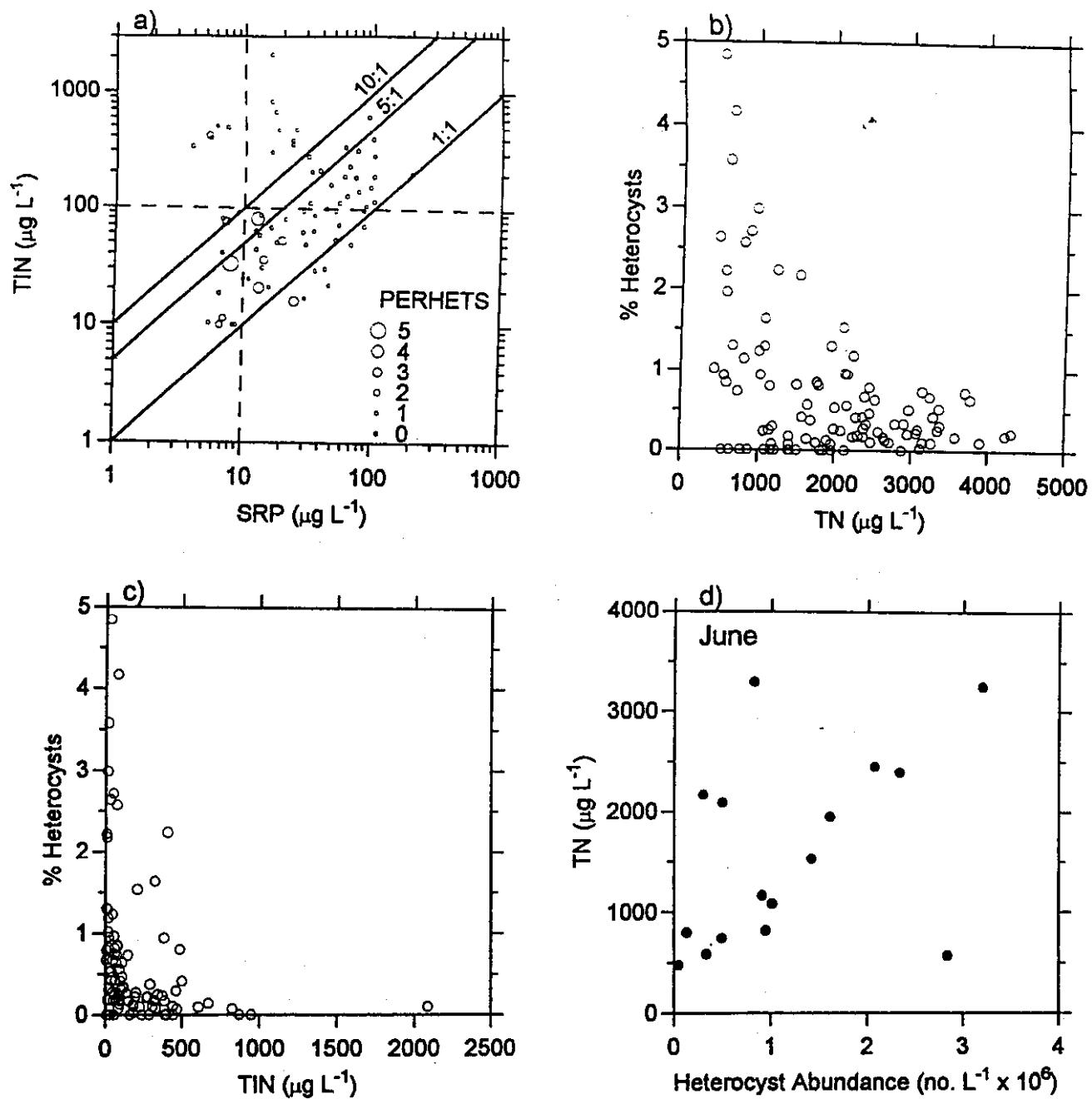


Fig. 1.16. Scatter plot of SRP versus TIN (a), with limits (dashed lines) drawn at $100 \mu\text{g L}^{-1}$ TIN and $10 \mu\text{g L}^{-1}$ SRP, symbol size represents heterocyst frequency (% heterocysts). Scatter plots of heterocyst frequency versus TN (b) and TIN (c), and TN versus heterocyst abundance in June (d).

was generally $>35 \mu\text{g L}^{-1}$ (Figs. 1.2 and 1.14). It is also apparent that throughout the range of SRP and TIN concentrations found in Upper Klamath Lake, that TIN:SRP ratios generally remained less than 10:1 by mass, with the majority of sample dates $<5:1$ by mass (Fig. 1.16a). As expected, the frequency of heterocysts was inversely related to both TN and TIN (Fig. 1.16b,c), with the highest potential nitrogen fixation (as indicated by heterocyst frequency) occurring at low levels of TN and TIN. Moreover, although *Aph. flos-aquae* began to increase in early June of 1996 (Fig. 1.2), levels remained low ($\sim 10 \text{ mg L}^{-1}$ biomass) until early July when TIN decreased dramatically (Fig. 1.14). It seems that high TIN in 1996 may have suppressed continued *Aph. flos-aquae* biomass development; however it is puzzling that *Aph. flos-aquae* still represented $>90\%$ of the total phytoplankton biomass (Fig. 1.3), and that heterocyst frequency remained constant through the period of TIN increase and decline (Fig. 1.14). Confirmation of the importance of nitrogen fixation in the early period of bloom dominance (i.e., June) is indicated by the positive relationship (with the exception of 4 outliers) between heterocyst abundance and TN (Fig. 1.16d).

TP was highly correlated with Chl during the period of rapid algal biomass increase in June (Fig. 1.17a), weakly correlated in July and August (Fig. 1.17b,d), and moderately correlated in September (although with greater variability and lower slope than June; Fig. 1.17d). The extremely high slope in June ($\beta_1 = 1.63, P < 0.0001$) indicates a period of high CHL yield or algal biomass per unit TP, with little impediment from other limiting factors. Relationships in subsequent months were more variable due to greater variability in physiological state of the bloom. This period was typically characterized by periods of bloom senescence or collapse (Fig. 1.2), when CHL levels remained low even during high levels of P.

Levels of SRP were generally 10-20 $\mu\text{g L}^{-1}$ (Fig. 1.12) prior to pH-induced internal

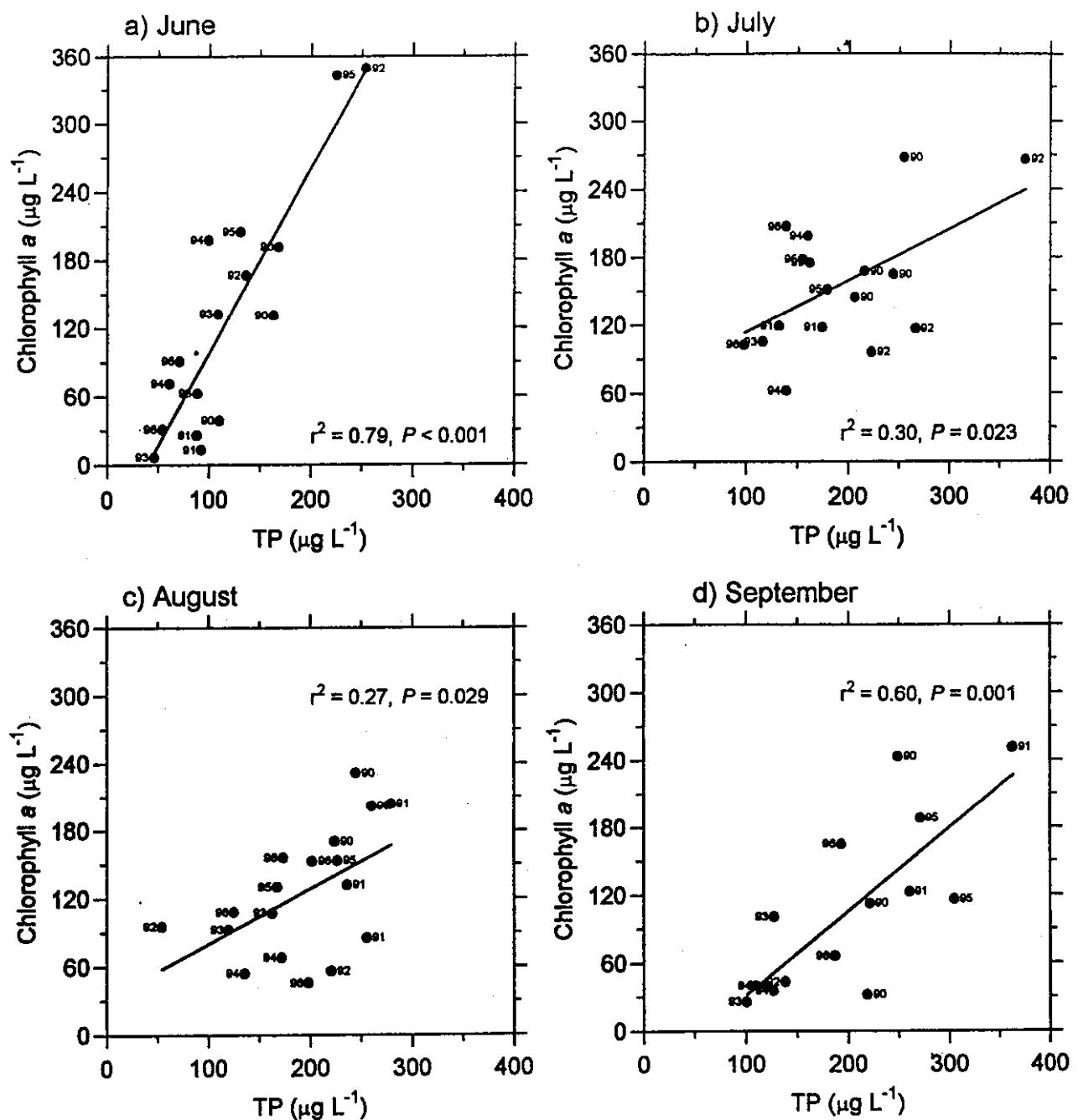


Fig. 1.17. Scatter plots of chlorophyll a versus TP in June (a), July (b), August (c), and September (d). Symbol labels refer to years.

loading of SRP in June (see above), and then either remained constant or decreased during the initial period of rapid algal biomass increase. The fact that June SRP levels remained low in the water column despite high internal loading of SRP, and that large increases in TP occurred at the same time (Fig. 1.12), indicates rapid algal uptake and incorporation of internally-loaded SRP. Following the decline of the first algal peak (Figs. 1.2 and 1.12), SRP increased and remained elevated through the growth season in 1990, 1991, 1995 and 1996 (Fig. 1.12). In 1992 and 1994, both years when the *Aph. flos-aquae* bloom collapsed early and did not recur, SRP initially increased following the first bloom, but then declined to ~ 10 µg L⁻¹ for the remainder of the growing season (Fig. 1.12). In 1993, SRP increased only slightly, and then remained at ~20 µg L⁻¹ through the season. It is clear that SRP remained elevated through the growth season (although less so in 1993) subsequent to the initial biomass peak in years when *Aph. flos-aquae* continued to dominate at high levels. Conversely, during both years when *Aph. flos-aquae* did not recur following the first peak, SRP declined to low levels.

Some interesting patterns emerge from further examination of nutrient dynamics during the early bloom declines and subsequent dominance by non-*Aph. flos-aquae* species in August of 1992 and 1994 (Fig. 1.3). It should first be stated that there do not appear to be any obvious physical factors which prevented the bloom from continuing in 1992 and 1994. Temperature, light, and water column stability (Figs. 1.8 and 1.9) were all within the range of other years when *Aph. flos-aquae* blooms persisted. As mentioned above, SRP declined to low levels during August of 1992 and 1994 when non-*Aph. flos-aquae* species dominated (Fig. 1.18a). SRP was also low in 1993 (although not as low as 1992 and 1994) when *Aph. flos-aquae* represented 100% of the biomass (Fig. 1.19a). An examination of the TIN:SRP ratio reveals that 1992 and 1994 had intermediate ratios when compared to other years, and

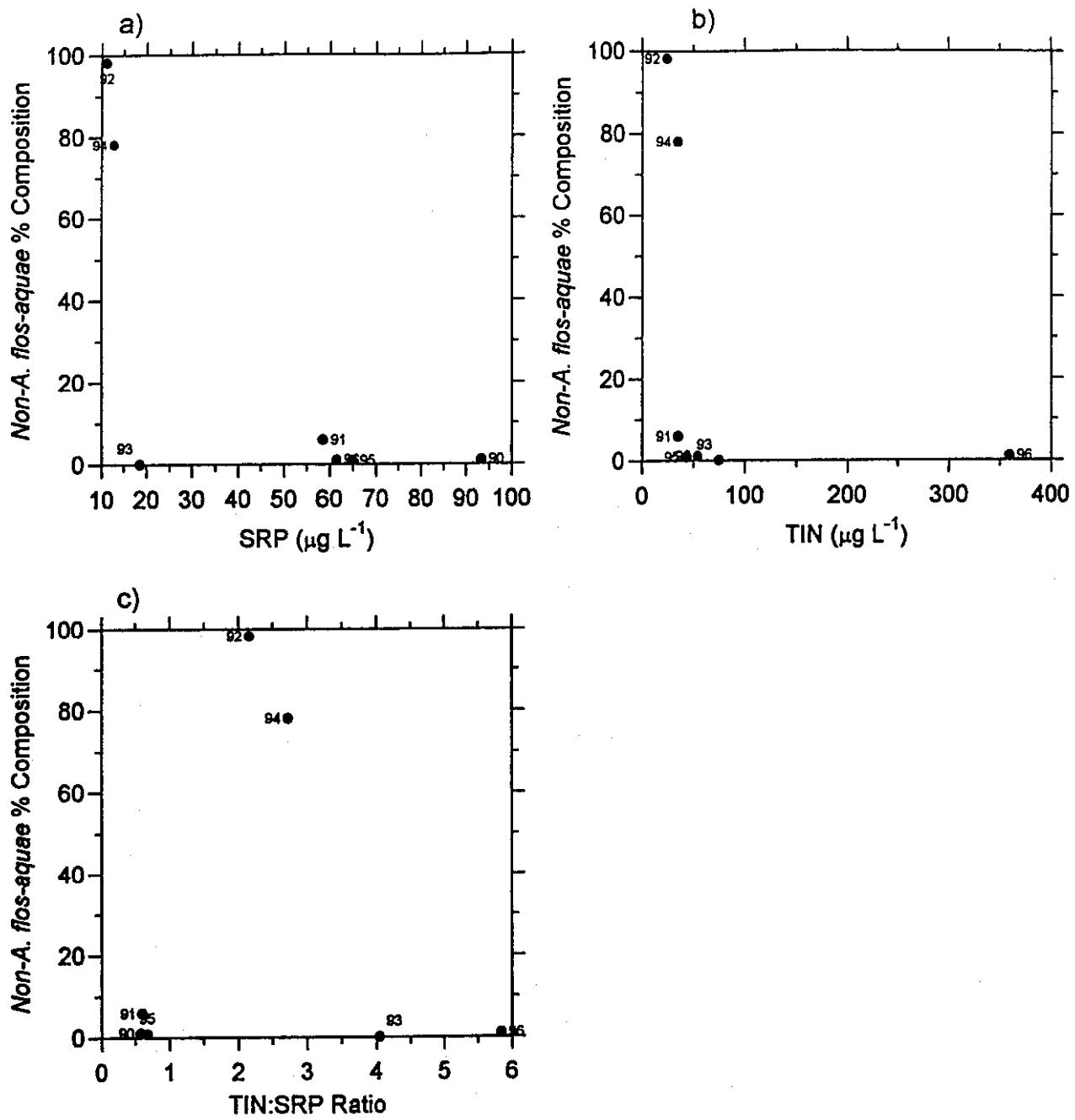


Fig. 1.18. Scatter plots of the percent composition of all non-*Aph. flos-aquae* species versus SRP (a), TIN (b), and the TIN:SRP ratio in August. Symbol labels refer to years.

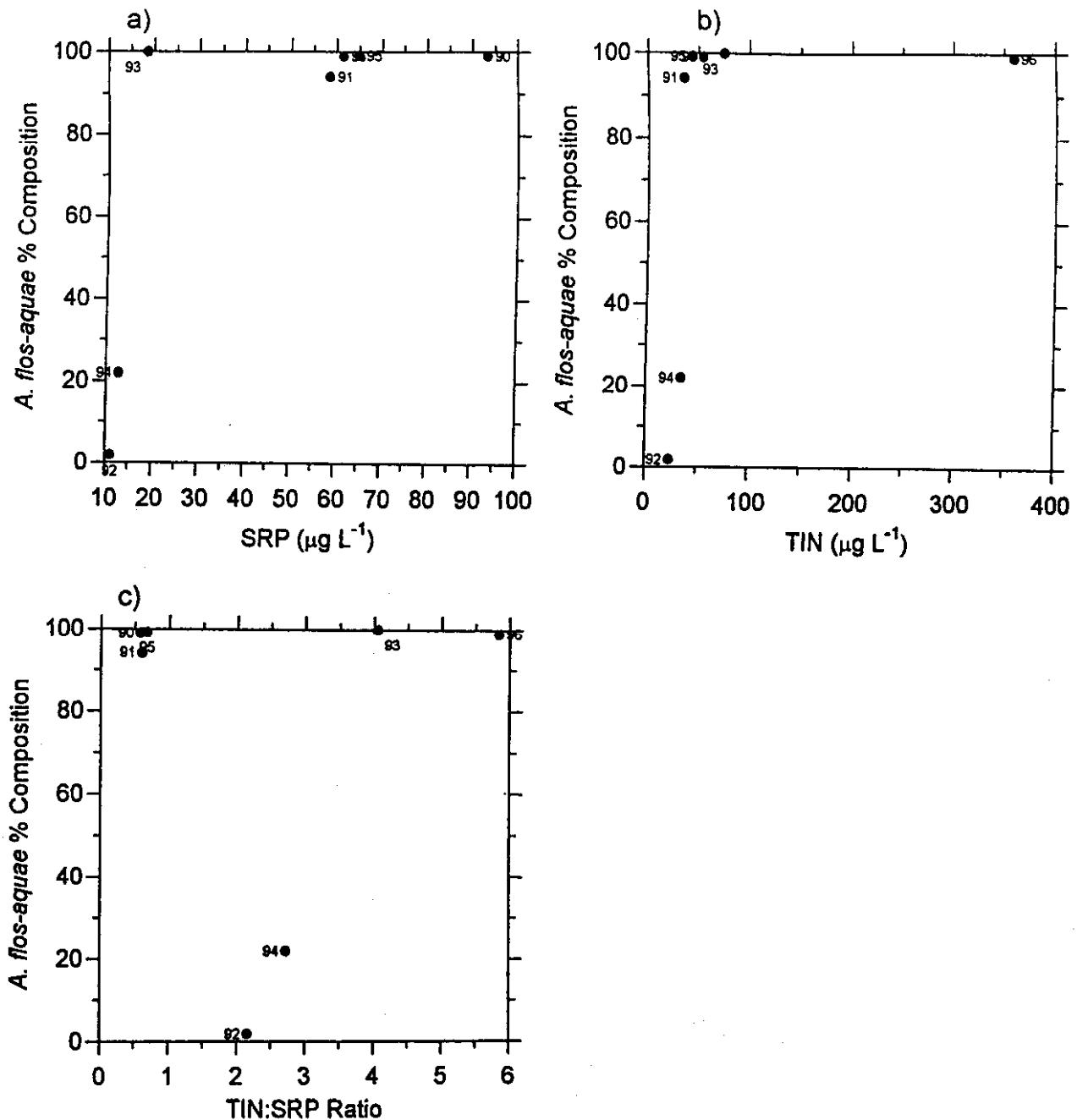


Fig. 1.19. Scatter plots of the percent composition of *Aph. flos-aquae* versus SRP (a), TIN (b), and the TIN:SRP ratio in August.

that years with both lower and higher ratios experienced >90% dominance by *Aph. flos-aquae* (Fig. 1.18c). As expected, the inverse of these relationships is seen when comparing *Aph. flos-aquae* composition to these same variables (Fig. 1.19a,b,c). The group of years (1990, 1991, and 1995) at the low end of the TIN:SRP spectrum (Figs. 1.18c and 1.19c) are characterized by higher SRP (Figs. 1.18a and 1.19a) but only slightly higher TIN than 1992 and 1994 (Figs. 1.18b and 1.19b). The years at the higher end of the TIN:SRP spectrum (1993 and 1996) are characterized by considerably higher TIN (more than double in 1993 at 75 $\mu\text{g L}^{-1}$; and substantially higher in 1996) and higher SRP than either 1992 or 1994 (Fig. 1.18b).

It appears from these trends that dominance by *Aph. flos-aquae* may require a threshold SRP concentration, and that despite what appear to be favorable conditions (i.e., low TIN:SRP ratios and low TIN; cf. Smith 1995) in 1992 and 1994, non-nitrogen fixing species dominate. In 1993, a year that had only slightly higher SRP (but maybe enough to overcome limitation), but twice the TIN, nitrogen fixing *Aph. flos-aquae* dominated. In addition, because heterocyst frequency generally remained low during the August period, especially when compared to the early season period preceding the increase in *Aph. flos-aquae* (Fig. 1.14), it is likely that both non-nitrogen and nitrogen fixing species are utilizing TIN. The water column concentration of TIN is likely the net result of regeneration and uptake, resulting in large pulses when algal uptake is low during bloom decline.

Relative effects of zooplankton on bloom dominance

As stated earlier, it does not appear that *D. pulicaria* plays a large role in bloom initiation. However, there is indication that increasing levels of *D. pulicaria* can influence both

the magnitude of the initial bloom, and subsequent dominance patterns and magnitude of later season phytoplankton populations. It is clear that even at low *D. pulicaria* biomass, the potential exists for large blooms (e.g., 1992; Fig. 1.20), and that during 1996, the second *Aph. flos-aquae* peak in July 1992, and the late season peak in 1995, *D. pulicaria* remained quite low, yet *Aph. flos-aquae* produced large peaks. However, it is also clear that during certain years or parts of years *Aph. flos-aquae* and *D. pulicaria* covaried (e.g., 1991, 1993, and 1995; Fig. 1.2), and that a weak positive relationship is evident between *D. pulicaria* biomass and Chl in June (Fig. 1.20). In fact, the two June sample dates (1990 and 1995) with the highest *D. pulicaria* biomass also had very high algal biomass (~200 and 350 µg L⁻¹ Chl; Fig. 1.20).

In order to determine if *D. pulicaria* had an overall effect on *Aph. flos-aquae* and the other major phytoplankton taxa over the entire growing season (June-September), I regressed seasonal mean *D. pulicaria* biomass against the biomass of *Aph. flos-aquae*, Cryptophytes, Chlorophytes, and Chrysophytes (Fig. 1.21). In all cases, among-year differences in *D. pulicaria* biomass were significantly related to among-year differences in biomass of respective phytoplankton groups. Moreover, there was a positive effect on *Aph. flos-aquae*, and negative effects on cryptophytes, chlorophytes, and chrysophytes (Fig. 1.21). *D. pulicaria* is clearly having a significant negative impact on the biomass of more edible species, and at the same time appears to enhance the biomass of *Aph. flos-aquae*. Enhancement of *Aph. flos-aquae* biomass by *D. pulicaria* may be occurring directly through grazing mortality of competitors (as indicated by the reduction in the taxonomic groups comprised of smaller more edible species), and indirectly through *D. pulicaria* nutrient regeneration of SRP and NH₄ (e.g., Sterner 1990). In fact, there is a significant positive relationship between *D. pulicaria* biomass and SRP during the summer growth season (Fig. 1.22a), although the wide

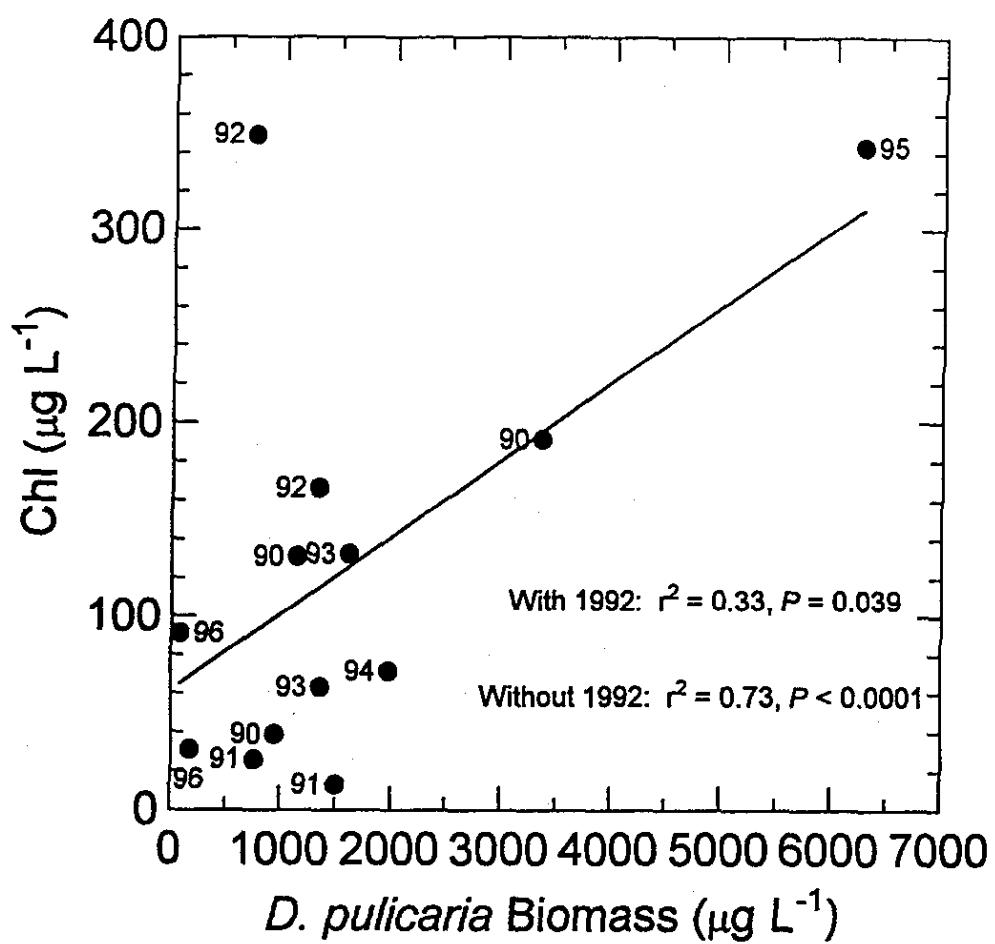


Fig. 1.20. Scatter plot of lake-wide mean Chl versus *D. pulicaria* biomass in June.

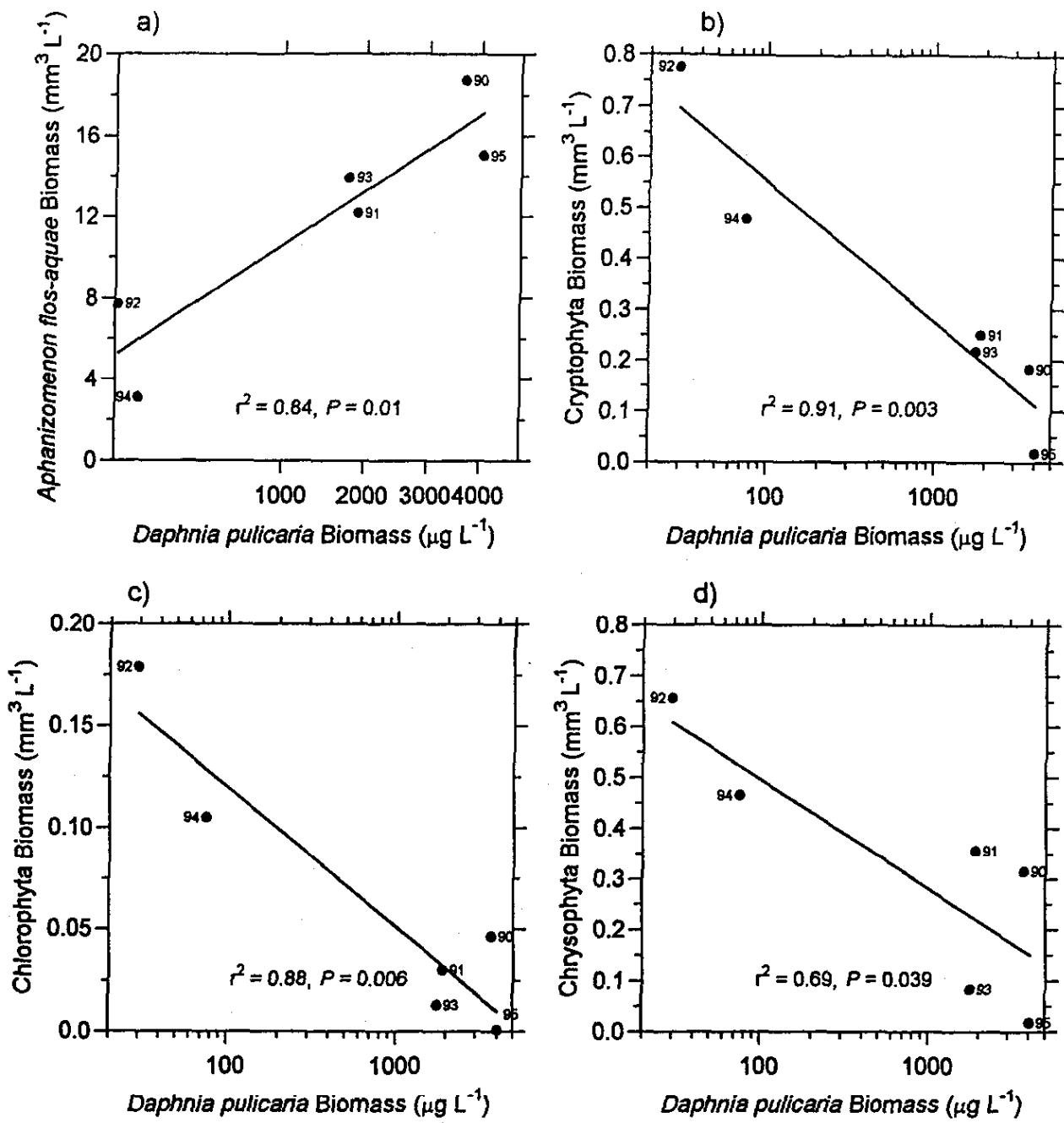


Fig. 1.21. Scatter plots of seasonal mean *D. pulicaria* biomass versus biomass of *Aph. flos-aquae* (a), cryptophytes (b), chlorophytes (c), and chrysophytes (d). Symbol labels refer to years.

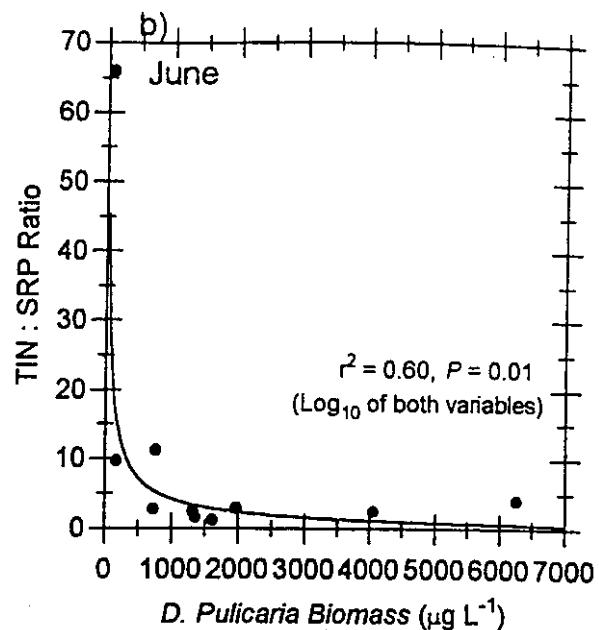
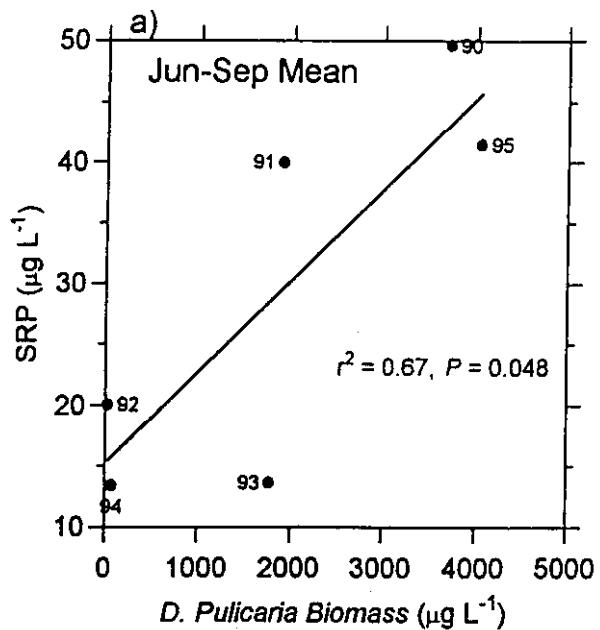


Fig. 1.22. Scatter plots of seasonal mean SRP versus *D. pulicaria* biomass (a), and TIN:SRP ratio versus *D. pulicaria* biomass in June (b). Symbol labels refer to years.

scatter is likely induced by interannual variability in sediment loading of SRP. However, the variable input of TIN (mainly NH₄) regenerated from sediment and water column decomposition precluded the ability to see a similar relationship between *D. pulicaria* biomass and NH₄ on a seasonal basis. In June, however, there was a very strong inverse relationship between *D. pulicaria* biomass and the TIN:SRP ratio (Fig. 1.22b). Promotion of low TIN:SRP ratios by *D. pulicaria* may further enhance already favorable conditions for nitrogen fixation.

Discussion

Aphanizomenon flos-aquae far exceeds other phytoplankton species in its ability to exploit environmental conditions in Upper Klamath Lake. This is evidenced both by its extreme dominance throughout the growing season (Fig. 1.3), and the substantially higher biomass it attains even when compared to periods of dominance by other species (Fig. 1.1). Although physical factors clearly influence the annual timing of the initial late-spring/early-summer *Aph. flos-aquae* bloom (Figs. 1.10 and 1.11), continued dominance and attainment of high biomass levels is likely due to a combination of nutrient and zooplankton factors. Low levels of TIN during the late-spring period promote increases in heterocyst abundance and frequency, allowing *Aph. flos-aquae* to replace inferior nitrogen competitors through N-fixation. This conclusion follows from resource competition theory, which predicts that superior nitrogen competitors should attain community dominance in nitrogen-limited systems (e.g., Tilman 1982). In addition, both TIN:SRP ratios (generally < 5:1 by mass), and TN:TP ratios (ranging between 5:1 and 20:1 by mass), are within the range of expected dominance by N-fixing cyanobacteria (Smith 1983). A further lowering of the TIN:SRP ratio occurs as the

increasing late-spring population of *Aph. flos-aquae* develops, and sediment regenerated SRP driven by photosynthetically-elevated pH increases. In response to the increased availability of SRP, along with the increasingly favorable TIN:SRP ratios, *Aph. flos-aquae* attains massive proportions (lake-wide mean biomass as high as 60 mg L⁻¹ wet wt, and 400 µg L⁻¹ Chl).

It should be noted that elevated ratios of TN:TP in Upper Klamath Lake usually occurred following periods of likely N-fixation and subsequent incorporation of this N source into algal biomass, and there is a clear pattern of concomitant increases of both TN and TP as the bloom increases in Upper Klamath Lake. Increases in TN and TP during the early period of bloom initiation may be partially due to benthic recruitment of *Aph. flos-aquae* flakes from sediments (*cf.* Osgood 1988; Barbiero and Kann 1994). However, it is apparent that while benthic recruitment may be important to serve as bloom inoculum, the majority of increase in N and P concentration occur as the bloom progresses and N-fixation and sediment-regenerated P takes place. This underscores the ability of *Aph. flos-aquae* to effectively enhance its own environment through both N-fixation and increased solubilization of P due to the ability to photosynthetically elevate pH to high water column levels (9.5-10.5).

Following the initial early-summer growth period there is generally a brief period of bloom decline. This decline may be caused by a combination of nutrient (Healey and Hendzel 1976) and light limitation, although the causes of cyanobacterial bloom crashes are not clearly understood; see Paerl (1988). This bloom decline was followed by a second period of *Aph. flos-aquae* growth and dominance in five of the seven years studied. Due to regeneration of N previously input to the system through N-fixation occurring during the initial bloom, the concentration of TIN was generally higher than during the first bloom period. It also appears, based on reduced heterocyst frequency, that N-fixation is substantially lower than during the

first period of increase, and that sources of regenerated TIN may supply the bulk of the N needed for *Aph. flos-aquae* growth. Nedoma et al. (1993) also found heavy blooms of *Aph. flos-aquae* occurring under conditions of persistent high inorganic nitrogen, and Pechar (1992) determined that ammonia released from sediments and recycling in the plankton was the main source of N for *Aph. flos-aquae* (>50%). Direct uptake of ammonia by *Aph. flos-aquae* was recorded by Murphy and Brownlee (1981), and Horne and Commins (1987) noted a reduction in nitrogen fixation in *Aph. flos-aquae* due to increased inorganic nitrogen being supplied to them by zooplankton. Because N-fixation is light dependent (Paerl 1990), and light extinction coefficients increase over the growing season in response to increased algal density (Fig. 1.9), it is likely that the ability of *Aph. flos-aquae* to efficiently fix N will be reduced as the season progresses. Also, due to the high energy requirement of N-fixation (reviewed in Paerl 1990), direct uptake of dissolved-N should allow more energy to be diverted to growth instead of N-fixation.

The periods of Cryptophyte and Chrysophyte dominance in August of 1992 and 1994 were characterized by TIN:SRP ratios that were intermediate to those of other years when *Aph. flos-aquae* dominated, similar TIN (to at least 3 of the other years when *Aph. flos-aquae* dominated), and the lowest SRP of all other years. This pattern suggests that SRP plays a large role in *Aph. flos-aquae* dominance. I propose that *Aph. flos-aquae* dominance during the late summer depends upon 1) adequate levels of TIN to complement N-fixation (due to light limitation and the need to increase growth rates to compete with smaller algal cells), and 2) adequate supplies of water column SRP to support cell growth and N-fixation. High levels of SRP should be necessary for *Aph. flos-aquae* to maintain a competitive advantage in the presence of smaller r-selected species (e.g., *Cryptomonas* and *Rhodomonas*), which are

thought to be better competitors at low levels of P (Reynolds 1984). Large colonial blue-greens are poor competitors for P and therefore require high P levels to dominate (Sommer 1989), and because smaller cells provide greater surface area to volume than large cells, small cells have an advantage when demand for P is intense due to a greater number of P uptake sites relative to cellular need (e.g., Mazumder et al. 1988). In addition, Paerl (1990) indicates that adequate cellular phosphorus is essential for the creation of ATP molecules which are required in high numbers for the reduction of the N₂ molecule during the N-fixation process. Thus even at low TIN:SRP ratios (<1-5 by mass), high concentrations of SRP are important in maintaining *Aph. flos-aquae* dominance.

Although accurate information on temporal patterns of zooplanktivory by Upper Klamath Lake fish populations is not available, it is likely that *D. pulicaria* remains at low population densities prior to the bloom partially due to small but consistent levels of fish predation. However, as the bloom progresses and elevated pH and low dissolved oxygen conditions occur, foraging by fish becomes restricted (see introduction). Predation rate on *D. pulicaria* thus declines as the season progresses, and *D. pulicaria* populations should increase due to relaxed zooplanktivory. Based upon generally stable levels of *D. pulicaria* biomass (and abundance) prior to bloom development, and the fact that bloom peaks occur in both the presence, absence, and at low levels of *D. pulicaria* biomass, it does not appear that *D. pulicaria* is necessary for transition from spring-dominant Cryptophyta and Chrysophyta to summer dominance by *Aph. flos-aquae*.

Sterner (1989a) similarly noted that while succession toward dominance by large inedible blue-greens did not necessarily require *Daphnia* grazing, *Daphnia* grazing may contribute to a succession already in progress. Similar conclusions were made by Lynch

(1980) and Lynch and Shapiro (1981), who found that *Daphnia* were typically associated with *Aph. flos-aquae*, but that decreases in *Daphnia* density did not preclude dominance by *Aph. flos-aquae*. In Upper Klamath Lake, however, it is clear *D. pulicaria* is positively correlated with *Aph. flos-aquae* on a seasonal basis, and that suppression of more edible species occurs (Fig. 1.21). This provides direct empirical evidence from a non-experimentally manipulated lake system that efficient grazing by large *Daphnia* can reduce densities of smaller, more edible algal cells, thereby shifting potential competitive advantage away from these smaller, faster-growing species.

The data presented in this study are thus consistent with previous studies which indicate that preferential grazing on more edible, faster growing competitors favors dominance of grazing-resistant filamentous cyanobacteria (Porter 1977; Haney 1987; Liebold 1989; Sterner 1989a,b, Vanni and Tempte 1990; Elser and Goldman 1991). In enclosure experiments using water from the northern arm of Upper Klamath Lake (Agency Lake), Ehinger (1992) also showed increased dominance by grazing-resistant species (e.g., *Aph. flos-aquae* and *Microcystis aeruginosa*) in the presence of *D. pulicaria*, but unlike *in situ* trends overall biomass of *Aph. flos-aquae* tended to decrease. Pechar (1992) also showed a significant positive correlation between *Daphnia* abundance and *Aph. flos-aquae* abundance in Czechoslovakian fish ponds. These trends of apparent enhanced biomass and domination by *Aph. flos-aquae* in the presence of large *Daphnia* are contrary to Sarnelle (1992, 1993), who concluded from enclosure experiments that *Daphnia* did not promote dominance of inedible species, and that *Daphnia* grazing retarded succession to another colonial cyanophyte, *Anabaena flos-aquae*. This likely reflects the relative edibility of *Anabaena* vs. flake forming *Aph. flos-aquae*, where *Anabaena* filaments were able to be at least partially ingested by

Daphnia. In other words, depending on relative edibility, not all “grazing-resistant” species will show similar successional or biomass responses to the presence of large *Daphnia*.

Both the quantity and N:P ratio of zooplankton-regenerated nutrients can be important determinants of phytoplankton community structure and biomass. (Lehman 1980; Elser et al. 1988; Sterner 1990, Sterner et al. 1992). Stoichiometric theory indicates that low ratios of N:P regenerated by zooplankton should shift phytoplankton toward N-limitation, and that high regenerated N:P ratios should shift phytoplankton toward P-limitation (cf. Sterner et al. 1992). Under joint conditions of zooplankton-mediated N-limitation and low N:P ratios, nitrogen fixing algae would be expected to dominate (cf. Smith 1983). However, there is conflicting evidence in the literature on the specific effect of *Daphnia* on the water column N:P supply ratio. Elser et al. (1988), and Urabe (1993) both provide evidence that the N:P release ratio is higher for *Daphnia*-dominated communities. In contrast, experiments by Sterner and Hessen (1994) indicate *Daphnia* should release compounds with a low N:P ratio, and an empirical study by Wen and Peters (1994) suggested that cladocerans release excreta with low N:P ratios and should intensify N limitation. Differences in food quality may partially account for these discrepancies (cf. Urabe 1993). However, data from Upper Klamath Lake are consistent with *Daphnia* release of low N:P excreta; a high biomass of large *D. pulicaria* is associated with low water column TIN:SRP ratios (Fig. 1.22b). Maintenance of low to moderate TIN:SRP ratios by *D. pulicaria* may thus be an important mechanism for maintaining a favorable competitive environment for *Aph. flos-aquae*.

Pechar (1992) concluded that in enclosures with *Daphnia Aph. flos-aquae* gained nitrogen with a minimum expenditure of energy resulting in higher *Aph. flos-aquae* growth rate, and conversely that a decrease in growth occurred in enclosures without *Daphnia* where

NH_4 was exhausted. Thus, in addition to the role that *Daphnia* may have in maintaining a favorable TIN:SRP environment and reducing faster growing algal competitors, they also may reduce the need for N-fixation through provision of recycled inorganic nitrogen (cf. Horne and Commins 1987). Moreover, given the apparent role of SRP in maintaining *Aph. flos-aquae* dominance through the season, SRP excretion by *D. pulicaria* (Fig. 1.22a) may also be an important mechanism contributing to relative dominance of *Aph. flos-aquae* in Upper Klamath Lake. Ehinger (1992) also showed a positive relationship between *Daphnia* biomass and concentrations of both SRP and $\text{NH}_4\text{-N}$ in enclosure experiments. Despite what seem to be favorable TIN:SRP ratios for *Aph. flos-aquae* dominance in Upper Klamath Lake, elevated supplies of both SRP and TIN appears to be essential for continued promotion of *Aph. flos-aquae* biomass and dominance. This supports the idea that it is important to consider the actual concentrations of N and P as well as their ratios (Horne and Commins 1987; Paerl 1988).

Conclusions

The patterns of cyanobacterial dominance in Upper Klamath Lake generally agree with Sterner (1989a), who concluded that *Aph. flos-aquae*'s superiority as a nitrogen competitor under nitrogen limiting conditions, together with its high resistance to grazing by *Daphnia*, allows it to become strongly dominant in the water column. It also appears that seasonal succession toward *Aph. flos-aquae* and continued seasonal dominance in Upper Klamath Lake depends not only upon low TIN:SRP ratios, but also on high SRP concentrations, and adequate levels of TIN during periods when SRP is low and/or reduced light conditions retard nitrogen fixation. Periods of *Aph. flos-aquae* dominance in Upper Klamath Lake occurred

both in the presence and absence of high levels of *D. pulicaria*, indicating that dominance is, at times, independent of *D. pulicaria*. However, *D. pulicaria*'s clear suppression of more edible algal competitors, regeneration of TIN and SRP, and apparent enhancement of low TIN:SRP ratios, can contribute to both dominance and biomass of *Aph. flos-aquae*.

Contrary to classical trophic cascade theory, which predicts that algal biomass in general should be low when large *Daphnia* are dominant in lakes with reduced planktivory, high algal biomass is consistently found in the presence of large *Daphnia* in Upper Klamath Lake. Although the use of food web manipulation to improve water quality (e.g., Shapiro et al. 1975; Carpenter et al. 1985) has become somewhat common, this method of lake restoration can be confounded by changes in size structure and resistance to grazing in the phytoplankton (e.g., Lathrop et al. 1996; Ramcharan et al. 1996; Post et al. 1997). Caution should thus be taken when biomanipulation through enhancement of large *Daphnia* is being considered in lakes that may be prone to dominance by grazing-resistant nitrogen-fixing taxa.

In fact, increased planktivory and its subsequent suppression of large *Daphnia* in Upper Klamath Lake could either shift the phytoplankton composition towards smaller algal species, or possibly reduce the magnitude of *Aph. flos-aquae* blooms. A shift toward these smaller species could potentially have desirable effects on water quality, especially given that the ability of such smaller, non N-fixing species (e.g., *Cryptomonas* spp.) to exploit growth conditions in Upper Klamath Lake and attain the massive bloom proportions that *Aph. flos-aquae* does, will ultimately be limited by their inability to fix nitrogen in this high-phosphorus, low-nitrogen system.

Upper Klamath Lake represents an ecological system whose behavior does not conform to that predicted by simple linear food chain models. These models indicate that in

even-linked systems (i.e., systems where herbivores are released from predation), plant biomass will not show a strong positive response to increasing resource availability (e.g., Hairston et al. 1960; Fretwell 1977; Oksanen et al. 1981). In his classification of a large cross section of North American lakes as either dominant even-link (large *Daphnia* present) or odd-link ecosystems, using the presence vs. absence of both *Daphnia* and planktivorous fish, Mazumder (1994c) tested the prediction that algal biomass (indicated by Chl) should not increase significantly along the potential productivity gradient of dominant even-link ecosystems. Mazumder (1994c) rejected this hypothesis; he empirically showed a pattern of positive algal biomass response to TP in even-link lake ecosystems, but the magnitude of this response to nutrients was significantly less than in odd-linked systems. While the results for Upper Klamath Lake (classified as an even-linked system) also indicate increased algal response to increasing TP, they also show a similar or even greater algal response to TP (slope=1.63) than for Mazumder's (1994c) dominant odd-link systems (greatest slope was 1.24 for meso- to eutrophic systems). While Mazumder (1994c) acknowledges that the positive algal response to TP in dominant even-linked systems may be due to accumulation of ungrazable large algae with increasing nutrient availability, he does not address the concept presented here; one where large *Daphnia* may actually enhance both dominance and biomass of large grazing-resistant blue-green algae.

Upper Klamath Lake thus provides an example of an aquatic ecosystem where high biomass of algae is attainable over a range of high TP concentrations, even in the presence of efficient grazing by high density of large-bodied *Daphnia*. Given that the blue-green algal biomass response to TP in Upper Klamath Lake (closed circles Fig. 1.23) is within the range experienced by other blue-green prevalent systems analyzed by Smith (1995) (Fig. 1.23), it is

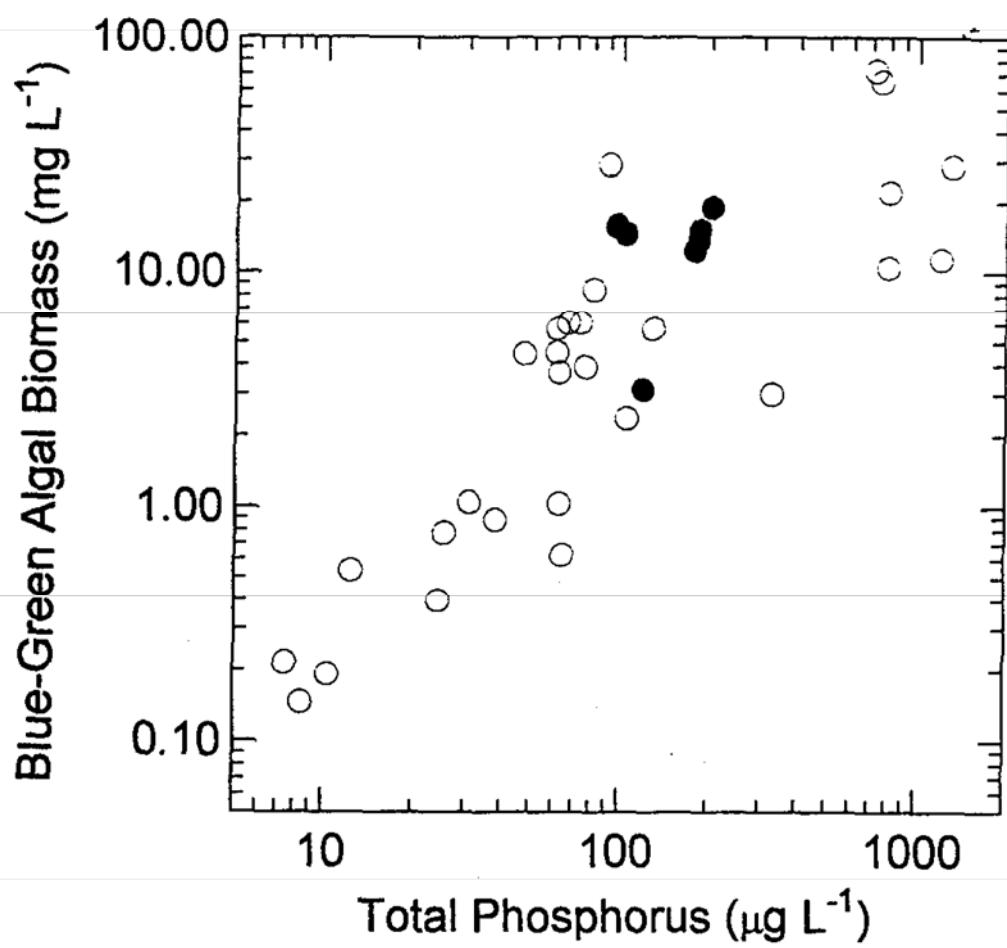


Fig. 1.23. Scatter plot of summer mean blue-green algal biomass versus summer mean TP in North American and Swedish lake systems (open circles; data from Smith 1985), and summer mean blue-green algal biomass versus summer mean TP in Upper Klamath Lake (solid circles; ●).

likely that similar enhancement by large *Daphnia* is occurring in some of these systems as well. Further cross-sectional analysis of dominant odd- vs. even-linked lake ecosystems should include an evaluation of phytoplankton size structure, and more specifically the presence or absence of large grazing-resistant blue-green species.

Chapter 2

**Chlorophyll as a Predictor of Elevated pH in a Hypereutrophic Lake: Estimating the
Probability of Exceeding Critical Values for Fish Success Using Parametric and
Nonparametric Models**

Introduction

Summer algal blooms are a consistent feature of eutrophic and hypereutrophic lakes worldwide (Reynolds 1987; Smith 1990). These algal blooms dramatically reduce water clarity, and frequently cause taste, odor, and filtration problems in water supplies (Bierman et al. 1984; Cooke et al. 1986; Ryding and Rast 1989). In many such lakes algal blooms are accompanied by water quality-caused fish kills that can be costly (AFS 1992) and can result in a complete restructuring of the fish community (Barica 1975a,b 1978; Vanni et al. 1990). As a result, multi-year monitoring programs are typically undertaken in order to evaluate the potential deleterious effects of water quality parameters on fishery resources. Because the magnitude and extent of a water quality variable of concern is often linked to the dynamics of another controlling factor (e.g., algal biomass), the development of an objective plan which minimizes risk to fishery populations requires a quantitative framework that (*i*) relates fish populations to the water quality variables of concern, and (*ii*) subsequently relates these variables to manageable watershed or lake characteristics.

Quantitative approaches to the effects of water quality on fish populations have previously been proposed by Barica (1975b, 1978) and by Mericas and Malone (1984), who developed water chemistry-based fish kill models. Unfortunately, the utility of these quantitative models is limited because historical records of fish kills are typically poor due to inconsistent reporting, rapid predation by avian and fish predators, settling of dead fish to

benthic areas, and the difficulty in observing kills of smaller larval or juvenile fish. Furthermore, models based solely on kills do not account for deleterious population-level effects from sublethal or chronic levels of the water quality variable. An alternative approach is presented here based on (*i*) documented physiological limits for fish success, and (*ii*) the probability of exceeding threshold values of the water quality variable of concern as a function of a controlling variable.

Accomplishment of (*ii*) above requires a modification of traditional approaches that utilize either cross-sectional or within-lake (based on time series or lake station) linear regression models to relate a variable of concern to its controlling factor (e.g. chlorophyll *a* to total phosphorus) (Dillon and Rigler 1974; Reckhow and Chapra 1983). These models typically only predict the summer mean response of the dependent variable, and such means are of limited utility because it is more likely to be the frequency with which threshold water quality conditions are violated that will dictate relative success of the fish population. The frequency or probability of exceeding threshold water quality values at various levels of an independent variable provides a more useful approach for evaluating risk to fishery populations.

In this paper I present and discuss the development of two empirical models to evaluate fish success relative to the probability of exceeding threshold water quality values. The first model extends the linear regression approach to express the prediction of the dependent variable as a probability of exceeding physiological limits. The second is based on Heiskary and Walker (1988) and Walker and Havens (1995) who, building on the efforts of Walsmley (1984), recognized that impairment of lake use is more sensitive to the frequency and severity of events (e.g., algal blooms, phosphorus concentration, and transparency) than

to average conditions, and have proposed a nonparametric cross-tabulation method to describe frequency of the dependent variable as a function of the independent variable. The risk assessment aspect of this method also has previously been primarily recreation-oriented, with chlorophyll and transparency the major foci of water quality assessment and management. I extend this method here for use in risk assessment of fishery success, based on the probability of exceeding known physiological limits (usually LC₅₀, or some measure of chronic stress) of water quality parameters. I also develop the predictive capability of this method by modeling the frequency response of the variable of concern, and by validating the model with independent data.

In the case of Upper Klamath and Agency Lakes, Oregon, the preservation and restoration of endangered fish species is one of the most important goals for lake restoration efforts. Because of the moderate alkalinity of the lakes (50-70 mg L⁻¹ as CaCO₃), the buffering capacity of the water is relatively low, and the excessive algal blooms (Fig. 2 introduction) cause significant water quality deterioration due to elevated pH (Fig. 3 introduction) as the inorganic carbon equilibria ($H_2O + CO_2 \rightleftharpoons H_2CO_3 \rightleftharpoons CO_3^{2-} + H^+$) shifts to the left as phytoplankters assimilate CO₂ and HCO₃⁻ during photosynthesis. Bioassays have shown that pH values >9.55 cause a loss of equilibrium in native *Chasmistes brevirostris* juveniles (Falter and Cech 1991), and short-term acute lethality tests (96 hr LC₅₀) indicate that mortality of juvenile *Chasmistes brevirostris* occurs when pH values >9.76 are reached (Bellerud and Saiki 1995). Other studies have also shown that photosynthetically-elevated pH can impair fish habitat and limit fish success (EIFAC 1969; Alabaster and Lloyd 1980), and the extent, frequency, and duration of elevated pH events in Upper Klamath Lake make pH a primary variable of concern for the evaluation of fishery risk. In this paper I demonstrate

how the methods described above can be utilized to evaluate the risk of exceeding various pH levels over a range of algal biomass as estimated by chlorophyll *a* (Chl).

Methods

Data collection

Limnological measurements were made in Upper Klamath and Agency Lakes from June 1987 through September 1996 in order to monitor both water quality and available fish habitat in the lake. Samples were taken at monthly intervals except when prevented by ice cover from 1987-1989, and were taken biweekly or occasionally weekly during the ice-free season from 1990-1996. In general 10 sites (excluding the Lee Shore Site in Agency Lake; Fig. 1 introduction), which was sampled only in 1990) were sampled on each date. The exceptions to this were in 1990 when a subset of sites (ER, SB, MN, PB, and AS) in the northern portion of the lakes was sampled on some dates, and in 1996 when only 6 (PM, ML, ER, SB, MN, and AS) of the 10 sites were regularly sampled. Depth profiles of pH were measured using a Hydrolab Surveyor® multi-parameter probe at each sample site. Because the lake is polymictic and only undergoes weak and intermittent stratification, a depth-integrated water sample of the entire water column was taken coincidentally with the pH profiles. This was accomplished by combining a minimum of three replicate hauls of a weighted 5 cm diameter plastic tube at each site. A portion was then analyzed spectrophotometrically for Chl and phaeophytin (Nusch 1980; APHA 1985). In addition to these recurrent samples, continuous records of pH and dissolved oxygen were occasionally obtained at selected sites using a moored Hydrolab DataSonde® remote recorder to determine diel variability.

Model development

In order to improve interannual consistency in sampling frequency, data utilized in model development and validation were limited only to years when biweekly measurements were available (1990-1996), and only to dates corresponding to a biweekly frequency. Depth-weighted mean values for pH and integrated Chl measurements during the June-September period of elevated pH were then used in subsequent model development. Sensitivity of parameter estimates to utilizing a subset of sample sites in computation of sample date means (hereafter referred to as lake-wide means) was negligible based on a comparison of subset means to means computed using all sites (data not shown). To allow for independent validation of model performance, the first 5 years of data (1990-1994) were used as a model development data subset, and the last 2 years (1995 and 1996) were used for validation.

Regression-based probability model

Linear regressions were performed between lake-wide mean pH and Chl on two subsets of data: 1) June-September lake-wide means, and 2) June only lake-wide means. Lake-wide means were computed from open-water sites in Upper Klamath Lake only. An additional regression was performed using the individual Agency Lake site AS. The assumptions of linear regression were evaluated using residual and normal probability plots, autocorrelation of residuals, estimates of skewness and kurtosis, and Kolmogorov-Smirnov tests of fit (Kleinbaum et al. 1988; Wilkinson 1996). Chl data were transformed to their common logarithms to improve linearity and to reduce heteroscedasticity. When the assumptions of linear regression are met, one can assume that the distribution of the dependent variable at fixed values of the independent variable is normal (Kleinbaum et al.

1988). Then based on probabilities associated with the standard normal distribution and utilizing the predicted mean and standard error from the regression computation, the prediction can be re-expressed as the probability of exceeding chosen values of the dependent variable. This was accomplished in this study by 1) predicting mean pH (pH_{pred}) at given Chl values from the linear regression equations, 2) computing the standard error of the estimate (S_{yx} , as estimated from the square root of the error or residual mean sum of squares; Kleinbaum et al. 1988), 3) normalizing a chosen critical pH value (pH_{crit}) to its standard score (Z; c.f. Zar 1984) based on the following equation:

$$Z = \frac{pH_{crit} - pH_{pred}}{S_{yx}} \quad (1)$$

and 4) computing the proportion (expressed as a percent) of the normal distribution that lies beyond the computed Z value utilizing the equation:

$$\text{Probability of } pH > pH_{crit} = 100(1 - zcf(Z)) \quad (2)$$

where zcf denotes the standard normal cumulative distribution function (Wilkinson 1996) (any standard normal cumulative probability table can be used to look up Z; e.g. Table A-1, Kleinbaum et al. 1988). In this manner the probability of obtaining values greater than pH_{crit} was computed for the range of Chl data.

Nonparametric cross-tabulation probability model

The same subset of pH and Chl measurements used to develop the above models was used in development of the following nonparametric model. However, instead of using lake-wide means as above, the analysis was performed on paired pH and Chl measurements from individual lake sample sites and dates. Following Heiskary and Walker (1988) and Walker and Havens (1995) the data were: 1) ordered by ascending Chl concentration, 2) divided into a chosen number of intervals, 3) the median Chl for each interval was computed, 4) the frequency of pH observations that exceeded chosen pH_{crit} values was computed within each of the intervals, and 5) this computed exceedence frequency (expressed as a percent of the total observations within each interval) was then plotted against the median Chl value for each interval. In order to quantitatively describe the relationship expressed by this plot, and to make the model more useful for predictive purposes, a logistic equation was used to describe the relationship between exceedence frequency of chosen pH_{crit} values and Chl. Equation parameters for the logistic model were estimated using Systat® (Wilkinson 1996) nonlinear regression procedures using the following equation:

$$Frequency\ of\ pH > pH_{crit} = \frac{pH_\infty}{1 + e^{(\beta_0 - (\beta_1 Chl))}} \quad (3)$$

where pH_∞ is the asymptotic limit for pH_{crit} , β_0 is a location parameter for the curve, β_1 is a slope parameter, and Chl is the median Chl value of an interval. The fit was evaluated using residual plots, standard errors of the parameter estimates, and R^2 values.

Values chosen for pH_{crit} were the same for both the nonparametric and parametric models, and were selected based on a literature survey of the physiological limits of elevated

pH on both fishes in general and those specific to the Upper Klamath system.

Results and Discussion

Establishment of pH_{crit}

An important step in development of the models outlined here is the choice of critical values of the variable of concern (in this case pH_{crit}). These values must be chosen based on the known relationships between pH and fish success. Although excursions of pH beyond these critical limits only suggest a strong likelihood that a negative fish response will occur, and do not themselves necessarily guarantee the occurrence of a fish-kill, avoidance of high pH water masses would be a minimal behavioral response. In an overview of stress assessment in fishes, Beitingen (1990) noted that behavior plays an important role in habitat selection, and that an animal's behavior tends to limit it to an environment far narrower than that which it can physiologically tolerate. As a result, stressed fish populations are often restricted to limited areas of tolerable water quality where food limitation and crowding may lead to negative effects on fish success, as reflected in reduced survivorship, growth, and reproduction.

In addition, at critical pH levels far lower than those derived from acute lethality tests (e.g., LC 50's), sublethal effects or long-term exposures can result in an increased susceptibility to disease, impaired growth and reproductive ability, and increased sensitivity to other factors. For example, exposure to elevated pH has been found to inhibit olfactory responsiveness (Hara 1976), reduce carbohydrate and liver glycogen levels (Arrilo et al. 1979), increase blood ammonia concentrations (Randall and Wright 1989), and increase mucous secretion, eye damage, and epithelial necrosis in the esophagus (Daye and Garside

1976). Interactions with other environmental factors such as ammonia and dissolved oxygen availability (EIFAC 1969; Alabaster and Loyd 1980; Soderberg et al. 1983; Russo 1985; Bergerhouse 1992) may result in actual pH tolerance limits that are well below those determined from short duration bioassays. Moreover, these effects may be dependent upon the life stage of the fish. For example, Bergerhouse (1992) showed significant differences in tolerance between 3, 8, and 10-day old walleyes exposed to elevated pH. Such sublethal effects can strongly influence future survivorship, growth, and reproduction. Given the variability induced by the above behavioral, ontogenetic, and sublethal factors on physiological tolerance to elevated pH, it is important to select limits that encompass the most conservative pH values with respect to fish success.

In their overview of water quality criteria for European freshwater fishes, EIFAC (1969) concluded that pH values between 9 and 10 are harmful to many fish species, and that pH values >10.0 are typically lethal. Similarly, Alabaster and Lloyd (1980) concluded that chronic exposure to pH values >10.0 was harmful to *all* fish species studied. In contrast, Alabaster and Lloyd (1980) have concluded that pH values in the range 6.5-9.0 are typically harmless to fish, although the toxicity of other environmental factors such as ammonia may potentially be affected by pH in this range. Bioassays specific to the two endangered fishes of the Upper Klamath system show large interspecific, and life-stage dependent variability in short-term acute lethality tests (96 hr LC₅₀; Monda and Saiki 1993; Bellerud and Saiki 1995). However, the most conservative value from these tests (pH=9.76) was the lower 95% confidence limit of the 96 hr LC₅₀ for juvenile *Chasmistes brevirostris* (Bellerud and Saiki 1995). When coupled with the pH 9.55 loss of equilibrium value from Falter and Cech (1991), these results suggest that the probable critical upper pH limit for fish success in

Upper Klamath Lake lies between pH values of 9.5 and 10.00. Given this pH range along with the potential unknown chronic or sublethal population effects described above, it is difficult to determine an exact value for pH_{crit} . It was therefore decided to develop the models using a range of four pH_{crit} values (9.00, 9.50, 9.75, and 10.00). Because pH 9.75 approaches the lethal level, pH 9.50 is a likely protective level that would encompass sublethal effects as well.

Spatial and temporal pH dynamics

Photosynthetically-elevated pH values in Upper Klamath and Agency Lakes frequently fall within or exceed the apparent thresholds described above. Although episodic diel reductions in pH occur, pH values frequently remain above 9.5 for several days at a time at open water and near shore sites (Fig. 3 introduction). Moreover, sites along the opposite shore from the prevailing winds (lee shore) exhibit more extreme daily fluctuations due to the wind driven accumulation of algal biomass (Fig. 3 introduction). Values of pH prior to the algal growing season range between 7.50 and 8.00, but begin to rise as lake productivity and algal biomass increases in mid-May, and peak sometime during the June-September growing season (Fig. 2.1). Seasonal high and low pH values coincide with highs and lows in chlorophyll α (Fig. 2.1).

The timing and magnitude of Chl and elevated pH events exhibits significant interannual and seasonal variability (Figs. 2.2 and 2.3). In addition, although part of the same lake system, Agency Lake typically exhibits more extreme pH and Chl fluctuations as well as differences in timing when compared to Upper Klamath Lake sites (Figs. 2.2 and 2.3). For example, the Agency Lake site (AS) consistently achieved higher pH values in June, and lower

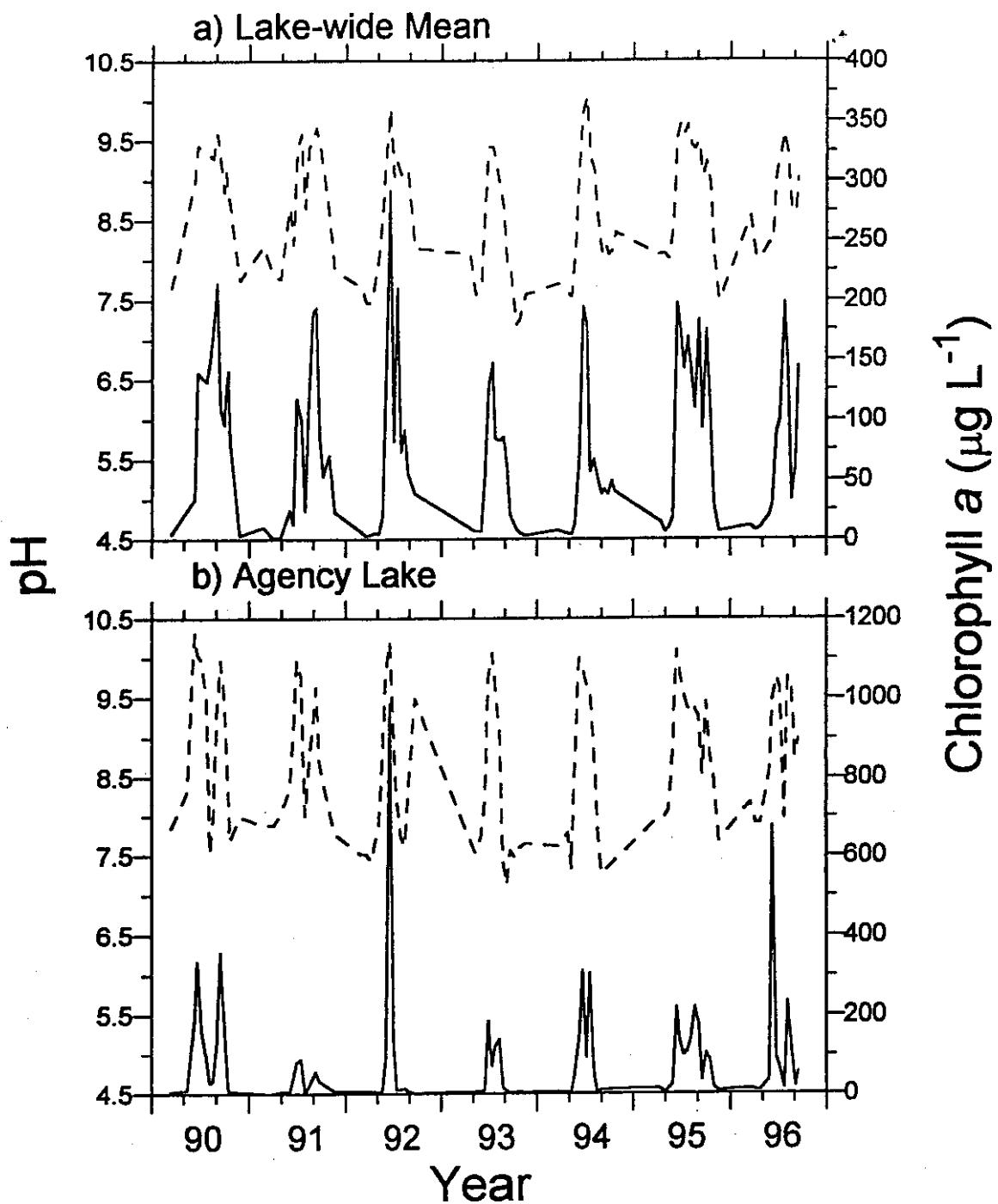


Fig. 2.1. Seasonal trends in lake-wide mean pH (dashed line) and chlorophyll α ($\mu\text{g L}^{-1}$; solid line) in Upper Klamath Lake (a), and at the Agency Lake site AS (b), 1990-1996.

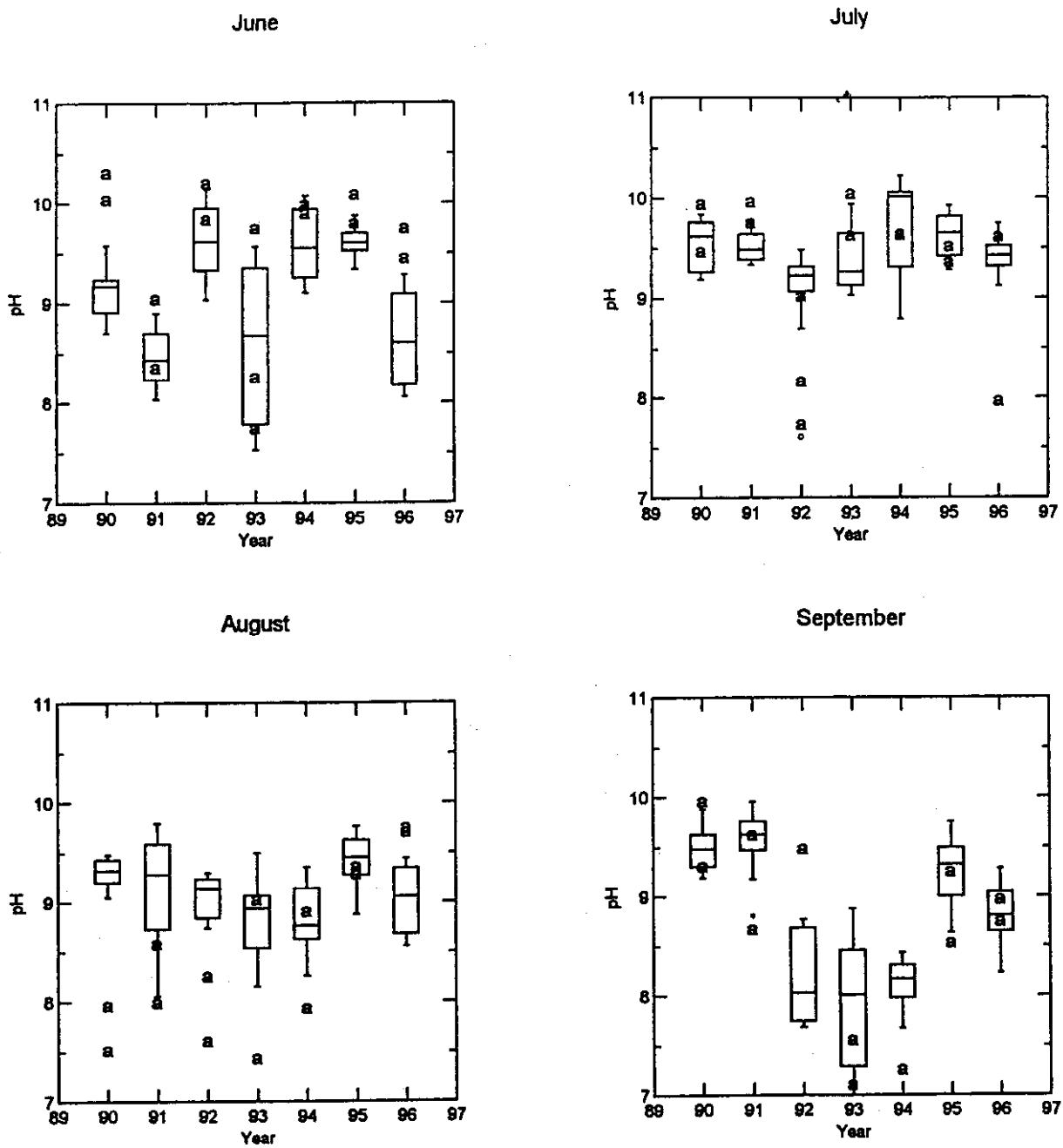


Fig. 2.2. Box plots of water column mean pH versus year (1990-1996) during the June-September growing season for individual Upper Klamath Lake sites. Values for the Agency Lake site AS are plotted separately and are denoted by a lower case "a". The bottom and top edges of the boxes are the 25th and 75th percentiles, while the horizontal line within the box is the 50th percentile (median). The whiskers extend to the highest and lowest observation unless they are more than 1.5 box-lengths long; observations outside this range are plotted as circles (outliers; < 3 box lengths) or asterisks (extreme values; > 3 box lengths).

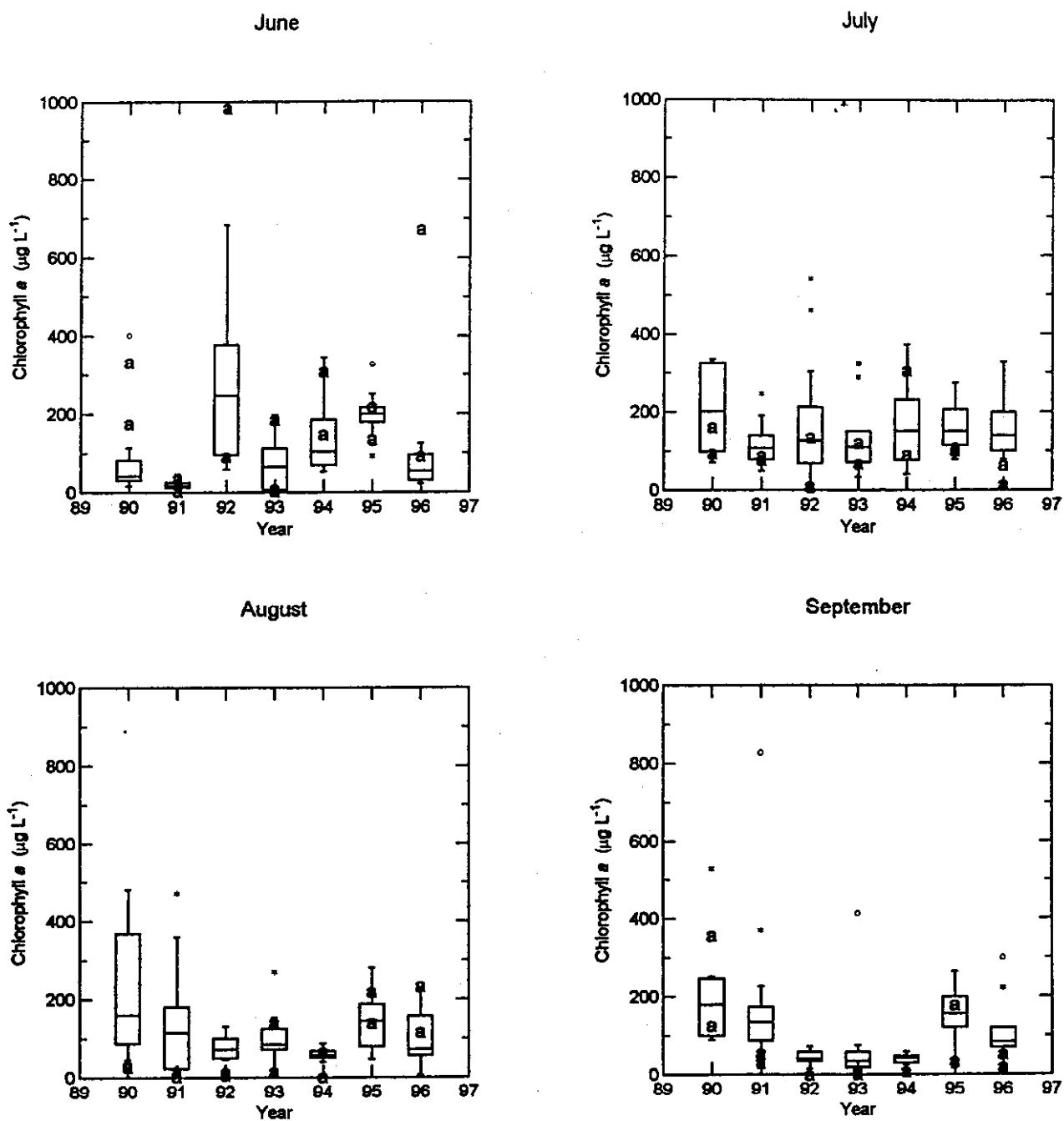


Fig. 2.3. Box plots of water column mean chlorophyll *a* versus year (1990-1996) during the June-September growing season for individual Upper Klamath Lake sites. Values for the Agency Lake site AS are plotted separately and are denoted by a lower case "a". The bottom and top edges of the boxes are the 25th and 75th percentiles, while the horizontal line within the box is the 50th percentile (median). The whiskers extend to the highest and lowest observation unless they are more than 1.5 box-lengths long; observations outside this range are plotted as circles (outliers; < 3 box lengths) or asterisks (extreme values; > 3 box lengths).

pH values in August (Fig. 2.2). This results from earlier bloom development, and earlier and more complete bloom crashes in the shallower Agency Lake (Fig. 2.3). With the exception of 1990 and 1991 when some of the highest pH values of the growing season occurred in September, maximum pH values typically occur in June or July (Fig. 2.2), when the algal bloom is in a rapid growth phase. Subsequent bloom crashes cause pH to decline in July or August (Fig. 2.2). Elevated pH's are typically less severe in September due to cooler water temperatures, more variable solar radiation, and shorter day lengths, all of which influence primary production rates and subsequent photosynthetically-elevated pH's. However, when summer-like conditions persist into September, pH values greater than 9.50 can still be present over a wide range of sites (e.g. 1990 and 1991; Fig. 2.2).

Spatial variability in pH among Upper Klamath Lake sites can be large, although on many occasions when elevated pH events occur, the distribution is exhibited lake-wide (Fig. 2.2). Likewise, Chl can also exhibit a high degree of spatial variability with occasional outliers and extreme values (Fig. 2.3).

Linear regression models

Hypereutrophic lakes are particularly susceptible to photosynthetically driven changes in pH as algal blooms develop over the course of the growing season (Wetzel 1983), and a strong degree of covariation was evident between pH and Chl concentrations in Upper Klamath and Agency Lakes (Fig. 2.1). However, in order to model the relationship between these two variables one must first evaluate the appropriateness of the data set. Because regression statistics are biased when correlations exist between observations that are proximate in time or space, one must carefully evaluate the effects of serial and spatial

autocorrelation when working with multi-year and or multi-site data from a particular lake (Reckhow and Chapra 1983). This can be accomplished through visual assessment of residuals, computation of first order and higher autocorrelations, and the Durbin-Watson D statistic computed on the residuals (Kleinbaum et al. 1988). In the case of Upper Klamath and Agency Lakes these measures indicated that utilizing paired pH and Chl measurements from all sites and dates was inappropriate (data not shown). It was therefore decided to develop the regression-based models utilizing only biweekly lake-wide means. Moreover, because timing and magnitude of pH and Chl values at the Agency Lake site AS (Figs. 2.2 and 2.3) differed from Upper Klamath Lake sites, it was determined that reduced bias in computation of lake-wide central tendency was best achieved by performing separate analyses for the two lakes.

Due to seasonal variance and the presence of outliers and extreme values in Chl (Fig. 2.3), these data were generally lognormally distributed in Upper Klamath Lake (this was confirmed by comparing both log transformed data and non-transformed data with the normal distribution using Kolmogorov-Smirnov one-sample tests (cf. Wilkinson 1996; Zar 1984) so that the geometric mean provided the best estimate of lake-wide central tendency. When the goal of regression models is to make predictive or probabilistic statements regarding future conditions, one can not emphasize enough the importance of both accurately reflecting central tendency when combining spatial or temporal data for model input, and ensuring that the basic assumptions of linear regression are not violated. For example all estimates of uncertainty and probability partially rely on the computation of S_{yx} which could be underestimated considerably due to sample size (n) inflation when autocorrelation is significant.

Despite the controlling effect of time of day the sample was collected, temperature,

photoinhibition, self shading, solar irradiance (intensity and duration), and physiological state of the bloom on photosynthesis (Reynolds 1984) and subsequent elevated pH, Chl was found to be a strong predictor of pH for all linear regression models (Table 2.1; Fig. 2.4), with 72% and 73% of the observed variation in pH explained by Chl for the lake-wide mean and Agency Lake models. A third model developed from lake-wide means during June explained 95% of the observed variability in pH, and despite a lower sample size ($n=11$) there was considerably less error in the model estimate ($S_{yx}=0.165$) when compared to the models developed from June-September data. Models developed from June-September data encompass a wide range of bloom conditions, including rapid growth and bloom collapse, and the photosynthetic response per unit Chl would be expected to vary with these different physiological bloom states. In contrast, June is always a period of rapid algal growth and increasing pH, and as such would not be affected by the variability induced by collapsing or more senescent blooms. This is evident in the lower S_{yx} and in the higher predicted pH at given Chl when compared to the June-September lake-wide mean model. The importance of the June model is apparent given that the early season bloom development period is a critical time period for larvae and juveniles of the two endangered sucker species as they enter and rear in the lake environment.

Because the concentration of phaeophytin increases when chlorophyll degradation occurs, it was thought that the ratio of phaeophytin to Chl (Phae/Chl) would provide a relative index of the physiological state of the bloom. The addition of this new variable to the lake-wide June-September model was significant ($P = 0.001$), producing a predictive equation of the form:

$$pH_{pred} = 6.800 + 1.277(\log Chl) - 0.615(Phae/Chl); \quad (4)$$

$$R^2 = 0.79, S_{yx} = 0.282, P < 0.0001$$

Table 2.1. Summary statistics for regressions of pH on chlorophyll α (Chl α) in Upper Klamath and Agency Lakes, Oregon. Regression model is $\text{pH}_{\text{pred}} = \beta_0 + \beta_1(\log \text{Chl } \alpha)$; all regressions and parameter estimates were significant at $P < 0.0001$.

Model	Parameters			Regression	
	β_0	β_1	SS_{yx}	r^2	n
Lake-wide Mean	6.396	1.398	0.317	0.72	43
June-September Dates					
Lake-wide Mean	6.809	1.260	0.165	0.95	11
June Dates Only					
Agency Lake (AS Site)	6.859	1.265	0.533	0.73	37
June-September Dates					

Note: β_0 is the intercept, β_1 is the slope, S_{yx} is the standard error of the estimate, and r^2 is the coefficient of determination.

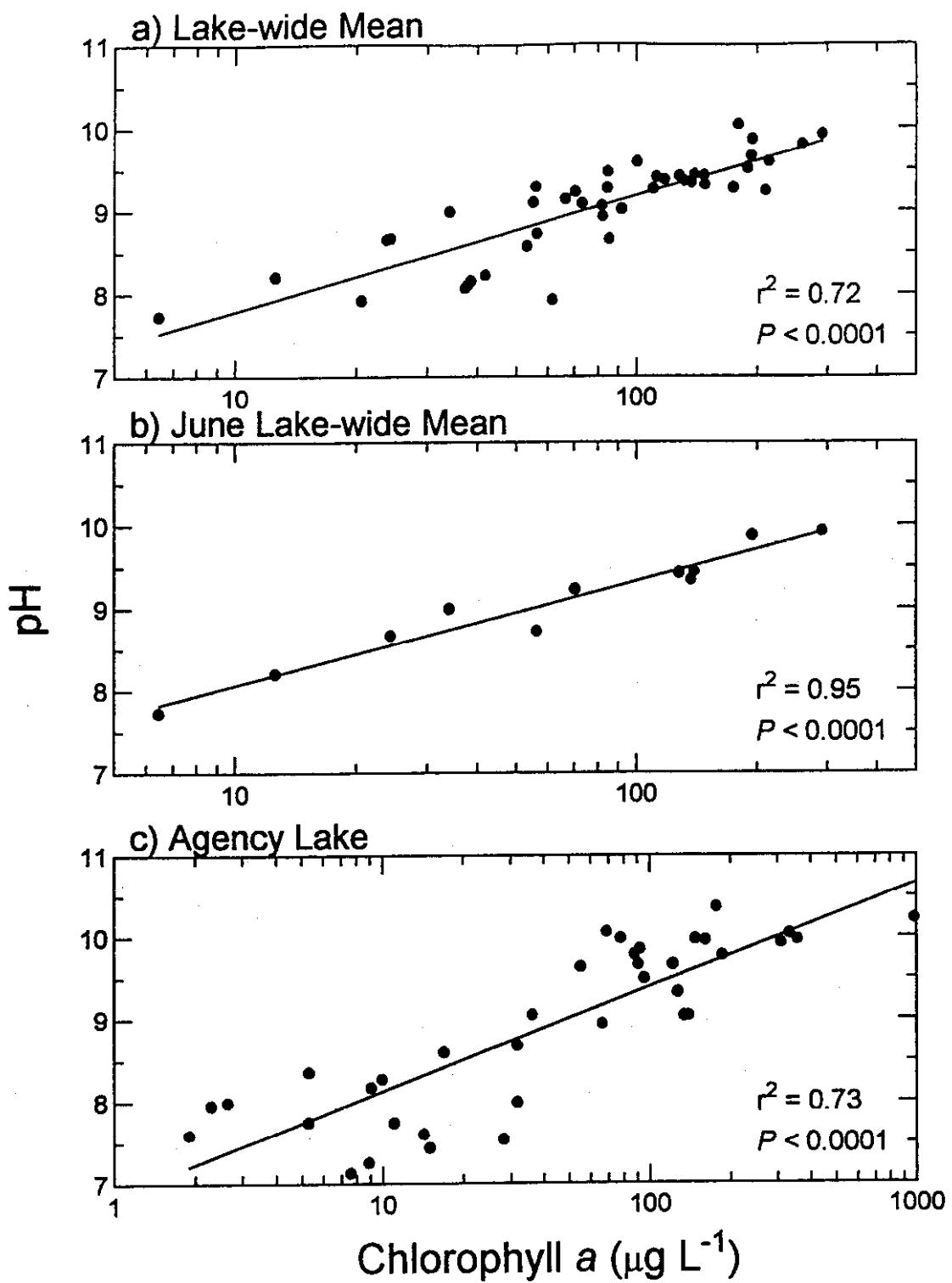


Fig. 2.4. Scatter plots of pH versus chlorophyll *a* ($\mu\text{g L}^{-1}$; log scale) for Upper Klamath Lake June-September (a) and June only (b) lake-wide means, and for the Agency Lake site AS (c), 1990-1994. Regression lines (solid lines) are computed from parameters in Table 1.

This new model explains an additional 7% of the variability in pH, and S_{yx} decreases by ca. 11% when compared to the June-September lake-wide model with Chl only. As would be expected if the Phae/Chl ratio is providing a true index of physiological state of the bloom, the coefficient is negative indicating a reduction in predicted pH as the ratio increases. Moreover, the intercept and Chl slope values of this multiple regression model are nearly identical to those of the June only bivariate model (Table 2.1), indicating that when physiological state is accounted for, pH_{pred} will be similar for both the June only and June-September models.

Probability of exceedence models

The establishment of pH_{crit} values based on the physiological limits of pH tolerance by fish, along with the observed relationship between algal biomass and pH in Upper Klamath Lake (Fig. 2.4), provides the empirical basis for a probabilistic approach to the modeling of fish success.

Regression-based probability model

By combining the regression equations from Table 2.1 with equations 1 and 2, the probability of exceeding the chosen pH_{crit} values is computed from the following equation:

$$\text{Probability of } pH > pH_{crit} = 100(1-zcf) \left(\frac{pH_{crit} - (\beta_0 + \beta_1(\log Chl a))}{S_{yx}} \right) \quad (5)$$

where $\beta_0 + \beta_1(\log Chl)$ equals pH_{pred} and the portion of the equation within the large parentheses equals Z. The statistical basis for this model stems from the fact that by meeting the assumptions of linear regression (hence the strict attention paid to evaluating these

assumptions), one can assume that pH_i is normally distributed with mean $\beta_0 + \beta_1 Chl_i$ (where $i=1,2,\dots, n$) and constant variance $S^2_{y|x}$ (Kleinbaum et al. 1988). Thus for any Chl input to the regression models a mean pH and standard error can be computed, and from this any proportion of a normal distribution which lies beyond a chosen value can be computed based on the normal probability density function.

The result of equation 5 when applied to the range of Chl data for each of the three models in Table 2.1 is a series of probability curves for each chosen pH_{crit} value (solid line; Fig. 2.5). For example Fig. 2.5a shows that for the lake-wide mean June-September model $P(pH_{crit} > 9.50)$ (the probability of exceeding $pH_{crit} > 9.50$) is 60% at $Chl = 200 \mu g L^{-1}$, while it is only 18% at $Chl = 100 \mu g L^{-1}$. For these same Chl values using the June model $P(pH_{crit} > 9.50)$ was 90% and 18% respectively (Fig. 2.5b), while for the Agency Lake model $P(pH_{crit} > 9.50)$ was 70% and 40% respectively (Fig. 2.5c). Given the healthier physiological state of the June blooms, it is not surprising that a higher probability of exceedence is predicted per unit Chl for this model. The effect of physiological state on the predicted probability of exceedence for the Upper Klamath Lake June-September model can be illustrated by holding the Phae/Chl ratio constant in Eq. 4, and computing a series of probability curves for each Phae/Chl constant by substituting Eq. 4 for pH_{pred} in Eq. 5 (Fig. 2.6). This plot clearly shows reduced probability of exceeding pH_{crit} as the Phae/Chl ratio increases. It is interesting to note that $Phae/Chl = 0$ produces results similar to the June model (Fig. 2.5b), while $Phae/Chl = 0.25$ produces similar results to the lake-wide mean June-September model (Fig. 2.5a). Predicted exceedence values per unit Chl are higher for the Agency Lake model also, very likely due to its shallower depth. Because the models are based on an integrated water column Chl value, inclusive of algal cells both in and out of the photic zone, it follows that

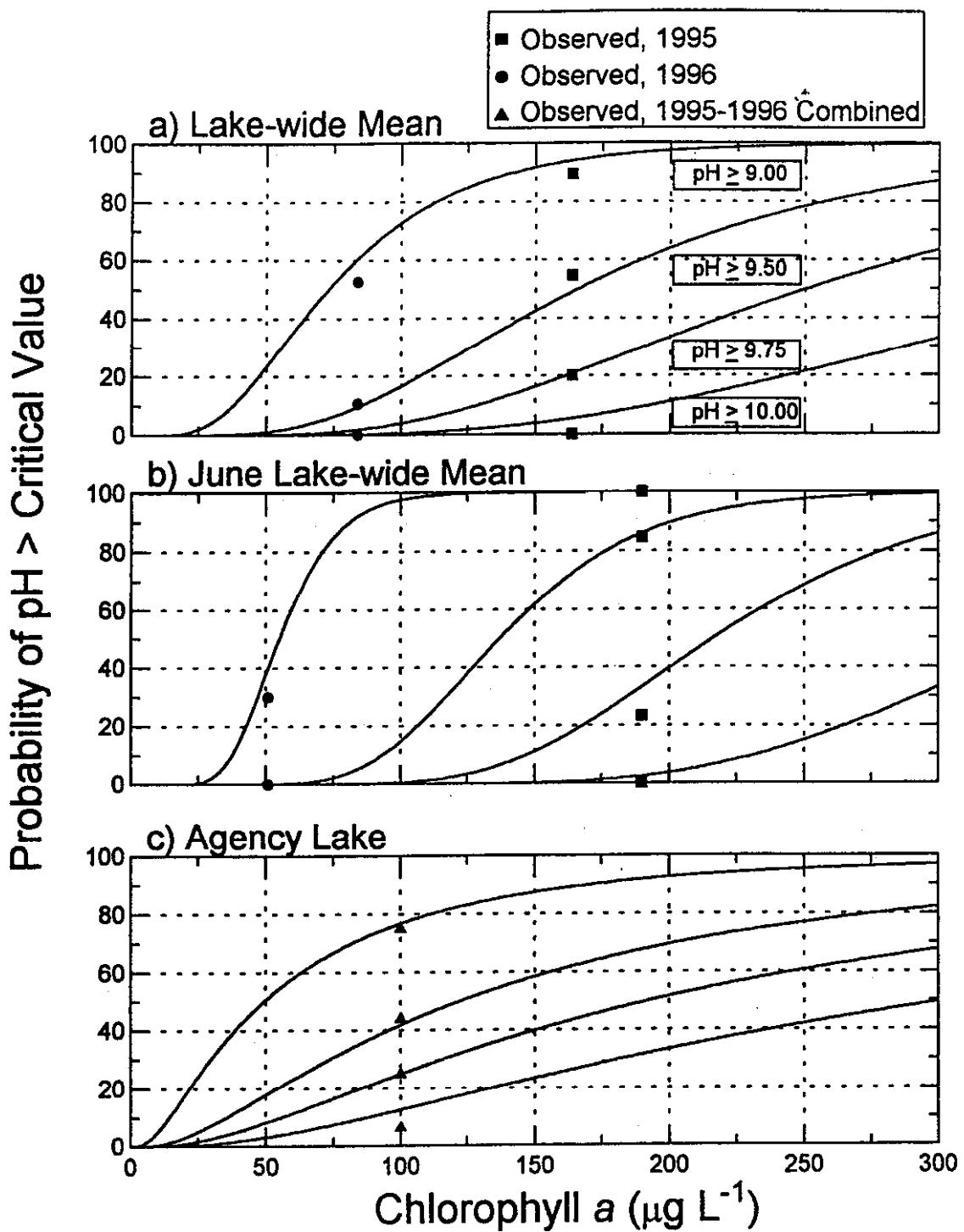


Fig. 2.5. Probability plots for regression-based probability models of exceeding four critical pH levels as a function of chlorophyll *a* concentration ($\mu\text{g L}^{-1}$) in Upper Klamath and Agency Lakes, Oregon. Probability curves (solid lines) are computed from Eq. 5 with input parameters from Table 1 (model subset descriptions for a, b and c are the same as for Fig 7). Symbols represent observed exceedence frequencies from the independent model validation data set (1995 and 1996) and are plotted against mean chlorophyll *a* (see text for detailed explanation).

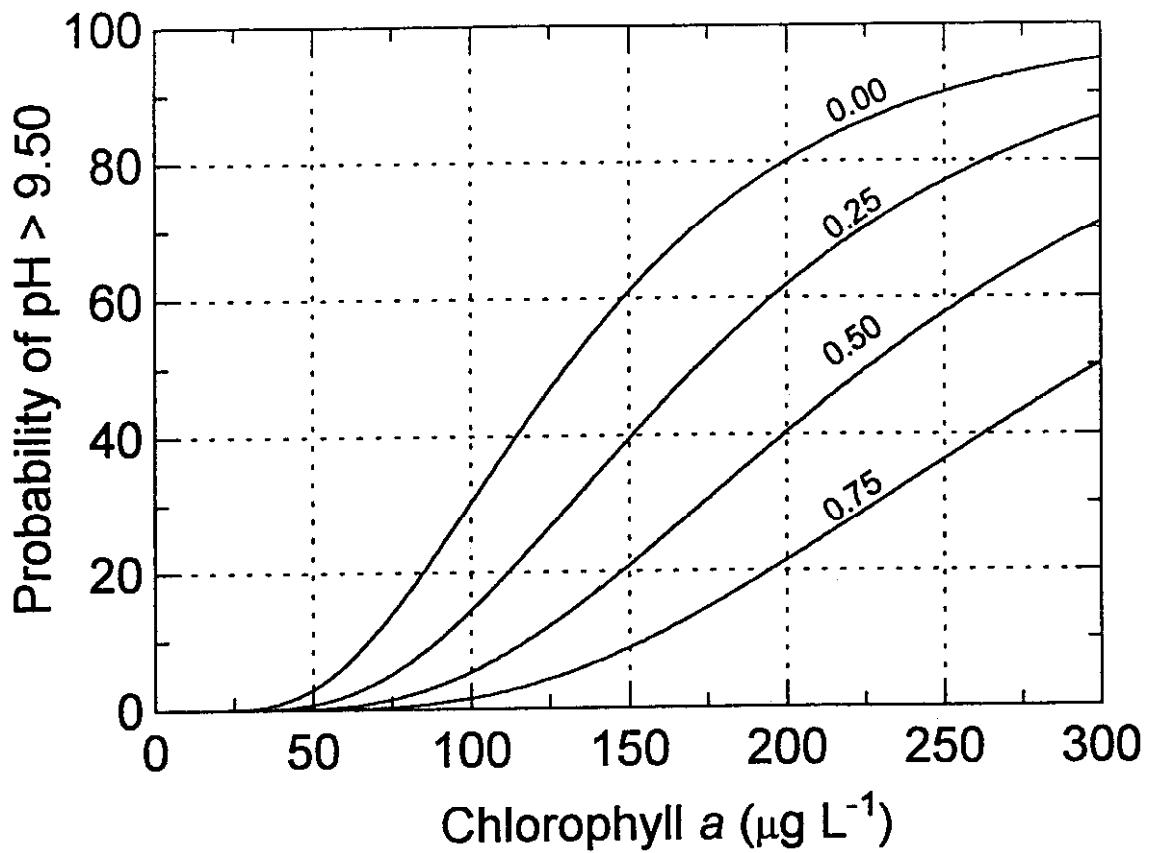


Fig. 2.6. Probability plots for the Upper Klamath Lake June-September regression-based probability model of exceeding $\text{pH} = 9.50$ at four constant levels of the phaeophytin to chlorophyll a ratio ($\text{Phae/Chl } a = 0.00, 0.25, 0.50, 0.75$). Probability curves (solid lines) are computed by substituting Eq. 4 for pH_{pred} in Eq. 5.

photosynthesis (and subsequent pH increase) per unit Chl would be higher when mixing conditions experienced at shallower depths increase the amount of time that algal cells are exposed to more optimal light conditions.

Nonparametric cross-tabulation probability model

When the underlying assumptions of the regression-based probability model are not met, similar probability of exceedence curves can be generated using the nonparametric cross-tabulation procedure described above (see methods section). This procedure requires no assumptions about the shape or functional form of the relationship (Walker and Havens 1995); one simply computes exceedence frequencies for pH_{crit} values within the designated intervals of ordered and paired pH/Chl values. To maximize the number of observations, and to be inclusive of spatial and temporal variance, only one model utilizing all paired measurements from the Upper Klamath Lake subset ($n = 248$) was developed. This data set was divided into 6 intervals, with the number of samples within an interval (n_{int}) equal to 41 for intervals 1-5, and 43 for interval 6. The frequency of pH values which exceeded each of the chosen pH_{crit} values within an interval was then plotted on the median Chl value for the interval (solid circles in 2.7). Because these 6 data points appeared to approximate a logistic function, and the fact that it is not unexpected to find a density dependent relationship between photosynthesis and algal biomass (factors such as self-shading increase in importance as biomass increases), the logistic equation (Eq. 3; Table 2.2) was used to describe the apparent relationship between exceedence frequency and Chl (solid line in Fig. 2.7). It is evident that these models provide an excellent fit to the observed frequencies within the six intervals (solid circles; Fig. 2.7). Results were very similar to the lake-wide mean June-September

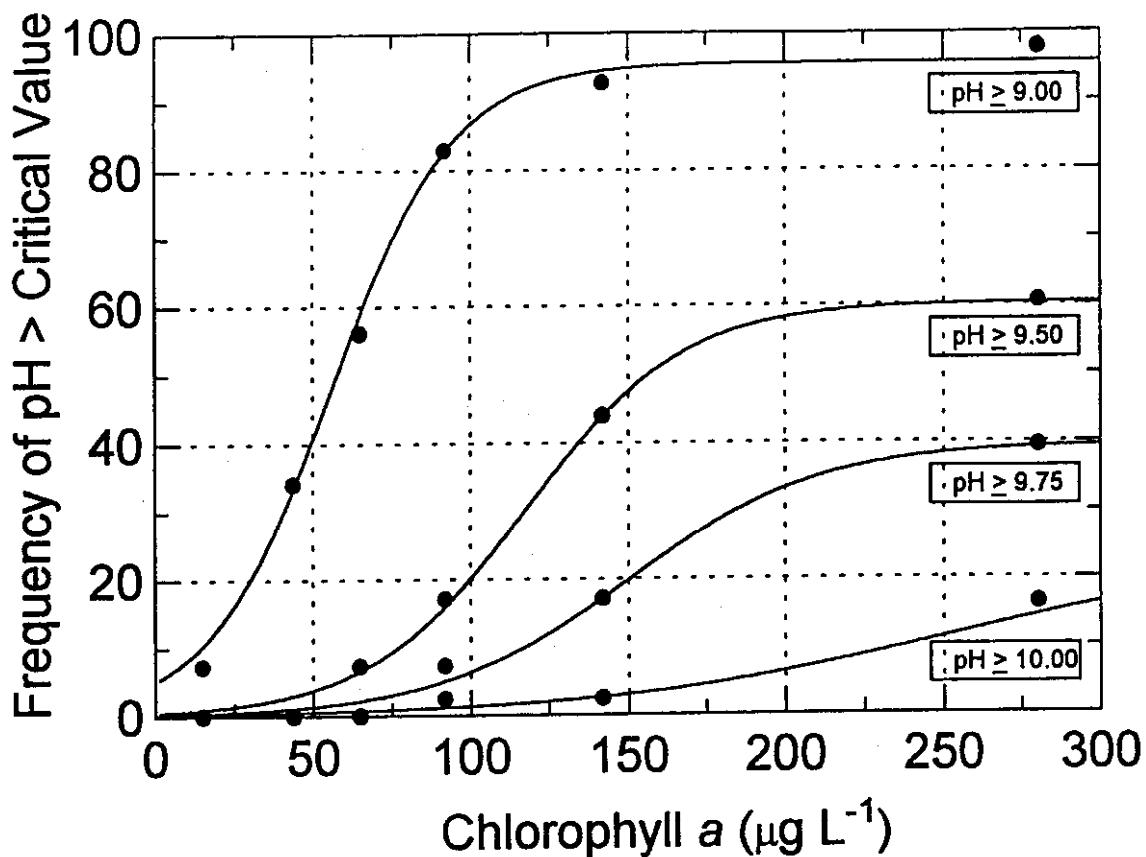


Fig. 2.7. Frequency plots for Upper Klamath Lake June-September nonparametric cross-tabulation probability models of exceeding four critical pH levels as a function of chlorophyll a concentration ($\mu\text{g L}^{-1}$). Frequency of exceedence curves (solid lines) are computed from Eq. 3 with input parameters from Table 2. Solid circles (\bullet) are the observed frequencies computed within six ordered and paired pH and chlorophyll a intervals and plotted on the median chlorophyll a of each interval.

Table 2.2. Parameter estimates and summary statistics for logistic probability models (Eq. 3) of exceeding pH_{crit} in Upper Klamath Lake, Oregon.

pH_{crit}	pH_c	β_0	β_1	S_{yx}	R^2
9.00	95.6 ± 2.185^a	2.878 ± 0.274	0.052 ± 0.005	3.001	0.99
9.50	60.3 ± 1.901	4.694 ± 0.400	0.040 ± 0.004	1.899	0.99
9.75	39.7 ± 1.970	4.970 ± 0.923	0.033 ± 0.007	1.879	0.99
10.00	18.0 ^b	5.143 ± 0.662	0.024 ± 0.003	0.818	0.99

^a ± standard error

^b value fixed based on plot

regression-based model, whereby the frequency of exceeding $\text{pH}_{\text{crit}} = 9.5$ is 59% at Chl a = 200 $\mu\text{g L}^{-1}$ and 20% at Chl = 100 $\mu\text{g L}^{-1}$.

Sensitivity to n_{int} and interval medians

Despite the lack of parametric assumptions in development of this model, an assessment of the model sensitivity to both n_{int} and use of an interval median (or any chosen measure of interval central tendency) to construct the exceedence plot is necessary to ensure an accurate description of the data. When n_{int} is small, one or two values within an interval can greatly alter the computed frequencies. For example if $n_{\text{int}} = 10$, then for every pH value which is below or exceeds pH_{crit} there is a 10% decrease or increase in the computed frequency within the interval. Applying this concept to model development, it is apparent that a large data set is required and that the number of intervals the data set is divided into can not be so great as to reduce n_{int} to an unacceptable level. However, the number of samples within an interval must be balanced against the need to have enough intervals to describe the shape of the relationship. For example a data set could be divided into 2 intervals to ensure high n_{int} , but this would not allow the functional shape of the relationship to be described. As can be seen from Fig. 2.8, where exceedence frequencies were computed for 1 interval (the entire data set; $n_{\text{int}} = 248$), 2 intervals ($n_{\text{int}} = 124$), and so on through 6 intervals, the functional shape based on 6 intervals (solid line) was relatively insensitive to interval choice. Likewise, computed exceedence frequencies for all interval choices were well described by the logistic function based on 6 intervals.

Because the plotted values (solid circles; Fig. 2.7) are based on median Chl values of each interval, each point actually represents a range of Chl values, and the described

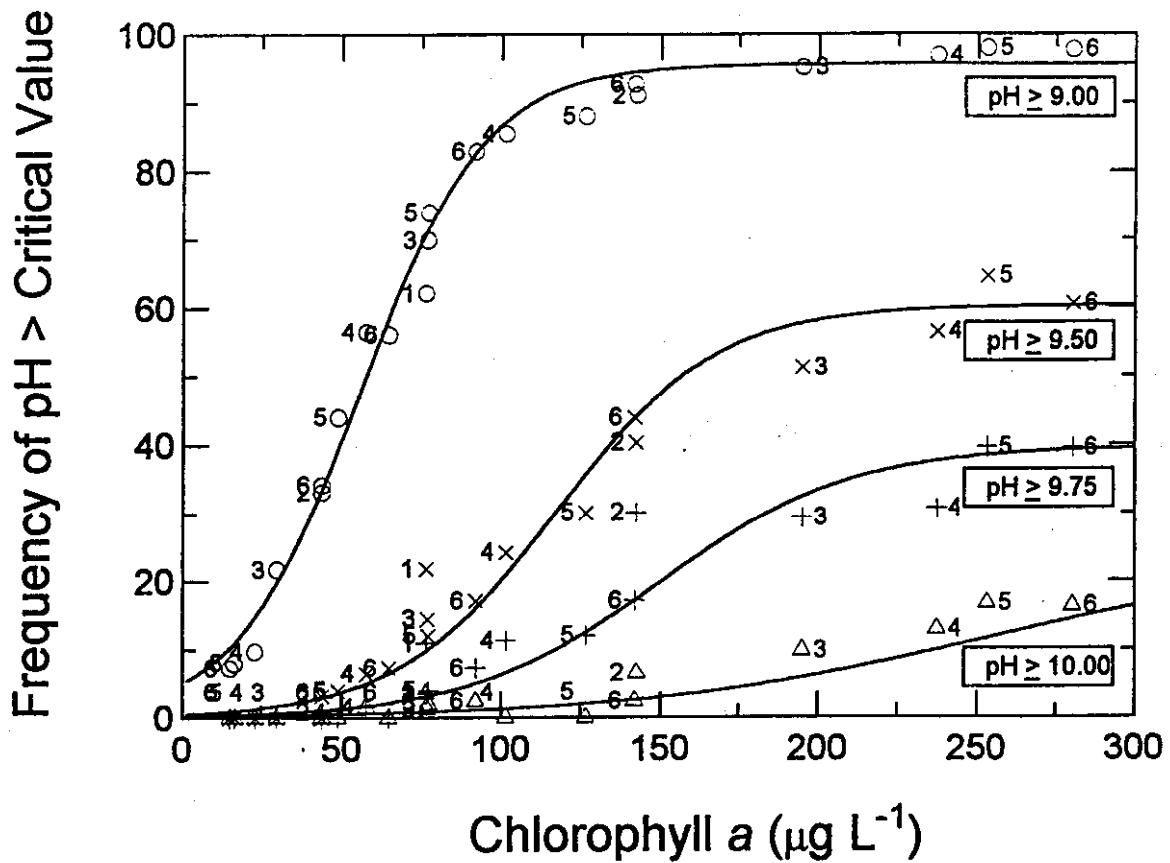


Fig. 2.8 Sensitivity of the frequency of exceedence models to interval choice and use of medians to represent interval central tendency. Frequency of exceedence curves (solid lines) are the same as those for Fig. 10, and are overlain on observed exceedence frequencies for 1 (the entire data set; $n_{\text{int}} = 248$), 2 ($n_{\text{int}} = 124$), 3 ($n_{\text{int}} = 83$), 4 ($n_{\text{int}} = 62$), 5 ($n_{\text{int}} = 50$) and 6 intervals ($n_{\text{int}} = 41$) which are plotted on their respective interval medians. The symbols denote each of the four pH_{crit} models ($\circ = \text{pH } 9.00$, $x = \text{pH } 9.50$, $+ = \text{pH } 9.75$, and $\Delta = \text{pH } 10.00$), and the symbol labels (numbers) refer to the number of intervals. In this way the label 1 shows up once for each model, the label 2 twice, etc..., through the label 6 which shows up six times.

functional shape could vary if the placement of these values along the abscissa changed due to an inappropriate description of the Chl variance within intervals. An evaluation of model sensitivity to this can be gained from Fig. 2.8, whereby each set of intervals < 6 produced completely different median Chl values from the 6 interval model, yet the frequencies associated with them were generally well described by the logistic functions. To evaluate the entire range of Chl, exceedence frequencies for the pH_{crit} value 9.50 were computed based on moving intervals ($n_{int} = 41$; the same as that for 6 intervals) of each successive set of 41 samples (1-41, 2-42, 3-43, etc... 208-248), and plotted on the median Chl of each moving interval (Fig. 2.9). As with Fig. 2.8, exceedence frequencies for Chl values falling between the 6 independent (non-overlapping) intervals were also relatively well described by the logistic model.

The excellent fit of the logistic equations to the observed data, and the fact that model sensitivity to both the number of intervals chosen and the use of median Chl values for intervals was minimal, provides the basis for use of the logistic functions to predict future conditions.

Model validation

While the above parametric and nonparametric based probability models provide excellent descriptions of the observed data, their predictive ability must be validated with independently-derived data. Walker and Havens (1995) proposed using the binomial distribution to compute standard errors of measured frequencies within intervals for the cross-tabulation model. However, this only provides an estimate of error in the descriptive model, and does not serve to validate the predictive capability of the models, nor does it describe

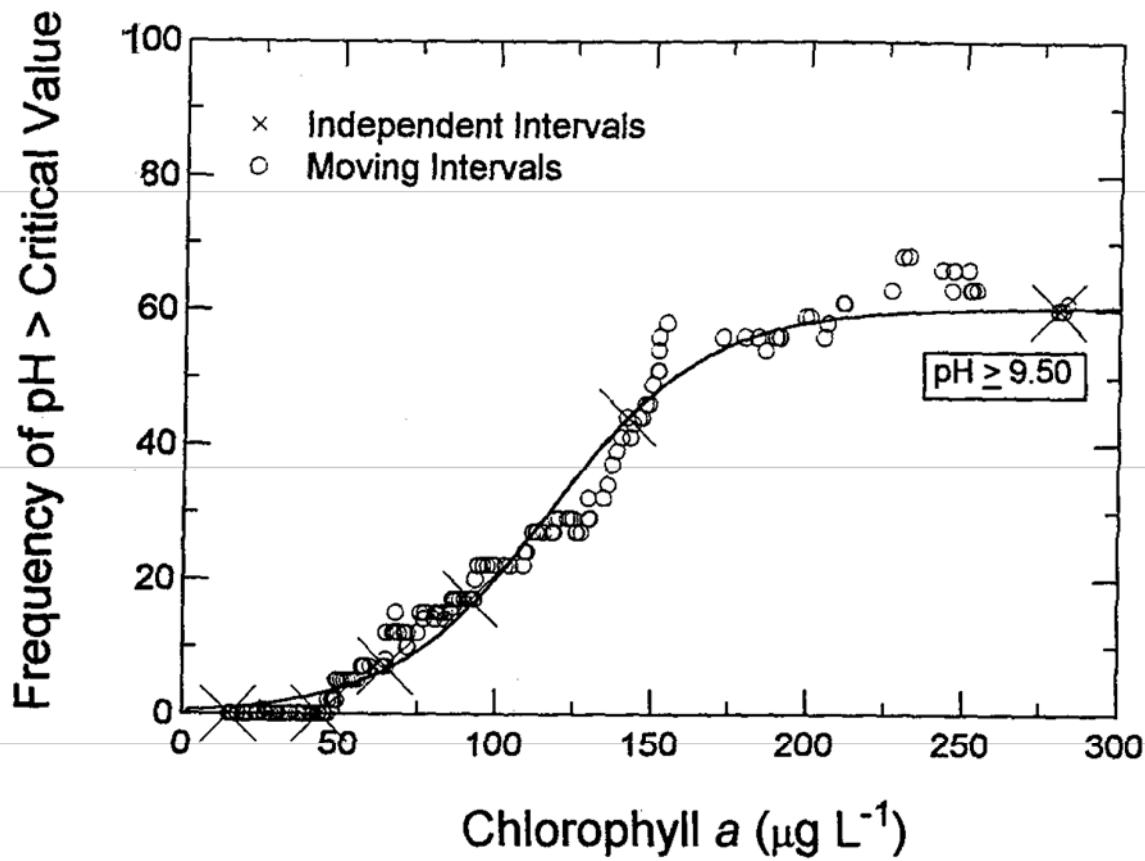


Fig. 2.9 Sensitivity of the modeled exceedence frequencies for $\text{pH}_{\text{crit}} = 9.50$ (solid line; the same as that from Fig. 10) to the use of medians to represent interval central tendency for the entire range of chlorophyll a . Exceedence frequencies (\circ) were computed based on moving intervals ($n_{\text{int}} = 41$; the same as that for the original 6 intervals) of each successive set of 41 samples (1-41, 2-42, 3-43, etc... 208-248), and plotted on the median chlorophyll a of each moving interval. This generates frequencies for 6 non-overlapping or independent intervals (\times), which are the same as the original 6 intervals from Fig. 10.

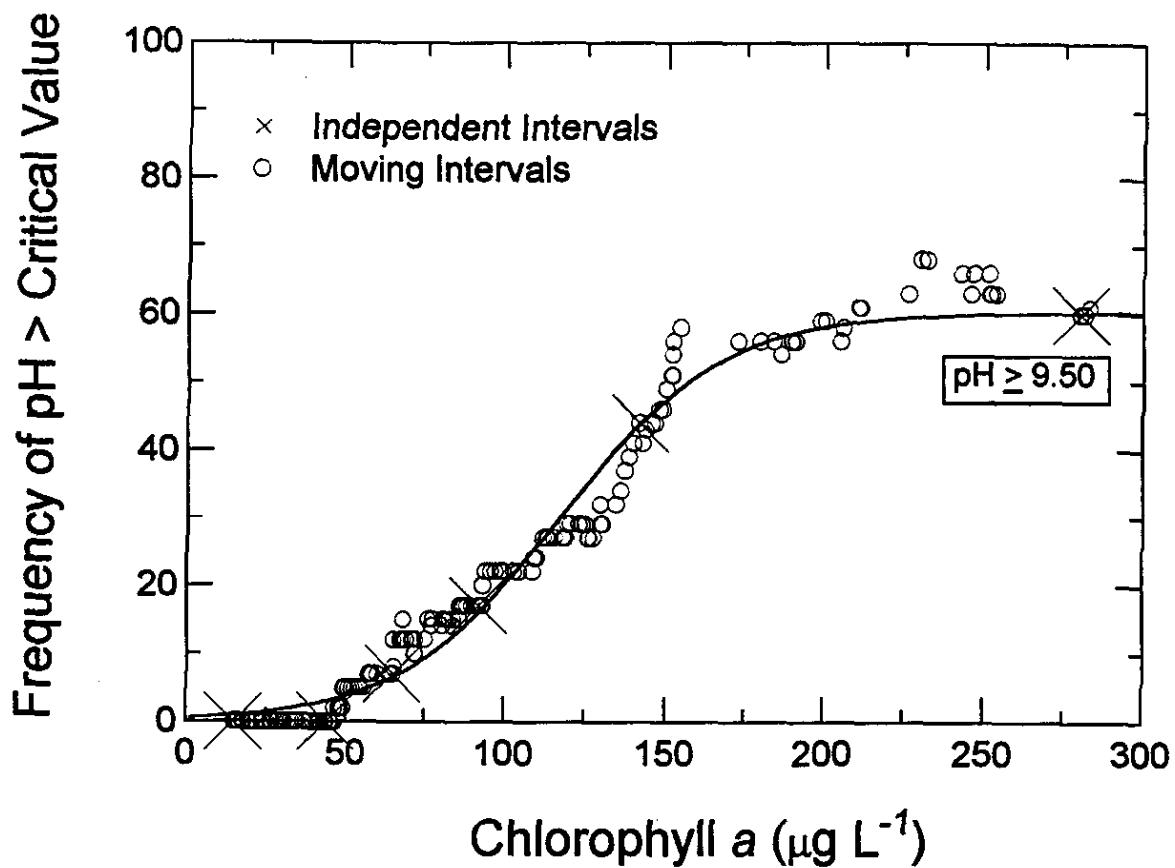


Fig. 2.9. Sensitivity of the modeled exceedence frequencies for $\text{pH}_{\text{crit}} = 9.50$ (solid line; the same as that from Fig. 10) to the use of medians to represent interval central tendency for the entire range of chlorophyll *a*. Exceedence frequencies (\circ) were computed based on moving intervals ($n_{\text{int}} = 41$; the same as that for the original 6 intervals) of each successive set of 41 samples (1-41, 2-42, 3-43, etc... 208-248), and plotted on the median chlorophyll *a* of each moving interval. This generates frequencies for 6 non-overlapping or independent intervals (X), which are the same as the original 6 intervals from Fig. 10.

prediction uncertainty. Likewise, the non-linear and linear regression statistics (Tables 2.1 and 2.2) are estimates of error in model fit to the observed data, and also do not describe prediction uncertainty. With the multi-year data base in Upper Klamath and Agency Lakes, all available data were not needed to formulate the model, and the predictive ability of the models could be verified from independently derived data.

For each year of the Upper Klamath Lake 1995-1996 validation data set the frequency of exceedence of pH_{crit} was computed as the number of observations (expressed as a percent of the total observations) at all sites and dates within the June-September and June only time periods that exceeded the chosen pH_{crit} values. The Agency Lake model is based on only one site, therefore data from both years were combined to ensure an adequate sample size for validation. Exceedence frequencies were paired with the mean Chl for each of the time periods and overlain on the parametric and nonparametric based probability plots (Figs. 2.5 and 2.10). With the exception of the nonparametric model for $\text{pH}_{\text{crit}} = 9.00$, which overpredicted exceedence frequency by ca. 25% in 1996 (Fig. 2.10), both plots qualitatively indicate good prediction by all models. A quantitative measure of the predictive ability of the models was assessed by regressing predicted values from the models with observed values from the model validation data set (Fig. 2.11). The predictive ability of all models was highly significant ($P < 0.01$; $r^2 > 0.95$), and the predicted regression lines were not significantly different from the 1:1 relationship between observed and predicted values ($\beta_0 = 0$; $\beta_1 = 1$). After Keller (1989) a quantitative measure of the predictive ability between the regression-based and nonparametric models was assessed through F-tests on the residual variability from the regression between observed and predicted values. This test showed no significant difference ($P > 0.10$) between the predictive ability of the two models. Despite a nearly two-

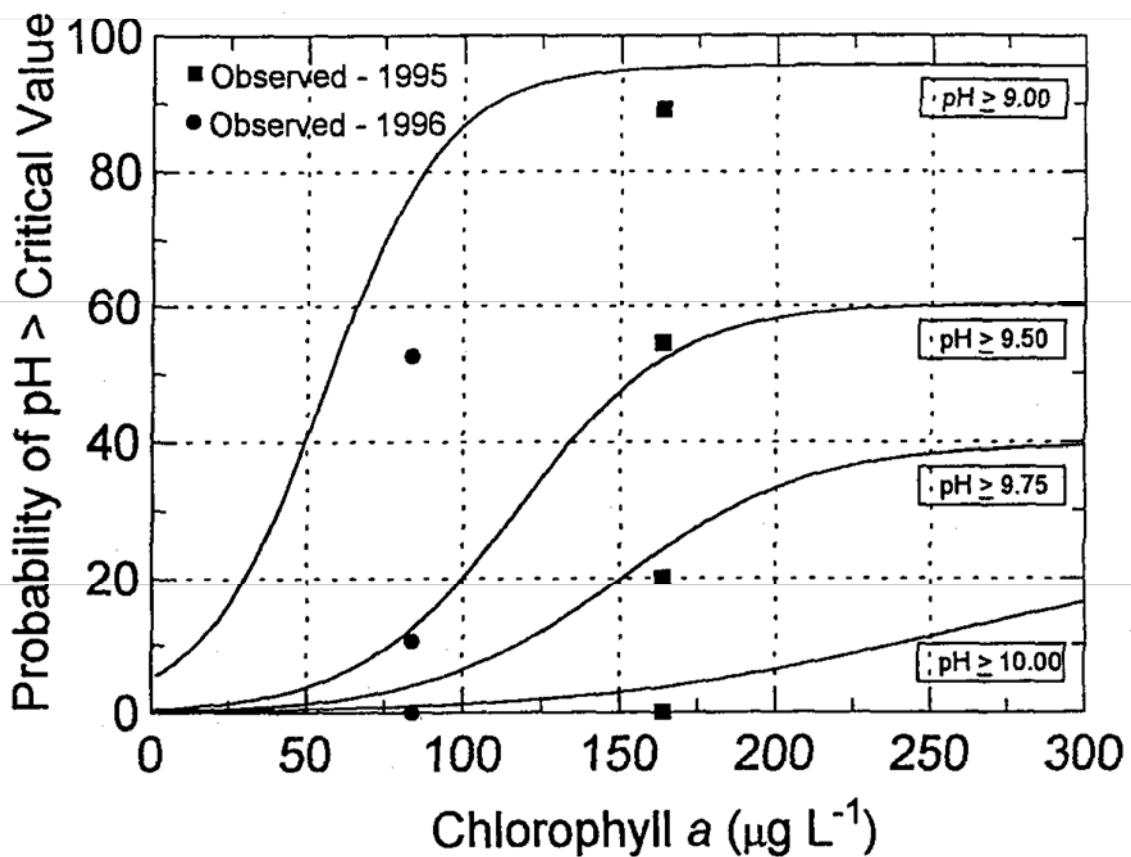


Fig. 2.10. Validation plot for Upper Klamath Lake June-September nonparametric cross-tabulation probability models of exceeding four critical pH levels as a function of chlorophyll α concentration ($\mu\text{g L}^{-1}$). Symbols represent observed exceedence frequencies from the independent model validation data set (1995 and 1996) and are plotted against mean chlorophyll α for the June-September time period.

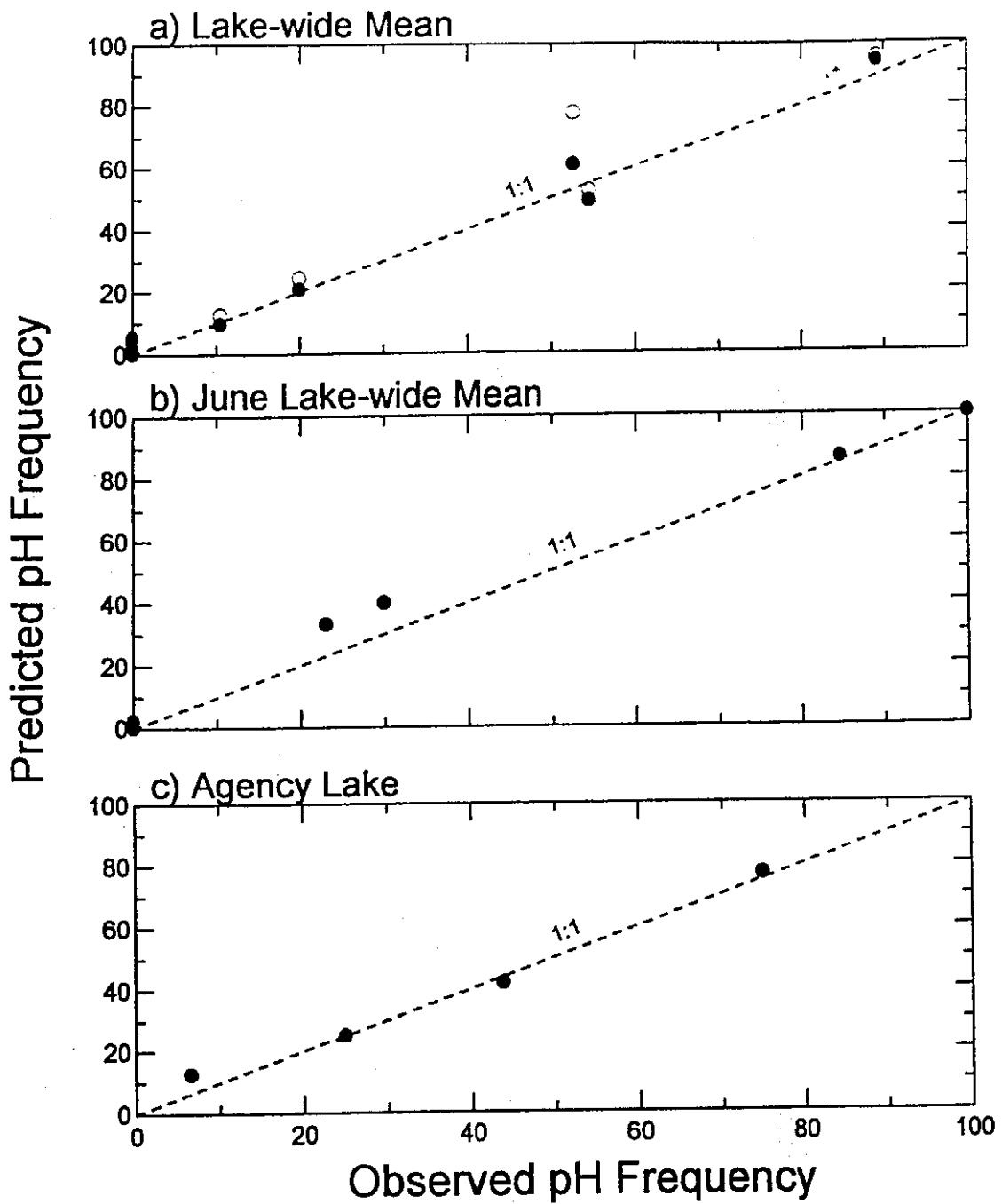


Fig. 2.11. Relationship between predicted exceedence frequency from the regression-based (●) and nonparametric (○) probability models and the observed frequency from the independent model validation data set (model subset descriptions for a, b and c are the same as for Fig 7; dashed line is the 1:1 relationship between the observed and predicted values). The regressions between the predicted and observed values were significant for all models ($P < 0.01$; $r^2 > 0.95$), and the predicted regression lines were not significantly different from the 1:1 relationship between observed and predicted values ($\beta_0 = 0$; $\beta_1 = 1$).

fold difference in June-September lake-wide mean Chl between 1995 ($164 \mu\text{g L}^{-1}$) and 1996 ($84 \mu\text{g L}^{-1}$), predicted exceedence frequencies for all pH_{crit} values were remarkably accurate. Seasonal or time period mean Chl provides a good indication of the expected probability of exceeding various pH_{crit} values, and therefore provide a good indication of the pH conditions experienced by fish both spatially and temporally at given seasonal mean algal biomass. These models clearly show that the frequency and severity of photosynthetically-elevated pH events decreases as Chl is reduced.

Practical Implications

These probabilistic models provide a versatile tool allowing an assessment of critical Chl concentrations for any chosen threshold pH values. In addition, the fact that exceedence frequencies can be well predicted from seasonal mean Chl allows integration with most TP and Chl eutrophication models which generally predict seasonal mean TP and Chl (Reckhow and Chapra 1983; Sas 1989). In large shallow hypereutrophic lakes with high external and internal nutrient loading such as Upper Klamath Lake, complete reversals of eutrophication are typically not technically or economically feasible. However, in shallow hypereutrophic lakes, chlorophyll α in general and blue-green algae in particular show substantial reductions in response to reduction in TP loading, even when TP concentrations remain in the hypereutrophic range ($>100 \mu\text{g L}^{-1}$ TP) after restoration (Jeppesen et al. 1990; Seip et al. 1992). In Upper Klamath Lake, our analysis shows that a nearly 45% reduction (72% for the June model) in the probability of exceeding pH 9.5 could be realized by reducing chlorophyll α from 200 to $100 \mu\text{g m}^{-3}$, still well within the hypereutrophic range.

A probabilistic approach has been used successfully in the assessment of lake trophic

state (OECD 1982; Reckhow and Chapra 1983), in the trophic state classification of South African lakes (Walmsley 1984), in the development of phosphorus criteria for Minnesota lakes (Heiskary and Walker 1988), and in the relationship of bloom frequencies to Chl (Havens 1994), and Chl to phosphorus (Walker and Havens 1995). Furthermore, Mericas and Malone (1984) related the probability of fish kills to the concentration of TP in six Louisiana lakes. Mericas and Malone (1984) then demonstrated that this probabilistic relationship could be linked to stochastic phosphorus loading models, and that this combined modeling framework could be used in the objective assessment of lake management alternatives designed to minimize the risk of summer fish kills. I suggest that the relationships illustrated here (Figs. 2.5 and 2.7) can similarly be used to provide guidelines for the reductions in chlorophyll *a* that will be needed to improve fish success, and thus can be used as the basis for development of an objective framework for the restoration of endangered fish populations in the Upper Klamath Lake system.

I also emphasize that a similar approach can be used in the evaluation of fish responses to other environmental factors. For example, fish success can be related to other important habitat quality parameters, such as the concentrations of dissolved oxygen and of unionized ammonia in the water column. Moreover, a great deal of recent effort has been made to develop methodologies for evaluating species risk (Sutter 1993), and I suggest that this general approach may prove useful in the future management of risk to other species as well.

Conclusions

The proper management of fisheries in water systems requires not only a knowledge of the environmental conditions that result in fish kills, but also an understanding of both the lethal and sublethal responses of fish to changes in water quality. In the analysis presented here, I have recognized the importance of considering both responses, and have (*I*) shown a clear relationship between algal biomass and photosynthetically-elevated pH, and (*ii*) used parametric and nonparametric methods to evaluate the risk of exceeding experimentally established critical pH limits for fish growth, survival, and reproduction at varying concentrations of chlorophyll *a* in Upper Klamath Lake and Agency Lakes, Oregon. The frequency with which certain critical values will be exceeded is more informative and less misleading than the pure regression approach which only predicts the mean pH response. The approaches presented here incorporate the inherent spatial and temporal variance in the independent and dependent variables, and reexpress it as the probability or frequency of conditions likely to be experienced by fish.

I have also discussed the assumptions involved in development of these models and provided a framework to test the sensitivity of the models to these assumptions. Once validated, these models permit an objective definition of the degree of water quality impairment, and provide a quantitative lake management tool. The risk assessment approach presented here (relating algal biomass → habitat quality parameter of concern → physiological tolerance → probability of exceedence → fish success) can be linked with existing eutrophication models to develop watershed management policies designed to improve fisheries in Upper Klamath Lake and Agency Lakes, Oregon. While the application of these

specific Upper Klamath and Agency Lake models to lakes of differing alkalinity, depth, and algal assemblages should be done with caution, I suggest that parallel relationships between algal biomass, pH, and fish success can be developed for other lakes as well. Due to the extensive seasonal and inter-annual variability typically observed in lakes (Jassby et al. 1990; Jassby et al. 1992), however, it should be emphasized that the development of such models should be based on multiple-year data bases where possible. The seven-year data base used to develop and validate the models presented here for Upper Klamath Lake captures the dynamic aspect of both inter- and intra-annual variability in this shallow system.

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