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Trophic Resource Partitioning Among Nine Sympatric Congeners
in an Ancient Tropical Lake

A Dissertation Submitted to the Graduate Faculty of
Baylor University
in Partial Fulfillment of the
Requirements for the Degree
of
Doctor of Philosophy

By
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May 2005

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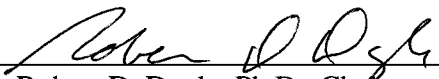
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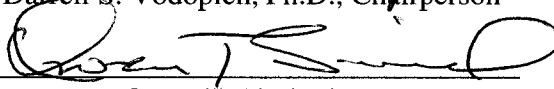
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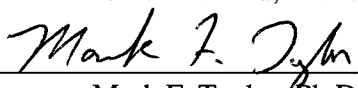
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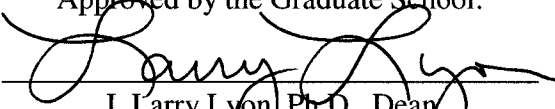

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ABSTRACT

Trophic Resource Partitioning Among Nine Sympatric Congeners in an Ancient Tropical Lake

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The maintenance of species diversity relies on factors such as competition, factors related to morphology, and the partitioning of spatial, temporal and trophic resources. Central Mexico's tropical Lake Chapala provides a rich diversity of nine sympatric congeners of *Chirostoma* which allows for studies related to the maintenance of species integrity. This research investigated factors of trophic partitioning, spatial distribution and the relationship of morphology to diet to reveal potential forces underlying the maintenance of species integrity. I investigated 1) correlations between dietary composition and morphology; 2) differences and partitioning of dietary resources; 3) ontogenetic influences on resource use; and 4) aspects of distribution and abundance. Results indicated that Jordani Group chirostomids are evenly distributed in Lake Chapala, while Arge Group species are skewed towards the eastern region. Morphologies have remained consistent over a 100 year period. Correlations between single morphological characteristics and dietary composition were not significant. Differences in dietary composition and the amounts of prey consumed were not observed on the basis of gender. Twelve major food categories were identified, all of which were shared by the

nine chirostomid species. Initial analyses indicated that the diets were broad with extensive overlap. More rigorous discriminant function analyses identified significant differences among the diets of the nine species. Although significant differences among the diets of the nine chirostomid congeners were detected, competition appeared to be dampened. High productivity, both primary and bacterial, combined with anthropogenic stresses such as over-fishing, human-induced declines in water quality and increased water demands have dampened competition for trophic resources among the nine sympatric chirostomid congeners.

TABLE OF CONTENTS

List of Figures	v
List of Tables	ix
Acknowledgments.....	xii
Dedication	xiii
Chapter One	1
Introduction.....	1
Competition.....	3
Competition and Resource Partitioning	5
Competitive Exclusion.....	5
Sympatriates versus Congeneric Sympatriates	8
Morphology.....	9
Development	10
Why study resource partitioning in Lake Chapala?.....	11
Lake Chapala, Jalisco, Mexico	11
A review of select literature on Lake Chapala.....	13
Why use chirostomid species as a research model?.....	14
A review of select literature for chirostomid fishes.....	15
Questions of formal research	16
Chapter Two.....	20
Methods and Materials.....	20
Sampling Areas	20
Seasonal Sampling	22
Field Collection techniques.....	23
Laboratory Techniques	24
Statistical Analyses	27
Morphological Analyses	27
Spearman's Rank Order Correlation.....	27
Discriminant Function Analysis and Morphology.....	28
Dietary Analyses.....	29
Student's <i>t</i> -test	29
Spearman's Rank Order Correlation.....	29
Discriminant Function Analysis and Diet.....	30

Chapter Three.....	33
Results.....	33
The Morphology of Chirostomid Fish.....	33
Species Diagnosis of the Jordani Group.....	34
<i>Chirostoma jordani</i>	34
<i>Chirostoma consocium</i>	36
<i>Chirostoma chapalae</i>	36
<i>Chirostoma promelas</i>	37
<i>Chirostoma sphyraena</i>	60
<i>Chirostoma lucius</i>	60
Species Diagnosis of the Arge Group.....	61
<i>Chirostoma arge</i>	61
<i>Chirostoma aculeatum</i>	61
<i>Chirostoma labarcae</i>	62
The Lake Chapala Community of Chirostomids.....	62
Dietary Composition of the <i>Chirostoma</i> spp. of Lake Chapala.....	70
The Diet of <i>Chirostoma aculeatum</i>	75
The Diet of <i>Chirostoma arge</i>	78
The Diet of <i>Chirostoma chapalae</i>	78
The Diet of <i>Chirostoma consocium</i>	81
The Diet of <i>Chirostoma jordani</i>	81
The Diet of <i>Chirostoma labarcae</i>	82
The Diet of <i>Chirostoma lucius</i>	83
The Diet of <i>Chirostoma promelas</i>	83
The Diet of <i>Chirostoma sphyraena</i>	93
Statistical Analyses of Dietary Data.....	98
Student's t-test.....	98
Spearman's Rank Order Correlation Analysis.....	101
Discriminant Analysis.....	102
MANOVA and Related Analyses.....	104
Chapter Four.....	114
Discussion.....	114
Relative Abundance and Distribution of Chirostomid Fishes.....	115
Ontogenetic Trends in Chirostomid Fishes.....	118
Dietary Differences Between Males and Females.....	119
Morphological Evaluations of Chirostomid Fishes.....	120
Dietary Differences Among Chirostomid Fishes.....	122
What Factors Shape Competitive Interactions of Chirostomids?.....	124
Overfishing.....	124
Productivity.....	126
System Stressors Water Quantity and Water Quality.....	126
Summary and Conclusions.....	129
Bibliography.....	131

LIST OF FIGURES

Figure 1.	<i>Chirostoma chapalae</i> shown above is a member of the Lake Chapala chirostomid species flock.....	1
Figure 2.	The hypothetical dietary niche breadth of a species in the absence of predators.....	6
Figure 3.	The addition of a second species into a system causes both species to narrow their dietary breadth.	6
Figure 4.	The addition of a third species results in competition for a common resource and a narrowing of niche breadth.	7
Figure 5.	Lake Chapala (depicted in blue) is located primarily in the State of Jalisco (Red) in Central Mexico.	12
Figure 6.	Chirostomid fishes available for sale in the City of Chapala downtown market.	15
Figure 7.	Bathymetric map of Lake Chapala during 1998-1999.	18
Figure 8.	Lake Chapala sampling areas shown from west (Jocotepec) to east (Ocatlan).	20
Figure 9.	Comparison of total lengths of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	38
Figure 10.	Comparison of standard lengths of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	39
Figure 11.	Comparison of head lengths, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	40
Figure 12.	Comparison of snout lengths, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	41
Figure 13.	Comparison of mandible lengths, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	42

Figure 14. Comparison of mouth heights, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	43
Figure 15. Comparison of mouth widths, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	44
Figure 16. Comparison of body depths, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	45
Figure 17. Comparison of caudal peduncle lengths, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	46
Figure 18. Comparison of pectoral fin insertions, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	47
Figure 19. Comparison of dorsal fin insertions, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	48
Figure 20. Comparison of anal fin insertions, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	49
Figure 21. Comparison of eye sizes, in millimeters, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	50
Figure 22. Comparison of gill raker numbers of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	51
Figure 23. Comparison of vertebrae numbers of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	52
Figure 24. Comparison of anal fin heights, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	53
Figure 25. Comparison of anal fin rays of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	54

Figure 26. Comparison of number of scales superior to the lateral line of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	55
Figure 27. Comparison of the number of pectoral fin rays of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	56
Figure 28. Comparison of median lateral line scales of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	57
Figure 29. Comparison of predorsal scales of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	58
Figure 30. Comparison of interdorsal scales of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999	59
Figure 31. The distribution of Jordani Group and Arge Group chirostomids is depicted for Lake Chapala during 1998-1999.....	70
Figure 32. The distribution of six chirostomid species of the Jordani Group at Lake Chapala from 1998-1999 are depicted.....	71
Figure 33. The distribution of three chirostomid species belonging to the Arge Group at Lake Chapala from 1998-1999 are shown.....	72
Figure 34. Dietary composition of <i>Chirostoma</i> spp. in Lake Chapala, Mexico (1998-1999)	75
Figure 35. Dietary composition of <i>Chirostoma aculeatum</i> in Lake Chapala, Mexico (1998-1999)	75
Figure 36. Dietary composition of <i>Chirostoma arge</i> in Lake Chapala, Mexico (1998-1999)	78
Figure 37. Dietary composition of <i>Chirostoma chapalae</i> in Lake Chapala, Mexico (1998-1999)	81
Figure 38. Dietary composition of <i>Chirostoma consocium</i> in Lake Chapala, Mexico (1998-1999)	82
Figure 39. Dietary composition of <i>Chirostoma jordani</i> in Lake Chapala, Mexico (1998-1999)	83
Figure 40. Dietary composition of <i>Chirostoma labarcae</i> in Lake Chapala, Mexico (1998-1999)	92

Figure 41. Dietary composition of <i>Chirostoma lucius</i> in Lake Chapala, Mexico (1998-1999)	92
Figure 42. Dietary composition of <i>Chirostoma promelas</i> in Lake Chapala, Mexico (1998-1999)	93
Figure 43. Dietary composition of <i>Chirostoma sphyraena</i> in Lake Chapala, Mexico (1998-1999)	98
Figure 44. Parametric scattergram of the diet of from the genus <i>Chirostoma</i> at Lake Chapala, Mexico, during 1998-1999.....	103
Figure 45. Parametric scattergram of the diet of from the genus <i>Chirostoma</i> at the Ajijic sampling station	105
Figure 46. Parametric scattergram of the diet of from the genus <i>Chirostoma</i> at the Chapala sampling station	105
Figure 47. Parametric scattergram of the diet of from the genus <i>Chirostoma</i> at the Jocotepec sampling station.....	106
Figure 48. Parametric scattergram of the diet of from the genus <i>Chirostoma</i> at the Mezcala sampling station	106
Figure 49. Parametric scattergram of the diet of from the genus <i>Chirostoma</i> at the Ocatlan sampling station	107
Figure 50. Parametric scattergram of the diet of from the genus <i>Chirostoma</i> during the March seasonal sampling.....	107
Figure 51. Parametric scattergram of the diet of from the genus <i>Chirostoma</i> during the July-August seasonal sampling	108
Figure 52. Parametric scattergram of the diet of from the genus <i>Chirostoma</i> during the December seasonal sampling.....	108
Figure 53. Composition of the four most significant food items that distinguish among diets of the Lake Chapala chirostomid species flock (1998-1999).....	113
Figure 54. A plot of the distributions of nine chirostomid species in Lake Chapala 1998-1999 show a two-tiered distribution.	116

LIST OF TABLES

Table 1.	Dietary components of <i>Chirostoma</i> species occurring in Lake Chapala, Mexico,, during 1998-1999. Parentheses indicate abbreviations used in Figures 35-44.	27
Table 2.	Species of <i>Chirostoma</i> occurring in Lake Chapala, Mexico,, during 1998-1999.....	34
Table 3.	Total catch of nine species of <i>Chirostoma</i> occurring in Lake Chapala, Mexico,, during 1998-1999 at five sampling stations	35
Table 4.	Seasonal catch of nine species of <i>Chirostoma</i> occurring in Lake Chapala, Mexico,, during 1998-1999	63
Table 5.	Total catch of nine species of <i>Chirostoma</i> occurring at the Ajijic sampling site at Lake Chapala during 1998-1999	65
Table 6.	Total catch of nine species of <i>Chirostoma</i> occurring at the Chapala sampling site at Lake Chapala during 1998-1999	66
Table 7.	Total catch of nine species of <i>Chirostoma</i> occurring at the Jocotepec sampling site at Lake Chapala during 1998-1999.....	67
Table 8.	Total catch of nine species of <i>Chirostoma</i> occurring at the Mezcala sampling site at Lake Chapala during 1998-1999	68
Table 9.	Total catch of nine species of <i>Chirostoma</i> occurring at the Ocatlan sampling site at Lake Chapala during 1998-1999	69
Table 10.	Relative catch of nine species of <i>Chirostoma</i> occurring at five stations in Lake Chapala, Mexico, during 1998-1999	73
Table 11.	Seasonal relative catch of nine species of <i>Chirostoma</i> occurring in Lake Chapala, Mexico, during 1998-1999	74
Table 12.	Dietary composition of <i>Chirostoma aculeatum</i> at five sampling stations in Lake Chapala, Mexico, (1998-1999)	76
Table 13.	Seasonal dietary composition of <i>Chirostoma aculeatum</i> in Lake Chapala, Mexico, (1998-1999)	77

Table 14. Dietary composition of <i>Chirostoma arge</i> at five sampling stations in Lake Chapala, Mexico, (1998-1999).....	79
Table 15. Seasonal dietary composition of <i>Chirostoma arge</i> in Lake Chapala, Mexico, (1998-1999)	80
Table 16. Dietary composition of <i>Chirostoma chapalae</i> at five sampling stations in Lake Chapala, Mexico, (1998-1999).....	84
Table 17. Seasonal dietary composition of <i>Chirostoma chapalae</i> in Lake Chapala, Mexico, (1998-1999)	85
Table 18. Dietary composition of <i>Chirostoma consocium</i> at five sampling stations in Lake Chapala, Mexico, (1998-1999)	86
Table 19. Seasonal dietary composition of <i>Chirostoma consocium</i> in Lake Chapala, Mexico, (1998-1999)	87
Table 20. Dietary composition of <i>Chirostoma jordani</i> at five sampling stations in Lake Chapala, Mexico, (1998-1999).....	88
Table 21. Seasonal dietary composition of <i>Chirostoma jordani</i> in Lake Chapala, Mexico, (1998-1999)	89
Table 22. Dietary composition of <i>Chirostoma labarcae</i> at five sampling stations in Lake Chapala, Mexico, (1998-1999).....	90
Table 23. Seasonal dietary composition of <i>Chirostoma labarcae</i> in Lake Chapala, Mexico, (1998-1999)	91
Table 24. Dietary composition of <i>Chirostoma lucius</i> at five sampling stations in Lake Chapala, Mexico, (1998-1999).....	94
Table 25. Seasonal dietary composition of <i>Chirostoma lucius</i> in Lake Chapala, Mexico, (1998-1999)	95
Table 26. Dietary composition of <i>Chirostoma promelas</i> at five sampling stations in Lake Chapala, Mexico, (1998-1999).....	96
Table 27. Seasonal dietary composition of <i>Chirostoma promelas</i> in Lake Chapala, Mexico, (1998-1999)	97
Table 28. Dietary composition of <i>Chirostoma sphyraena</i> at five sampling stations in Lake Chapala, Mexico, (1998-1999).....	99

Table 29. Seasonal dietary composition of <i>Chirostoma sphyraena</i> in Lake Chapala, Mexico, (1998-1999)	100
Table 30. Nonparametric discriminant analysis provides the Wilkes Lambda, a descriptive statistic which indicates differences in groups if significant. The probability that group separation is significant is indicated if the Wilkes Lambda is greater than the a priori probability, in this case 0.0001. All cases were found to indicate significant differences.	104
Table 31. The MANOVA results showing Wilkes' Lambda values, significant dietary variables and power metric (Kruskal-Wallis Chi-square) are shown. The Kruskal-Wallis result indicates a non-linear power of significance for each dietary variable.	111
Table 32. Descriptive discriminant analysis results indicate the five most significant dietary variables among the diets of the nine sympatric <i>Chirostoma</i> species at Lake Chapala, Mexico, during the 1998-1999 sampling period.	112

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CHAPTER ONE

Introduction

Trophic Resource Partitioning Among Nine Sympatric Congeners in an Ancient Tropical Lake

Nine fish species of genus *Chirostoma* live sympatrically in Lake Chapala, Jalisco, Mexico. Their morphologies and distributions are so similar that they can only be distinguished with magnified examination. Lake Chapala is an ancient lake, and these nine congeners have successfully maintained their species distinction and diversity despite living in a seemingly homogenous environment. Lake Chapala is a remarkably homogenous lake lacking the microenvironments and habitats that one might expect for such a large tropical lake. Habitat diversity is low, yet the lake supports a diversity of nine congeners of *Chirostoma* (Figure 1) living sympatrically and having similar feeding and spawning habits. If their niches extensively overlap, as they apparently do (all species consumed all food items), then why don't the stronger competitive species eliminate the weaker ones? How can such a homogenous environment support nine similar congeners when it is widely accepted that heterogenous environments are required for higher diversities (Zong-Ling et al. 2005)?

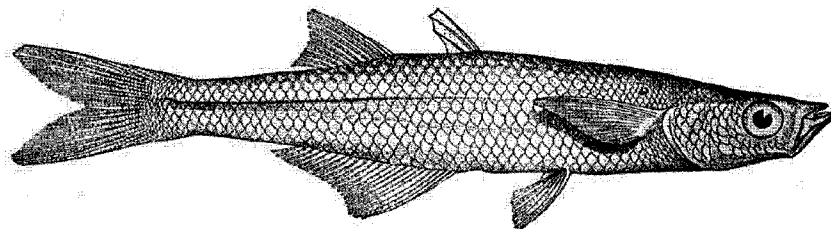


Figure 1. *Chirostoma chapalae* shown above is a member of the Lake Chapala chirostomid species flock (Graphic used with permission from the California Academy of Science).

Popular literature indicates that Lake Chapala was a portion of a larger “inland sea” in pre-Tertiary times. Lake Chapala likely was a member of several interconnected lakes which may have covered a significant portion of western Mexico. Additionally, Barbour (1973) stated that terraces along the banks of Lake Chapala are evidence of subsequent uplift activity. The current landscape was likely shaped by mid-Tertiary and Plio-Pleistocene volcanic activity and by uplifts during the mid-Pleistocene. As a result, historic drainage patterns of the region have continuously changed. The Rio Lerma once flowed to the west through a series of lakes, eventually flowing into the Pacific Ocean. Barbour (1973) stated that the mid-Pleistocene uplifts likely compartmentalized this flow pattern. Lake Chapala was along this path and received water from the Rio Lerma on the eastern end of the lake and lost water via a historical water outflow at the western end of the lake. At some point, uplifts prevented outflow of water in Lake Chapala from the western end of the lake and shifted it to the eastern end via the Rio Santiago.

Geological activities have shaped Lake Chapala and the entire basin and played a role in the development of fish community structure. The presence of a historic inland sea allowed for extensive distribution of species throughout the Mesa Central of Mexico. A subsequent recession of water via uplifts and volcanic activity landlocked these species. This geographical isolation resulted in allopatric speciation. Fossil evidence indicates that chirostomid species were likely descendants from a common *Menidia* and/or *Melaniris* ancestor. This research assumed that the age of this lake has provided ample time for speciation and establishment of niche partitions via competition. For the nine chirostomid species, the separation of niches, the reproductive isolation of species,

and the relationship of morphology to niche parameters should be well defined and stable.

This research identifies and examines factors or combinations of factors that keep these nine species reproductively isolated. If higher diversity triggers competition and partitioning of resources (de Merona and Rankin-de Merona, 2002), how do these species maintain their integrities? Previous research indicates that a variety of environmental factors often separate niches of sympatric animal species including those factors that partition resources. Major resources include food (diet), space (habitat), and time (life history pattern). However, in Lake Chapala space is not radically partitioned and the fish species intermingle in a remarkably homogenous habitat. Also, the lack of distinct winter-summer seasons in tropical environments potentially reduces the impact of temporal partitioning, i.e. spawning patterns are more diffuse. Thus, food is a likely resource that chirostomid species partition rigidly enough to maintain the integrity of nine different niches. Piet et al. (1999) stated that resource partitioning along trophic lines in fish more often contributed to coexistence than do spatial or temporal factors.

My approach to reconcile the diversity of chirostomids with the homogeneity of the habitat was to study details of the fishes' morphology, distributions and diets and to elucidate the variables of niche separation among species or groups of species. I examined morphology for factors potentially associated with diet partitioning and maintenance of species integrity in this homogenous, ancient, tropical lake. My research effort concentrated on dietary partitioning as the major focus of niche integrity.

Competition

When two or more species require a common resource that is insufficient to meet the needs of both, competition occurs and reduces the fitness of at least one of the species

(Pianka, 1983). The ultimate result of competition is the local extinction of the lesser species (Chan and Franke, 2004). Such competitors may be the same species (intraspecific competition) or different species (interspecific competition). Although intraspecific competition can affect an individual's success in acquiring a resource, interspecific competition has traditionally received more attention because it provides insight into the coexistence and persistence of species diversity in a biotic community. Typically, individuals compete for food, habitat and refugia.

When many species coexist in an ecological system, each species may exploit a common resource by slightly different means (MacArthur, 1958; Shoener, 1974; Gladfelter and Johnson, 1983; Yuma et al. 1998; Molles, 2000). Each coexisting species usually follows distinctive spatial (Prochazka, 1998; Richards et al. 2000), temporal (Alanara et al. 2001; Loladze et al. 2004), and trophic patterns (Chase et al. 2002; Zekeria et al. 2002). For example, animals in a common range may forage in different areas, feed at different times during the day (Giroux et al. 2000), or use different size classes of prey. Such resource partitioning may facilitate the coexistence of two or more species by dampening competition for a shared resource in their community; the more limited the resource, the sharper the partitioning.

Sympatric fish species often partition resources based on food availability (Chase et al. 2002), dietary preferences, spatial patterns (Denoel and Joly, 2001), temporal patterns (Iribarne et al. 2003) and patterns of ontogeny (Sibbing et al. 1998) and morphology (Knouft, 2003). Centrarchidae (sunfish) often partition resources. Frequently as many as eight species of sunfish coexist within a lake or river in North America. Most sunfish are similar morphologically and behaviorally. How then do they coexist without reducing their diversity through competition for resources?

One well-known study of competition involved the sunfish genus *Lepomis* (Baldigo, 1982). When stocked separately in ponds as yearlings, three sunfish species -- bluegill (*L. macrochirus*), green sunfish (*L. cyanellus*), and pumpkinseeds (*L. gibbosus*) -- used similar habitats and had a similar diet of invertebrates associated with aquatic macrophytes. When stocked together, bluegill and pumpkinseeds shifted their diets away from that of the more aggressive and competitively superior green sunfish. Bluegills shifted toward planktonic prey while pumpkinseeds shifted to benthic invertebrates. However, all three species responded to competition with reduced growth rates, indicating that competition reduced resources for each species.

Competition and Resource Partitioning

The claim that competition underlies resource partitioning is typically supported by the observation that some species narrow or widen their use along a resource gradient, such as available food, when another species is added or removed, respectively. Such resource partitioning is illustrated with the classic three-species model. Species A has a wide dietary breadth to exploit a wide range of food in the absence of competitors (Figure 2). When species B is first introduced, its diet may competitively overlap that of species A. Over time, selective pressures from interspecific competition will force species A and B to partition the resource, narrow their dietary breadth (Figure 3), and cause diets to diverge. This adjustment can be an evolutionary one occurring over many generations or a behavioral one in the current generation. The addition of species C will further narrow the dietary breadth of the other species as they compete for the common resource (Figure 4). Interspecific competition will either cause subsequent sympatric competitors to subdivide (partition) the resource(s) or may competitively exclude and eliminate a species.

Competitive Exclusion

Gauss (1934) stated that two or more species with similar ecological requirements can not live in the same place at the same time. He stated “as a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain peculiar kinds of food and modes of life in which it has

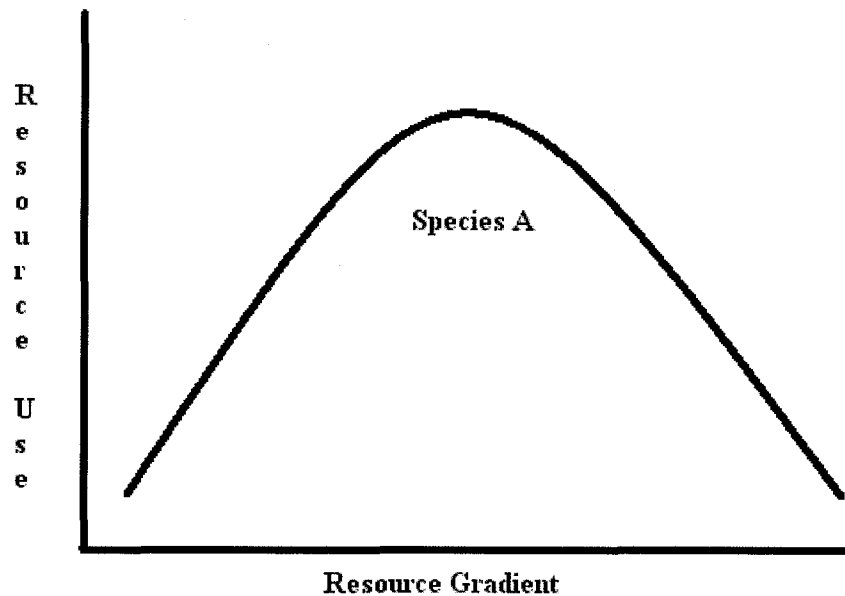


Figure 2. The hypothetical dietary niche breadth of a species in the absence of predators.

an advantage over its competitor.” This competitive exclusion principle states that no two (or more) species with similar ecological requirements can coexist in the same community since one species will more efficiently harvest resources and reproduce, leading to the local extinction of the other species. Kelt et al. (1995) found that the success of a species in a functional group also strongly decreased the likelihood of entry or success of another species into the same functional group.

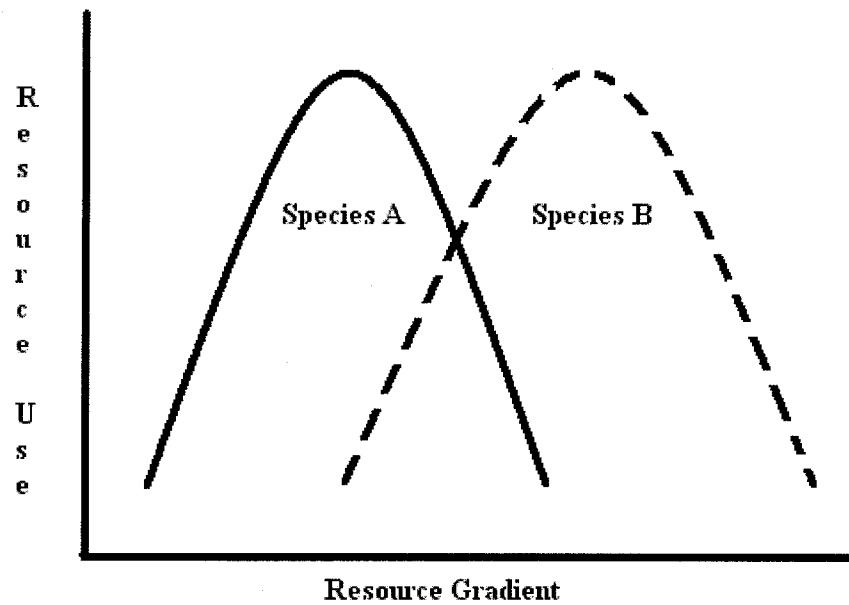


Figure 3. The addition of a second species into a system causes both species to narrow their dietary breadth.

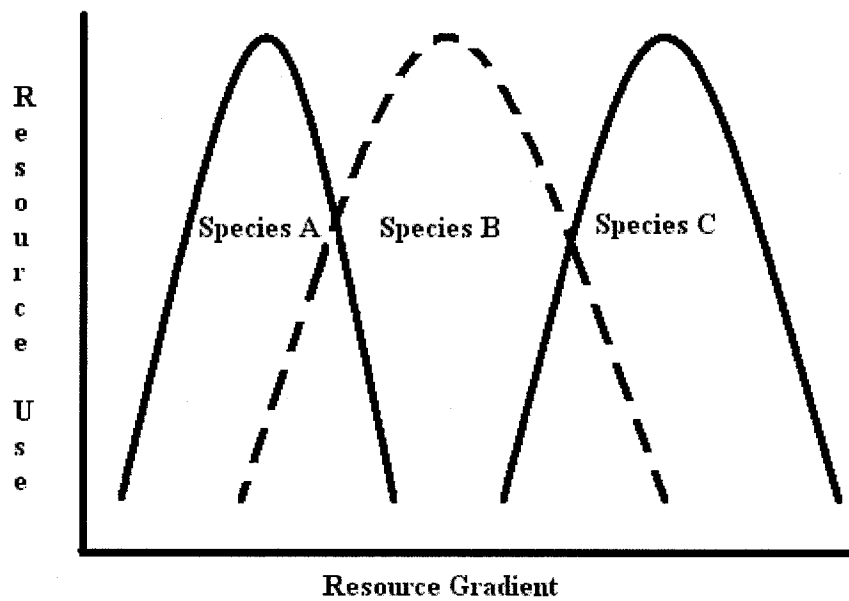


Figure 4. The addition of a third species results in competition for a common resource and a narrowing of niche breadth.

If ecologically similar species cannot coexist in the same niche per Gauss' widely accepted principle, then how different must two or more species be to coexist in the same habitat? How rigidly must sympatriates partition their resources? Do congeneric sympatriates partition resources even more rigidly? This fundamental question is inherent to investigations of resource partitioning and to this study.

Sympatriates versus Congeneric Sympatriates

Some ecologists currently argue that sympatric species of different genera are not necessarily relevant candidates for study of competition and resource partitioning. They contend that being sympatric does not constitute a significant sharing of the same resources. Sympatriates of multiple genera do not necessarily fit the Gaussian definition of ecological similarity. These ecologists argue that sympatric species do not fit the Gaussian principle because they do not have the exact same ecological requirements. These ecologists contend that the coexistence of two species (such as a largemouth bass and a bluegill) having such differing ecological requirements that they cannot be considered as ecologically similar even though they occupy the same apparent habitat. Strong (1980) adds that if competition for resources does occur, then its effects are so slight or inconsistent that it does not cause any noticeable ecological patterns. Reynolds (2002) suggests that such variability reduces competition to the point which makes exclusion unlikely.

Other ecologists argue that sympatric species by definition are ecologically similar and will compete for the same resources. These ecologists argue that competition for resources occurs and cannot be avoided since sympatriates occupy the same niche and utilize the resources inherent to that niche. Therefore, studies based on resource partitioning depend on an investigator's interpretation of ecological similarity among sympatric species.

I contend that congeneric sympatriates provide the most appropriate model for study of competition and satisfy the ambiguity of ecological similarity. Congeneric species are often assumed to be competitors due to their rigid taxonomic similarities and closely related behavior. Coexisting congeners have inspired research asking how they can coexist in the same apparent functional niche (Walsh and Fitzgerald, 1984; Lammens and Hoogenboezem, 1991; Encina and Granado-Lorencio, 1997). How do these congeners coexist in light of the Gaussian competitive exclusion principle? What separates their niches when morphology, behavior, and habitat are similar? The answer may lie in the partitioning of resources.

Sympatric species with similar needs, and congeners in particular, are widely assumed to be competitors. However, competition is clearly not the only factor that determines the structure of a community. Community structure is also influenced by resource availability (Chase et al. 2002; Huxel et al. 2002), biotic and abiotic interaction (Loladze et al. 2000; Muller et al. 2001; Nelson et al. 2001; Urabe et al. 2002, 2003), spatial (Richards et al. 2000; Denoel and Joly, 2001) and temporal patterns (Iribarne et al. 2003), patterns of ontogeny (Sibbing et al. 1998), morphological adaptations (Knouft, 2003) and the physical characteristics of the environment in which the organisms live (Holmgren and Appelberg, 2000; Litchman and Klausmeier, 2001). The overwhelming abundance of research on the coexistence of congeners, however, has focused on the partitioning of food resources.

Spatial and temporal partitioning plays a role in resource allocation. Fukushima and Smoker (1997) documented habitat segregation between sympatric pink and sockeye salmon based on niche breadth (depth, exposure to current) in an Alaskan stream. Sympatric populations of salmonids often follow a pattern of spawning habitat segregation in which one

species occupies more upstream reaches of a stream than the other species (Fukushima and Smoker, 1998). Spawning habitat segregation was observed among five sympatric salmonid congeners (*Oncorhynchus* sp.).

Morphology

Some studies of resource partitioning have found that variation in morphological adaptations is sufficient to separate some closely associated species. Futuyama (1986) stated that morphological features of coexisting animals often correlate with their available food and that differentiation of diet reduces competition among those animals with dietary overlap. Spencer (1995) added that differing foraging strategies necessarily implies morphological variation. Schoener (1974) adds that morphological differences in feeding apparatus suggest a functional relationship between use (function) and phenotype (structure), and that morphological differences correlate with resource partitioning behavior. Sibbing et al. (1998) and Sibbing and Nagelkerke (2001) made similar conclusions. Changes in morphometry related to ontogeny have also been performed to discriminate among species (Cadrin, 2000).

Morphological differences between species are often related to differences in resource use among coexisting species (Paine et al. 1982; Jakubowski 1996). Species of menhaden, for example, are similar in body size, external morphology, and are spatially and temporally sympatric. Castillo-Rivera et al. (1996) found that sympatric menhaden congeners partitioned resources based on differences in internal morphology.

Development

Competition among three species of *Lepomis* is more apparent in young fish and has an ontogenetic component (Baldigo, 1982). As fish age, they specialize more on different habitats. Older bluegill become adept at open water and suction feeding on zooplankton

while pumpkinseeds develop pharyngeal dentition to crush mollusks. Hence, competition is less among older fish under normal conditions (Werner and Hall 1979, Werner 1984, Mittelbach 1988, Osenberg et al. 1988, Wooten 1990).

Changes in resource use based on ontogeny are extremely common in fish (Labropoulou et al. 1999; Nemerson, 2001). Major ontogenetic shifts in fish feeding habits occur in many fish species (Livingston, 1982; Ross, 1986). Jepsen et al. (1997) reported that young-of-the-year piscivores shifted from invertebrate feeding to piscivory during spawning periods. Winemiller (1991) found a correlation between ontogenetic niche shifts and seasonality in the cichlid *Serranochromis* sp. of the Zambezi River and its floodplain.

Why Study Resource Partitioning in Lake Chapala?

Lake Chapala is an ideal site to study resource partitioning. Lake Chapala is unusually homogenous in depth, sediment type, and shoreline development which indicates that habitat differences are not solely responsible for the coexistence of the nine sympatric congeners of *Chirostoma*. Resource partitioning studies typically investigate habitat heterogeneity to explain the coexistence of sympatric species supported by niche separation. Due to a lack of habitat influence in Lake Chapala, other factors that support coexistence of nine congeneric fishes should be considered. Factors such as spatial and temporal phenomena, ontogeny, morphology, and diet may reveal answers to the paradox of high species diversity of congeners in a homogenous environment. These factors can be readily investigated at Lake Chapala.

Patterns of resource partitioning in which sympatric species use food items in different ways are well documented in fish. Studies of these animals are abundant because dietary partitioning is easier to detect in consumers, such as fish, that ingest food whole and have more easily identifiable gut contents (Allen 1995). For example, dietary overlap in nine

sympatric tropical piscivores was shown to be low during periods of falling water in Venezuelan creeks (Winemiller, 1989).

Lake Chapala, Jalisco, Mexico

Lake Chapala is the largest natural lake in Mexico and lies 42 km south of Guadalajara between 102° 42' 00" and 103° 25' 30" west longitude and 20° 6' 08" and 20° 18' 08" north latitude. Lake Chapala has a normal surface elevation of 1524 m above sea level. Most of the lake lies in the State of Jalisco with a small portion reaching into the State of Michoacan (Figure 5). The principal uses of the lake are irrigation, recreation, tourism, and fisheries as well as being the main water source of the Guadalajara metropolitan area (Limon et al. 1989) with an estimated population of nearly six million.

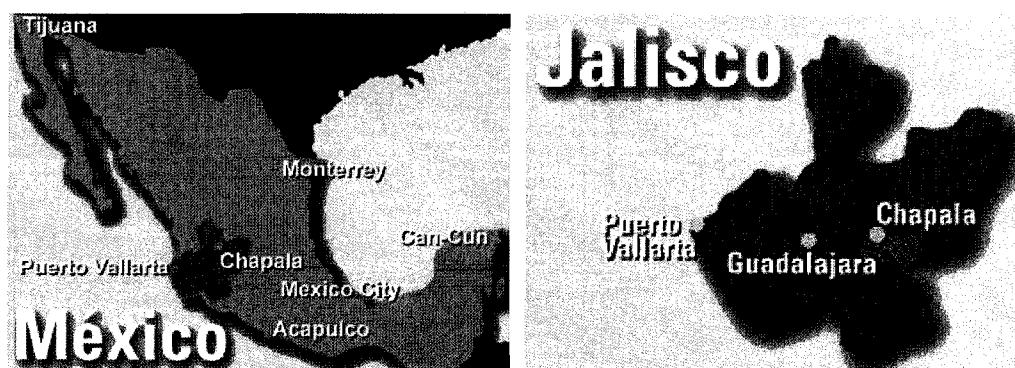


Figure 5. Lake Chapala (depicted in blue) is located primarily in the State of Jalisco (red) in Central Mexico.

Lake Chapala is a part of the Rio Lerma-Lake Chapala-Rio Santiago hydrological system and is an east-west oriented graben. The Rio Lerma is the primary water source for the lake. Outflow occurs to the Rio Santiago. However, evaporation (1900+ mm/year) annually removes almost three times the total annual rainfall (790 mm/year). To date, little information is known about the amount of outflow to groundwater sources (Davalos et al.

1989). Limon et al. (1989) described the physical and chemical limnology and hydrology of the lake.

Lake Chapala is an ideal system in which to study the coexistence of congeneric species. The lake contains an easily identifiable species list consisting of approximately 29 species of fish. Included in that list are nine sympatric species of *Chirostoma*. Lake Chapala is an ancient tropical lake and such lakes typically have high speciation. However, Lake Chapala has a relatively low diversity of fish species for a tropical lake, possibly due to its physical homogeneity.

A Review of Select Literature on Lake Chapala

Compared to more widely studied tropical lakes such as Lake Malawi, research on Lake Chapala has received significantly less attention and relatively few studies have been published. Research related to Lake Chapala in the past two decades has primarily been performed by a small but dedicated number of biologists. Past and present research efforts have investigated the limnology of the lake, productivity rates, physical and chemical issues, water quality issues and others. Fisheries studies have been limited. Current research has evolved towards a more holistic point of view due to a variety of factors including but not limited to water quality degradation, water quantity declines, cultural and social effects of a declining lake and other related topics.

Much of the seminal work performed at Lake Chapala was undertaken by two Baylor University biologists, Dr. Owen Lind and Laura Davalos-Lind. Their work has described the limnology of the lake (Davalos-Lind and Lind, 1993; Lind and Davalos-Lind, 2001; Lind, 2003), issues related to various aspects of productivity (Davalos et al. 1989; Lind and Davalos-Lind, 1991; Lind et al. 1992; Davalos-Lind, 1996; Lind et al. 1996; Lind et al. 1997; Davalos-Lind and Lind, 2001), the interaction of water quality and water quantity (Lind and

Davalos-Lind, 2002), the failure of fisheries models due to turbidity (Lind et al. 1994) and the movement of metals through the lake's food web (Lind et al. 2000). Additionally, they have coauthored numerous other studies and continue to investigate the dynamics and processes of Lake Chapala.

Comprehensive studies on Lake Chapala's limnology (Limon et al. 1989; de Anda et al. 2001), management (Limon et al. 1990), hydrology (de Anda et al. 1998), productivity (Hernandez-Aviles et al. 2001; Bernal-Brooks et al. 2002), biotic integrity (Lyons et al. 1995; Lyons et al. 2000; Moncayo-Estrada and Buelna-Osben, 2001), and trace metal pathways (Ford and Ryan, 1995; Hansen & Maya, 1997; Shine et al. 1998; Ford et al. 2000; Hansen & van Afferden, 2004) have contributed to the base of knowledge on the processes of the lake. Other studies such as those investigating declining fish yields (Lyons et al. 1998), water quality and quantity concerns (Fernex et al. 2001; van Afferden & Hansen, 2004), parasitology (Martinez-Aquino et al. 2004), weather effects (Filinov & Tereshchenko, 1999; Filinov, 2002; Tereshchenko et al. 2002) are available in peer reviewed literature. Holistic management studies which integrate social, cultural and ecological process (Mestre and Eduardo, 1997; Hansen and van Afferden, 2001) are becoming popular as well.

Why use Chirostomid Species as a Research Model?

The chirostomid species flock at Lake Chapala consists of nine sympatric congeners. It is rare to find this situation in natural environments because competitive interactions in long term populations of ecologically similar species usually lowers diversity. This species flock comprises the most important commercial fishery in the lake and is the primary food source of thousands of regional citizens (Figure 6).

Lake Chapala chirostomids were relatively easy to collect across the lake and taxonomic keys to the identification of the species were available. The nine congeneric

species of chirostomids were the most diverse of any genus in the lake. Additionally, it was more feasible to perform stomach content analysis on the larger chirostomids than that of the physically smaller species, such as Lake Chapala's goodeid or poeciliid fishes which also had less speciation. Economic importance, ease of capture, identification and stomach content analysis combined with the unusually high number of species make the chirostomid species flock an ideal set of study organisms.



Figure 6. Chirostomid fishes available for sale in the City of Chapala downtown market.

A Review of Select Literature for Chirostomid Fishes

Little information is available on the biology of chirostomid fishes in general and the chirostomid species flock at Lake Chapala in particular. Available related primary literature is typically restricted to the chirostomids of Lake Patzcuaro, an important but overexploited central mesa Mexican lake. Some of the most accurate and representative information available on chirostomid behavior at Lake Chapala was obtained from local fishermen.

More studies on *Chirostoma* species in Mexican lakes and streams have been performed than in Lake Chapala. Few studies however are related to those species that

are found in Lake Chapala. Studies related to development (Aguilar and Navarette, 1997; Reygadas, 1998; Martinez-Palacios et al. 2002; Blancas-Arroyo et al. 2004; Figueroa-Lucero et al. 2004; Martinez-Palacios et al. 2004; Morales-Ventura et al. 2004), parasitology (Cochran et al. 1996; Espinosa-Huerta, 1996; Guzman-Cornejo and Garcia-Prieto, 1999; Choudhury and Dick, 2000; de Leon et al. 2000; Moravec et al. 2000; Aguillar-Aguillar and Salgado-Maldonado, 2001; Choudhury, 2001; Salgado-Maldonado et al. 2001), food preference (Navarette et al. 1996), the role of chirostomid fishes in the calculation of biotic integrity (Lyons et. al., 2000) *Chirostoma* and ecosystem condition (Soto-Galera, 1999), diversity (Robles et al. 1997), fisheries management of regional lakes (Orbe-Mendoza et al. 2002), *Chirostoma* as a food choice of top vertebrate predators (Macias Garcia and Drummond, 1990), and genetics (Barriga-Sosa and Arredondo-Figueroa, 2000; Barriga-Sosa, 2002; Uribe-Alcocer et al. 2002; Barriga-Sosa et al. 2004) have been performed. The majority of available information on Lake Chapala chirostomids is found in gray literature or is passed on by word of mouth. Little information is available on the development, biology or ecology of Lake Chapala chirostomid fishes. One exception is the recent modeling study detailing the atherinid and goodeid spatial densities in Lake Chapala (Becerra-Munoz et al. 2003).

Questions of Formal Research

How do nine species of *Chirostoma* maintain their species integrity in Lake Chapala? The habitat of Lake Chapala is unusually homogenous. The lake banks and floor are comprised mainly of volcanic based ash and sand. A relatively small depth gradient of 0 to 6 meters occurs along the longest fetch (77 km). The waters surrounding two centralized islands (Scorpion Island and Mezcala Island) are used by all nine species during spawning

periods. No other apparent physical variation exists with enough variation to partition the nine chirostomid species. In this unusually homogenous lake, how then do these nine congeneric species maintain their integrities? To answer this broader question, the following specific research questions were investigated.

1. Do individual morphological characters correlate with dietary composition?

Individual morphological characters can play a role in the partitioning of trophic resources in fish communities (Sibbing and Nagelkerke , 2001; Knouft, 2003).

Morphological characteristics such as gape, mouth size, eye size and others are commonly investigated as a means to discern resource use in competition studies.

Morphological characteristics were compared to dietary data to investigate whether correlations occur between the two.

2. What are the relative abundances of the nine chirostomid species at Lake Chapala?

Little information is available on the relative abundance and distribution of chirostomid species at Lake Chapala. Relative catch data was tabulated based on the consistent catch effort for each sampling area. Inferences related to species distribution can be based on this data.

3. Do species distribute themselves along a West-East gradient along the longitudinal axis of Lake Chapala?

Three apparent depth zones occur in Lake Chapala. The main body of the lake is shallow with a mean depth of 3-4 meters (Figure 7). The maximum depth occurs in the central and eastern part of the lake. Preliminary sampling has shown that two of the nine *Chirostoma* species (*C. lucius* and *C. aculeatum*) occur in higher abundance in the deeper areas. These two are the largest of the chirostomid species. The other depth zone occurs near the inflow of the Rio Lerma and outflow of the Rio Santiago.

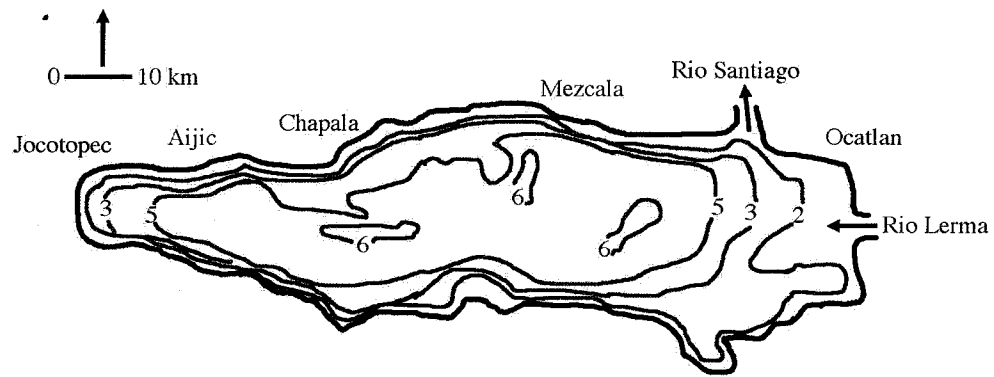


Figure 7. Bathymetric map of Lake Chapala during 1998-1999. Depth is in meters.

4. Do changes in diet related to ontogeny partition resources enough to maintain the integrity of nine species of *Chirostoma*?

Ontogenetic dietary shifts within a species and among species may explain the coexistence of juveniles and adults. No apparent differences in diet occur among the chirostomid congeners as juveniles. Preliminary data revealed that young-of-the-year and fry of all nine species share a common diet during the first several months of life. At this age, all species of chirostomids ate primarily small invertebrates and small amounts of algae, especially diatoms. At some point after the first several months of life, *Chirostoma* juveniles diverge in dietary preferences. Preliminary studies have indicated that diets diverged during the sub-adult and adult phases.

5. Do female chirostomids consume significantly more prey than males during periods before and during spawn?

A sexual partitioning of resources may exist in the chirostomid species. Preliminary data suggested that males consumed less prey than females during periods preceding spawn. This may allow for sexual partitioning to increase competitive success for gravid females during periods of lower prey abundance.

6. Does variation in dietary composition separate the species?

The lack of significant microhabitats and apparent temporal trends due to tropical influences mandate that dietary differences be investigated to determine whether differences in diet could be wholly responsible for the maintenance of species integrities. Food item differences may be the sole resource that chirostomid species partition rigidly enough to maintain the integrity of nine different niches.

CHAPTER TWO

Methods and Materials

Sampling Areas

Lake Chapala was divided into five sampling areas along the east-west gradient and parallel to the northern shoreline. Sampling areas were established near the cities of Jocotepec, Ajijic, Chapala, Mezcala, and Ocatlan (Figure 8). Although Lake Chapala was unusually homogenous, these areas represented the entirety of the lake and areas of major depth variation within the lake. In each sampling area, shoreline samples were taken using seine nets within 50 m of the shoreline. Pelagic (open water) samples were taken in open water >100 m from shore. Pelagic samples for the Mezcala area were taken closer to shore due to regulations for no fishing near Mezcala Island. The shoreline and pelagic catches for a sampling area were combined.

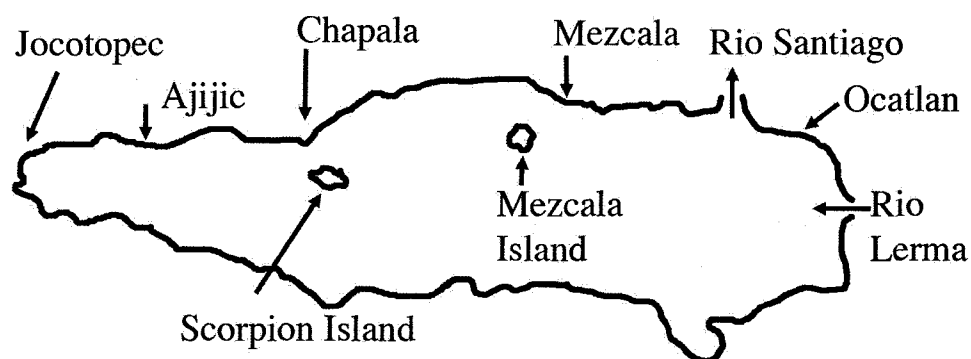


Figure 8. Lake Chapala sampling areas shown from west (Jocotepec) to east (Ocatlan).

The Jocotepec sampling area was on the westernmost end of Lake Chapala and was the shallowest area in the lake during the study. The Jocotepec area was characterized by muddy beaches and a depth of less than one meter. High turbidities occurred at this area due to normal suspended volcanic sediment (ash) and combined organic bacterial aggregates (COBA) as described in Lind and Davalos-Lind (2001) and moderate to heavy outflows from municipal discharges by the city of Jocotepec. Little vegetation occurred at this area during the study.

The Ajijic sampling area was similarly shallow with depths ranging from 0-1.5 m. The Ajijic area had readily accessible beach areas and open water and did not appear to be influenced by municipal discharges. Little vegetation occurred at the Ajijic area during this study.

The Chapala area provided easy access to sandy ash beaches and open waters. Scorpion Island was southeast of the city of Chapala (Figure 8). Water depths in the sampling areas ranged from 0-2.4 m. Higher turbidities likely influenced by heavy municipal discharges were noted at the Chapala area. Vegetation was moderate at the Chapala area and included perennial beds of water hyacinth (*Eichornia crassipes*) and *Potamogeton* spp. Commercial fisheries placed high numbers of gill nets in the waters around Chapala which made open water sampling difficult.

The Mezcala sampling area was characterized by rocky shoreline access, steep slopes, moderate depths of 0.5-3.6 m, and significant commercial fishing. Mezcala Island was located approximately one kilometer southwest of the Mezcala sampling area. The main water intake for the Guadalajara metropolitan district was near the Mezcala

sampling area. Vegetation was moderate and included *Eichornia crassipes*, especially in open water.

The Ocatlan sampling area was at the easternmost end of the lake and was the deepest sampling area in Lake Chapala. Beach access was difficult due to extensive muddy areas of deep sediment created by the riverine inflow of the Rio Lerma and outflow to the Rio Santiago. The water was normally turbid and depth was 0.6-6 m during the study period. Significant commercial fishing made open water sampling difficult at Ocatlan. Vegetation included permanent bankside mats of *Eichornia crassipes* and frequently dense mats of *Eichornia crassipes* in open water.

Seasonal Sampling

Three seasons were identified during preliminary sampling efforts. Lake Chapala's climate can be best divided into a rainy season (June-August) and a dry season (September-May) which included a cool dry season (November-January). These seasons correlated to spawning habits as well as weather conditions.

March samples taken during the mid-dry season coincided with the pre-spawn of chirostomid fishes. The nine chirostomid species at Lake Chapala begin to spawn in late April according to local fishermen.

Combined samples from July and August were taken during the active spawn. Most adult chirostomid fishes migrated to spawn in waters offshore from Scorpion Island or Mezcala Island (Moncayo-Estrada and Buelna-Osben, 2001). Local fishing regulations prohibited sampling chirostomid fishes offshore from the islands to help preserve the chirostomid fishery. Young-of-the-year and fry occurred in tremendous numbers during this season. First-year fingerlings were common in shoreline samples.

This sampling season was during the rainy season, although rains were below average during this two-year study.

December samples included the post-spawn of chirostomid development when the young-of-the-year likely become adults. This season was cool and the rainfall was low. No rains were noted during December samples in either 1998 or 1999.

Field Collection Techniques

Representative samples of fish were collected from Lake Chapala with seines and gill nets from the five sampling areas established along the banks of the lake and with boat trawls and gill nets at pelagic (open water) stations. Shoreline samples were taken with a 10 m x 1.3 m bag seine. The bag measured 1.3 m x 1.3 m and had a standard #30 (0.635 cm) mesh. Seine hauls were taken as described by Nielsen and Johnson (1992). Boat trawls were taken in pelagic areas >100 m from the shoreline. Local fishermen were enlisted to provide boats and nets. When depth inhibited boat trawls, gill nets provided by local fishermen were used for open water samples. Three to five one-minute trawls were taken to gather a representative pelagic sample from the area. The trawl net used was a standard hoop net with a 1-m diameter gape and a #30 mesh. Standard #30 mesh gill nets were used in pelagic areas when needed. Shoreline and pelagic samples were combined at each area.

All chirostomid fishes collected were counted in the field. Non-chirostomid fishes were released except for a few voucher specimens. Chirostomids were preserved in the field with buffered 30% formalin for later examination. Preserved specimens were returned to the Lago de Chapala Ecological Station (CES) laboratory, washed and stored in buffered isopropanol. CES is co-sponsored by the Universidad Autonoma de

Guadalajara and Baylor University. Those specimens not examined in the laboratory in Mexico were not washed and stored in alcohol. They remained in formalin and were transported back to Waco, Texas and examined at Baylor University. Voucher specimens were selected and stored at Baylor University. Voucher specimens have been offered to the Mayborn Museum at Baylor University and the University of Texas fish collection under the direction of Dr. Clark Hubbs.

Qualitative samples of prey were taken concurrently with the fish sampling and were examined to aid the identification of gut contents. Plankton tows were collected in the seine and trawl areas to obtain a qualitative sample of potential prey available to the fish. Plankton net contents were pooled and condensed in a #10 Wisconsin bucket and then preserved in 10% buffered ethanol. Three benthic dredge samples per area were also taken, and the sieved contents were pooled and preserved in ethanol.

Laboratory Techniques

The chirostomid individuals were identified in the lab. Identifications followed Barbour's (1973b) seminal taxonomic key to the species of *Chirostoma* and *Melaniris*. From each sampling effort at least 100 individuals of each species were randomly selected from the total catch of that species for analysis. If less than 100 individuals of a species were captured during a sampling effort, then all individuals were used for further analysis. After the identifications of the selected individuals were confirmed each fish was assigned a unique identification number for its catch location, season, year, and collector. A data analysis sheet was then made which included the fish identification number and areas for entry of subsequent morphological and dietary data.

Twenty four standard morphological and meristic measures were recorded for the sampled chirostomid fishes. Barbour (1973a) stated that individual characters that effectively separated species of chirostomid fishes are rare and found little utility in using them to differentiate between the species groups. However, Barbour noted that several meristic and morphological characters, used in concert, accurately distinguished among the species. Those characters included head length, mandibular length, dorsal fin insertion, anal fin height, median lateral scales, predorsal scales, interdorsal scales, pectoral fin rays, anal fin rays, gill rakers, and number of vertebrae.

Along with gender, 24 meristic and morphological characteristics were measured for each individual in the analytical sample. Measures and counts were performed in accordance with Hubbs and Lagler (1958) or when appropriate, with Barbour (1973). Barbour modified several characters in his redefinition of the genus. The number of median lateral line scales was modified to include the number of scales between the scapular arch to the end of the hypural plate. Predorsal scales were modified to include scales occurring on a line between the first dorsal fin and the head, inclusive of the large head/nape scale. Scales were only counted when the scale intersected the line between noted features by 50% of the scale width. Interdorsal scales included those scales between the first dorsal fin membrane and the origin of the second dorsal fin.

The characteristics included total length, standard length, snout length, head length, body depth, pelvic fin insertion, dorsal fin insertion, anal fin height, anal fin insertion, number of scales superior to the lateral line, number of median lateral line scales, number of predorsal scales, number of interdorsal scales, scale type, lateral line type, number of anal fin rays, number of pectoral fin rays, caudal peduncle length, eye

size, mouth width, mouth height, mouth (mandible) length, number of gill rakers and the number of vertebrae. Each characteristic was measured and recorded on the laboratory data sheet bearing the identification number of the individual fish. All data were then entered into an Excel spreadsheet and converted into Fortran and SAS eligible files for later statistical analyses.

After species identification and morphological examination, the entire digestive system (mouth to anus) was removed from each of the sub-sampled (≤ 100) of fish for each species. The gut contents were collected, and estimates of gut fullness were made for each fish and recorded. Digestive tracts and their contents were stored in labeled vials with 10% formalin until analyzed.

Most guts contained readily identifiable food items. Food item identification was sometimes problematic because of digestion, but resolution to taxonomic order or family was usually possible. If dismembered prey were encountered, only identifiable head capsules were recorded to avoid repetition of counts. The nine species of chirostomids in Lake Chapala consumed a diet categorized into twelve food choices (Table 1). Dietary percentages were recorded on the fish identification sheet. Qualitative samples of plankton and benthos taken during the sampling regime aided the identification of damaged organisms. Gut content data were entered into an Excel spreadsheet and converted into Fortran and SAS eligible files for later statistical analyses.

Table 1. Dietary components of *Chirostoma* species occurring in Lake Chapala, Mexico, during 1998-1999. Parentheses indicate abbreviations used in Figures 35-44.

Dietary Components		
Organic Matter (organic)	Crustaceans (Crust)	Ostracods (Ostra)
Vegetation (Veg)	Algae (Algae)	Copepods (Cops)
Chironomids (Chiro)	Amphipods (Amphi)	Rotifers (Rotif)
Fish (Fish)	Cladocerans (Clado)	Oligochaetes (Oligo)

Statistical Analyses

Morphological Analyses

Spearman's Rank Order Correlation. Spearman's rank order correlation coefficients were calculated to determine whether individual morphological characters correlated to dietary preferences. Of all the statistical analyses available based on ranks, the Spearman rank order correlation continues to be the most commonly used ranking statistic (Siegel and Castellan, 1988; Ott, 1993; Blest, 2000; McQueen et al., 2005). The Spearman's rank coefficient, r_s , compares two independent random variables (continuous or discrete) and measures association between the two variables. The statistic requires that both variables be measured in ordinal scale to ensure that the study parameters are ranked in two ordered series. This analytical method uses ranked data rather than actual data. Spearman's rank coefficient (r_s) values near one indicate strong correlation whereas a value near zero indicates poor correlation (Figure 9).

The Spearman Rank Order Coefficient was calculated based on the following Formula:

$$r_s = 1 - \frac{6\sum d^2}{N^3 - N}$$

The calculation of r_s is achieved by compiling a list of observations from two variables. A ranking is assigned to each X and Y variable. Ranks are assigned to each set of variables from 1 to N , where N is the number of observations. In the event of ties, ranks were averaged. The values of d^2 were calculated by determining the difference between the X and Y rankings for the i^{th} observation and squaring the value.

The Spearman correlation statistic was generated based on several variable combinations and were evaluated for instances of correlation between individual morphological characters and dietary compositions. Because nine variables were used in the Spearman's calculations, correlations were considered to be significant at the 0.05% level if the r_s value was 0.65 or greater. This significance level was calculated by plotting the Spearman's rank correlation coefficient versus the degrees of freedom and then identifying the intersection between the two variables (Altman, 1991). Microsoft Excel (2002) was used to calculate all Spearman's rank order correlation coefficients.

Discriminant Function Analysis and Morphology. Discriminant function analyses (DFA) were performed on the morphological data to validate species identifications, detect morphological variation from historical data and to set up the programming files for more complex dietary analyses.

DFA is widely used to analyze fish morphometric variation (Villaluz and MacCrimmon 1988, Humphries 1990, Douglas and Matthews 1992, Humphries 1993, Labropoulou and Eleftheriou 1997). DFA compared two or more groups (fish species)

using several variables simultaneously. DFA transformed measured variables into a set of canonical variables which become linear combinations of the original set of variables. The first canonical variable was constructed to provide the maximum separation of groups. The second canonical variable provides the next greatest separation and so forth. If the first two canonical variables explain a large percentage of the variation, then it is possible to represent the relative positions of the groups graphically in two dimensions (scattergram) based on the first two canonical variables.

Dietary Analyses

Student's t Tests. Two-tailed unpaired Student's *t*-tests (Snedecor and Cochran, 1989) determined if male chirostomids consumed significantly different quantities of prey than females in periods before, during, and after spawning periods and for all seasons combined. The TTEST function (a priori $\alpha = 0.05$) in Microsoft Excel XP (2002) was used on gut fullness data for each season and for each species to perform these calculations. Significant differences were assumed if $p < 0.05$.

Spearman's Rank Order Correlation. Spearman's rank order correlation coefficients were also performed to examine whether male and female chirostomids had similar prey compositions in periods before, during, and after spawn. Dietary compositions for each species and the combined genus were calculated, ranked and examined on the basis of males versus females. Microsoft Excel (2002) was used to calculate all Spearman's rank order correlation coefficients.

Dietary compositions were ranked for each sex and compared to determine if male and female diets were correlated. A lack of correlation would indicate that

differences existed in the dietary compositions of male and female chirostomids.

Conversely, positive correlations would indicate that diets were consistent and infer that males and females had similar diets during periods leading up to, during and following the spawn. Correlation analyses were performed on combined data from the March, July-August, and December samples, the combined data for all species and the combined data from Jocotepec, Ajijic, Chapala, Mezcala, and Ocatlan.

Discriminant Function Analysis and Diet. Dietary analyses were designed to discern whether differences in diet would reveal any potential partitioning of dietary resources and explain how the species flock maintained species integrity. Parametric stepwise DFA was applied to individual numerical percentages of each food item as discriminating variables to: (1) determine if the species' diets were different from one another based on percent consumption of various food items, and (2) identify the most important group of food items differentiating species' diets. This parametric test can effectively detect differences in diet among the nine chirostomid species even though the dietary data were not normally distributed. Huberty (1994) stated that parametric stepwise DFA was appropriate as a descriptive analysis technique when the purpose of the research was to describe group differences or to predict group membership on the basis of response variable measures. Similarly, Whitaker (1997) stated that parametric stepwise DFA validly represented variables in a discriminating model and could be used cautiously to imply differences among groups, especially if follow-up corroborative analyses were employed. Parametric stepwise DFA produced scattergrams that allowed initial visual assessments of differences among species. This DFA also provided statistical pairwise squared distances information and Mahalanobis distances to indicate

the significance of difference among species. The parametric stepwise DFA allowed preliminary assessed whether differences occurred among the diets of the nine chirostomid species. However, the data were not normally distributed as required, so additional nonparametric analyses were mandated.

Nonparametric DFA were performed since the assumption of normality was not needed. The discriminatory ability of the statistical model underlying this nonparametric analysis is measured by Wilkes Lambda (Λ) which indicates the probability that group separation is significant. Although the nonparametric stepwise DFA indicated significant differences in diets among species, it could not reveal which dietary components had variation most responsible for discriminating among species. Further examination of the data was required to discover which specific food items accounted for separation among the species. MANOVA was appropriate for this examination.

Whitaker (1997) stated that MANOVA tests combined with DFA can elucidate the variables most responsible for group separation when group differences were known to occur. Whitaker further stated that DFA are statistically interdependent with MANOVA results and recommend that MANOVA be performed. He concluded that DFA should be checked and validated with MANOVA results. However, MANOVA required that the most relevant variables (e.g. food items) be identified for inclusion in the test. I used canonical DFA to identify the most explanatory group of variables.

Fortran-based canonical descriptive DFA were performed to determine which group of dietary variables best discriminated among the diets of the nine chirostomid species. The canonical DFA proceeded by first choosing the one variable (food item) that contributed the most to discriminating among the species. Then it chose the most

discriminating pair of variables, then the most discriminating three variables, then the most discriminating four variables, etc. The procedure was repeated with larger groups until the addition of another variable no longer increased the explanation of variation by less than 5%. This procedure provided not only the most powerfully discriminating group of dietary variables, but also provided Wilkes Lambda, the likelihood ratio criterion that indicates significance.

The group of dietary components found to be most discriminating by canonical descriptive DFA were used to perform the MANOVA tests previously mentioned as a supplemental test to nonparametric DFA. DFA combined with MANOVA validate each test's results if the Wilkes Lambda values are consistent. Wilkes Lambda values were compared and reported. MANOVA provided a) the Wilkes Lambda, b) the dietary variable explaining the most significant differences in diet and, c) the Kruskal-Wallis Chi-Square statistic that indicated the rank order of significance for all the input dietary variables. The Kruskal-Wallis Chi-Square statistic is a weighted non-linear ranking based on the statistical interaction of the groups.

These statistical analyses determined if significant differences occurred among the diets of the nine species of chirostomid fishes at Lake Chapala. The above path of analysis indicated if a) differences existed among diets of the species, b) which food item or group of items was most responsible for explaining the variation among the diets, and c) the order of importance for those food items found to be responsible for defining the dietary variation. Except where noted, all statistical analyses were computed with SAS version 8.2 (SAS 2002) for all combined data, for collections from each area with seasons combined, and for combined data for each season.

CHAPTER THREE

Results

The Morphology of Chirostomid Fishes

All nine species of *Chirostoma* previously known to occur in Lake Chapala were captured during this study (Table 2). Samples of *Chirostoma* spp. from Lake Chapala during 1998-1999 included representatives of both major phylogenetic groups -- the Jordani Group and the Arge Group (Barbour 1973). A total of 22,416 chirostomid fishes were captured and identified to species level during this two year study. Of those, 17,946 were used for morphological and dietary analyses (Table 3). The analytical catch was comprised of 7,751 males and 10,195 females.

Of the 18 chirostomid species known to occur in the Central Mesa Region of Mexico, nine had been documented in Lake Chapala at the time of this study (Hansen and van Afferden, 2001). Meek reported the existence of *Chirostoma estor* in Lake Chapala in 1903, however his specimens likely came from Lake Patzcuaro (Barbour, 1974). It is not widely accepted that *C. estor* occurred in Lake Chapala. Barbour (2002) described a new species, *Chirostoma contrerasi*, occurring in Lake Chapala. *Chirostoma contrerasi* is not referred to in this study because the new species description was not available until 2002, long after species identifications were performed during this study.

Six Jordani Group species of *Chirostoma* were represented in Lake Chapala (Table 2). The Jordani Group is characterized by higher meristic characteristics, canals along the lateral lines and lacinate margined scales. Morphometric ranges have higher values in median lateral scales, 36-90; predorsal scales, 16-136; interdorsal scales, 0-29; gill rakers, 14-34; vertebrae, 35-47; pectoral fin rays, 10-18; and anal fin rays, 14-24 (Barbour, 1973). The

species range in size from the smallest (*C. chapalae*) to the largest (*C. lucius*) of the chirostomid fishes.

Table 2. Species of *Chirostoma* occurring in Lake Chapala, Mexico, during 1998-1999.

Jordani Group Species	Arge Group Species
<i>Chirostoma chapalae</i> (Jordan & Snyder 1899)	<i>Chirostoma arge</i> (Jordan & Snyder 1899)
<i>Chirostoma consocium</i> (Jordan & Hubbs 1919)	<i>Chirostoma aculeatum</i> (Barbour 1973)
<i>Chirostoma jordani</i> (Woolman 1894)	<i>Chirostoma labarcae</i> (Meek 1902)
<i>Chirostoma lucius</i> (Boulenger 1900)	
<i>Chirostoma promelas</i> (Jordan & Snyder 1899)	
<i>Chirostoma sphyraena</i> (Boulenger 1900)	

Three Arge Group species occur in Lake Chapala (Table 2). In contrast to the Jordani Group, the Arge Group generally has lower meristic values, smooth margined scales and pored scales along the lateral line (except *C. labarcae* and *C. aculeatum*). The Arge Group generally exhibited lower meristic values in median lateral scales, 36-51; predorsal scales, 15-32; interdorsal scales, 1-8; gill rakers, 12-26; vertebrae, 35-43; pectoral fin rays, 8-15; and anal fin rays, 10-19.

Species Diagnoses of the Jordani Group

Chirostoma jordani (Woolman 1894). *C. jordani* occurs throughout the lakes and rivers of central Mexico and is found in both fresh and brackish waters. This species was first described by Woolman in 1894. Consistent with available taxonomic keys, the individuals of *C. jordani* captured during this study were characterized by the following morphological features: total length, 50.9-105.5 mm; standard length 48.8-95.1 mm; snout length 4.8-9.7; head length, 12.1-24.9%; body depth, 17.0-20.1%; pectoral fin insertion, 33.2-37.6%; dorsal fin insertion, 45.1-49.9%; anal fin height, 13.8-20.3%; anal fin insertion, 46.0-58.4%; scales superior to lateral line, 3-6; median lateral line scales, 34-49; predorsal scales,

Table 3. Total catch of nine species of *Chiostoma* occurring in Lake Chapala, Mexico during 1998-1999 at five sampling stations.

	Sampling Area					
Species	Jocotepec	Ajijic	Chapala	Mezcala	Ocatlan	Combined Sites
Jordani Group						
<i>C. jordani</i>	1160	1147	1216	1228	948	5699
<i>C. consocium</i>	1017	1223	1219	1038	942	5439
<i>C. chapalae</i>	1041	941	1134	981	830	4927
<i>C. promelas</i>	667	607	756	527	639	3196
<i>C. sphyraena</i>	534	599	588	543	568	2832
<i>C. lucius</i>	19	22	39	79	164	323
Arge Group						
<i>C. arge</i>	19	65	117	272	470	943
<i>C. labarcae</i>	19	60	70	107	348	604
<i>C. aculeatum</i>	0	1	8	79	200	288

16-27; interdorsal scales, 0-7; scale type, smooth; lateral line type, canals; anal fin rays, 14-22; pectoral fin rays, 9-14; caudal peduncle length, 17.8-26.3%; eye size, 5.0-7.1 mm; mouth width, 3.7-5.2%; mouth height, 7.0-8.1%; mandible length, 7.2-9.2%; gill rakers, 13-23; and vertebrae, 35-42 (Figures 9-30). Means and ranges are consistent with historical data cited by Barbour (1973).

Chirostoma consocium (Jordan and Hubbs 1919). *C. consocium* occurs throughout the freshwater streams and lakes of Mexico. This species was described by Jordan and Hubbs in 1919. Consistent with available taxonomic keys, the individuals of *C. consocium* captured during this study were characterized by the following morphological features: total length, 66.3-139.6 mm; standard length, 61.0-125.0 mm; snout length, 7.1-9.5%; head length, 24.4-28.1%; body depth, 16.5-20.4%; pectoral fin insertion, 37.1-43.3%; dorsal fin insertion, 49.3-53.4%; anal fin height, 15.8-20.1%; anal fin insertion, 47.3-56.2%; scales superior to lateral line, 3-6; median lateral line scales, 52-68; predorsal scales, 44-77; interdorsal scales, 4-13; scale type, crenulate; lateral line type, canals; anal fin rays, 17-24; pectoral fin rays, 13-16; caudal peduncle length, 8.1-9.8%; eye size, 6.1-7.6 mm; mouth width, 4.1-6.3%; mouth height, 6.6-8.9%; mandible length, 9.1-11.1%; gill rakers, 14-29; and vertebrae, 42-46 (Figures 9-30). Means and ranges are consistent with historical data cited by Barbour (1973).

Chirostoma chapalae (Jordan and Snyder 1899). *C. chapalae* occurs throughout the freshwater Lerma River basin of central Mexico. This species was described by Jordan and Snyder 1899. Consistent with available taxonomic keys, the individuals of *C. chapalae* captured during this study were characterized by the following morphological features: total length, 59.6-105.3 mm; standard length, 55.1-94.0 mm; snout length, 5.1-9.8%; head length, 24.2-25.6%; body depth, 16.8-20.4%; pectoral fin insertion, 33.9-36.9%; dorsal fin insertion,

48.9-53.0%; anal fin height, 16.1-18.2%; anal fin insertion, 46.4-56.8%; scales superior to lateral line, 3-6; median lateral line scales, 43-55; predorsal scales, 27-48; interdorsal scales, 4-9; scale type, crenulate; lateral line type, canals; anal fin rays, 17-22; pectoral fin rays, 13-16; caudal peduncle length, 7.6-9.2%; eye size, 5.5-7.5 mm; mouth width, 3.9-5.8%; mouth height, 6.8-7.9%; mandible length, 8.6-9.4%; gill rakers, 25-29; and vertebrae, 43-45 (Figures 9-30). Means and ranges are consistent with historical data cited by Barbour (1973).

Chirostoma promelas (Jordan and Snyder 1899). *C. promelas* occurs throughout the freshwater Lerma River basin of central Mexico. This species was described by Jordan and Snyder in 1899. Consistent with available taxonomic keys, the individuals of *C. promelas* captured during this study were characterized by the following morphological features: total length, 89.5-178.1 mm; standard length, 83.0-159.0 mm; snout length, 10.4-12.6%; head length, 28.4-32.4%; body depth, 16.5-20.4%; pectoral fin insertion, 31.3-35.9%; dorsal fin insertion, 55.2-58.3%; anal fin height, 15.1-16.1%; anal fin insertion, 51.9-56.7%; scales superior to lateral line, 4-6; median lateral line scales, 51-68; predorsal scales, 44-66; interdorsal scales, 4-13; scale type, crenulate; lateral line type, canals; anal fin rays, 18-21; pectoral fin rays, 12-16; caudal peduncle length, 19.9-24.2%; eye size, 5.1-7.0 mm; mouth width, 6.6-9.0%; mouth height, 7.4-10.4%; mandible length, 11.3-13.2%; gill rakers, 22-29; and vertebrae, 43-46 (Figures 9-30). Means and ranges are consistent with historical data cited by Barbour (1973).

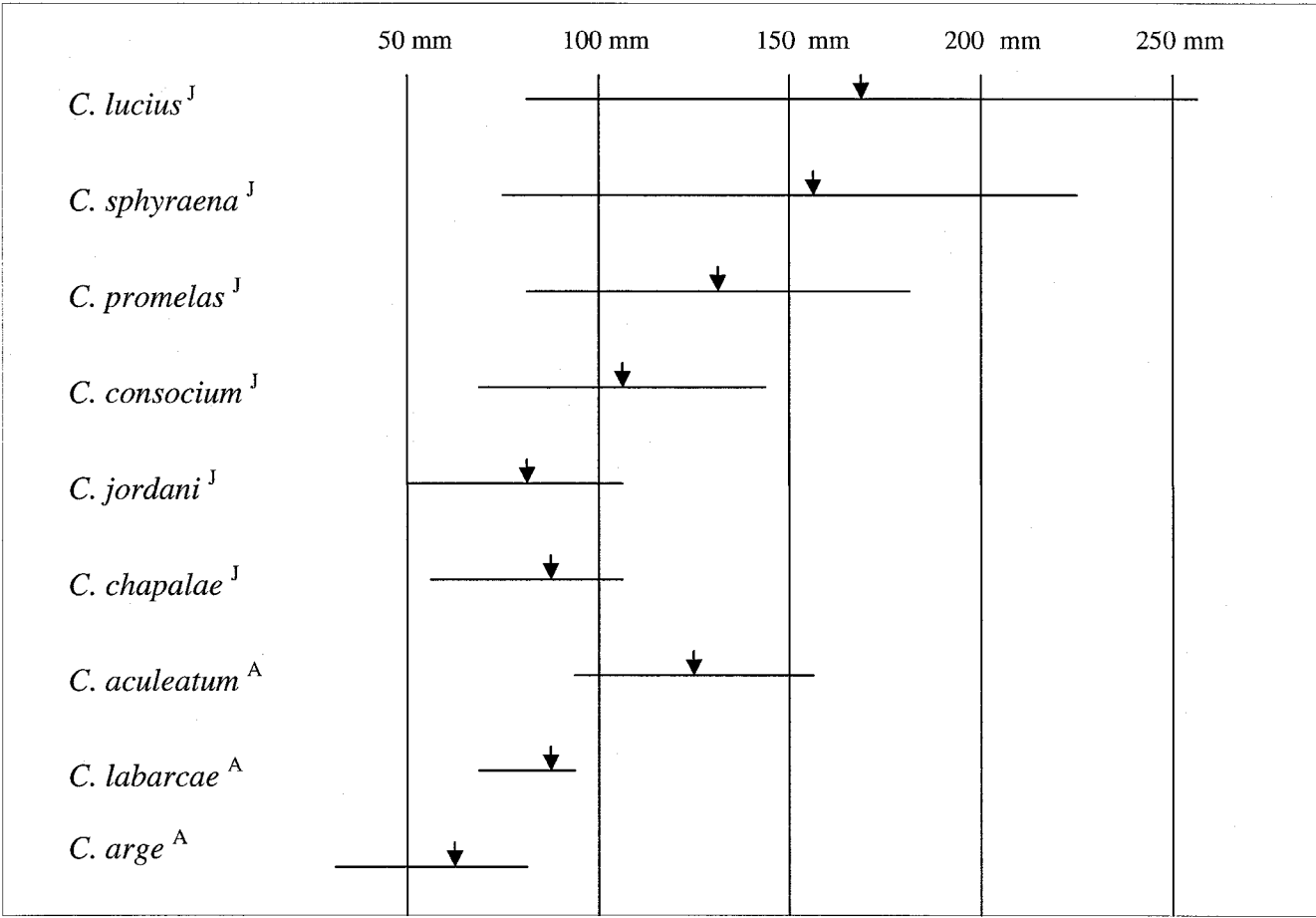


Figure 9. Comparison of total lengths of nine chiostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. J=Jordani Group, A=Arge Group.

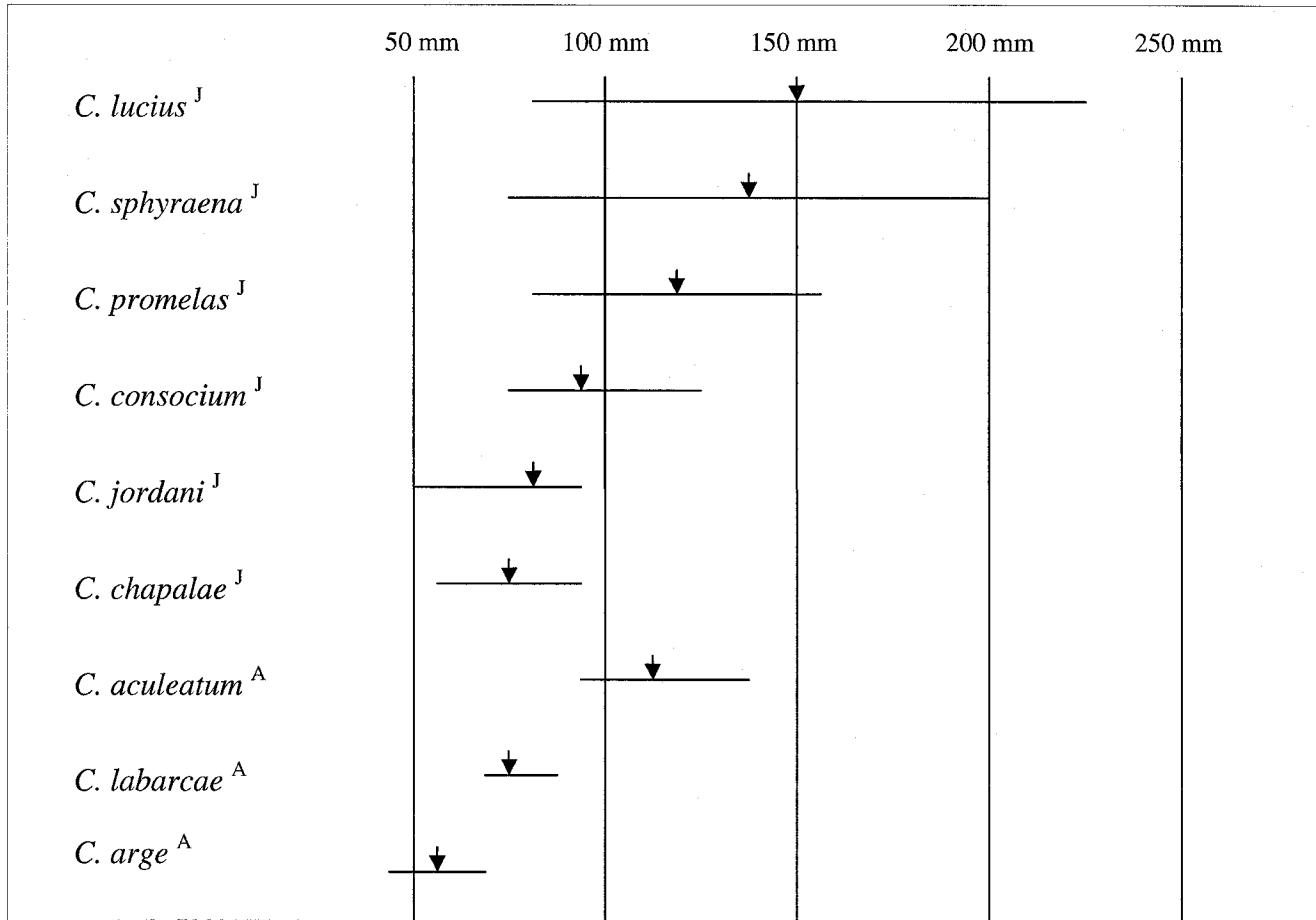


Figure 10. Comparison of standard lengths of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. J=Jordani Group, A=Arge Group.

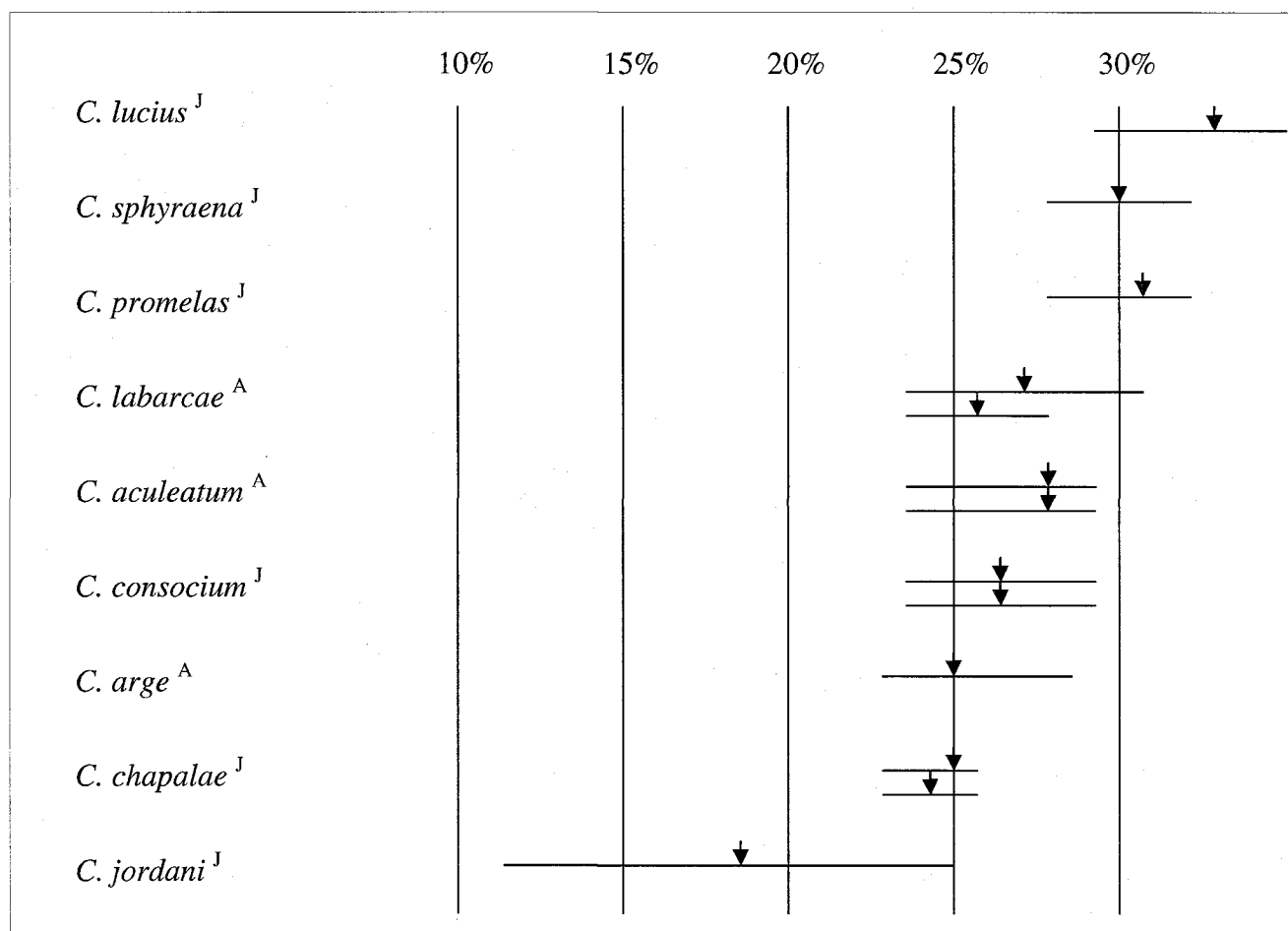


Figure 11. Comparison of head lengths, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. Red lines and arrows indicate historical comparison data from Barbour (1973). J=Jordani Group, A=Arge Group.

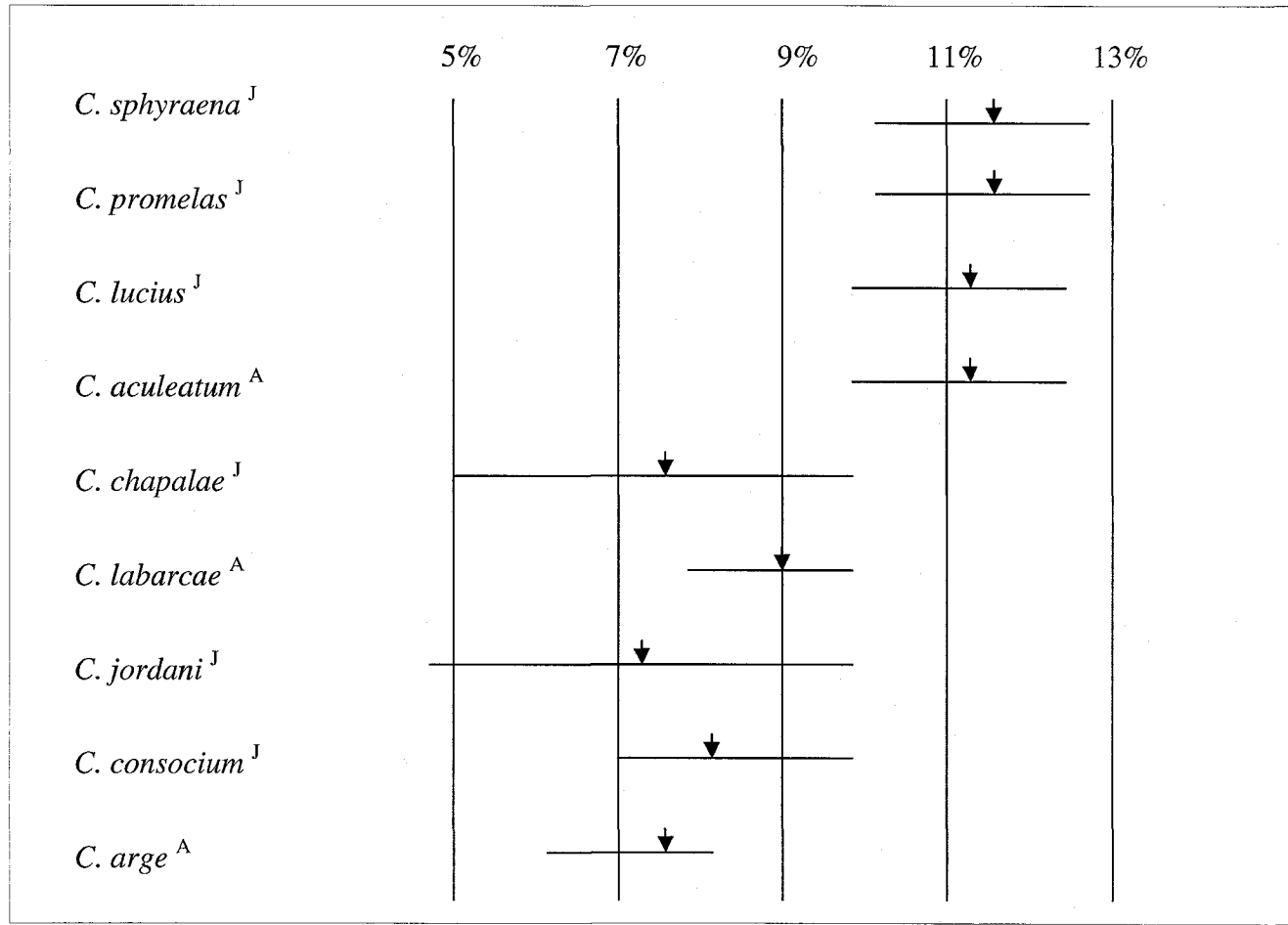


Figure 12. Comparison of snout lengths, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. J=Jordani Group, A=Arge Group.

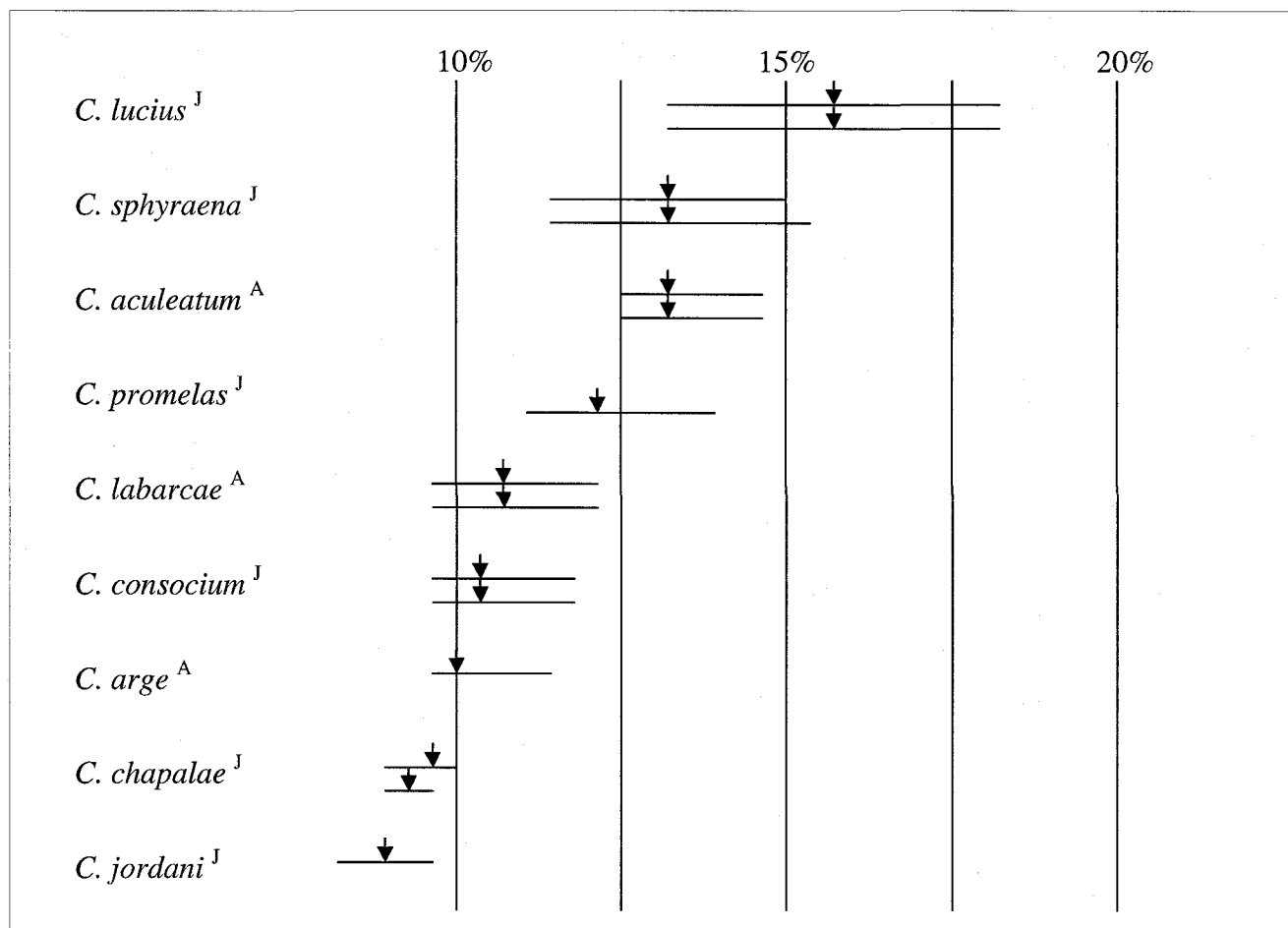


Figure 13. Comparison of mandible lengths, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. Red lines and arrows indicate historical comparison data from Barbour (1973). J=Jordani Group, A=Arge Group.

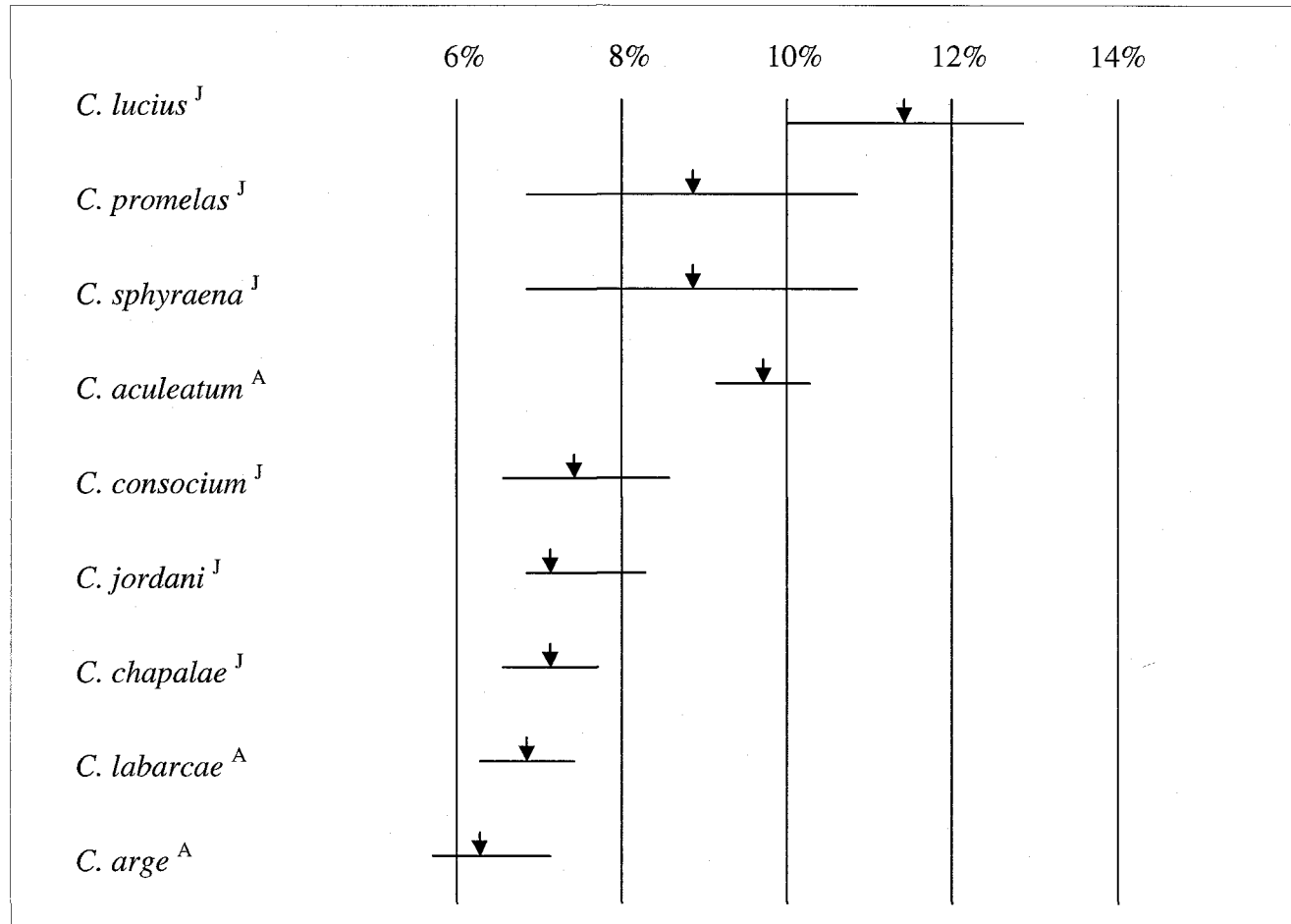


Figure 14. Comparison of mouth heights, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. J=Jordani Group, A=Arge Group.

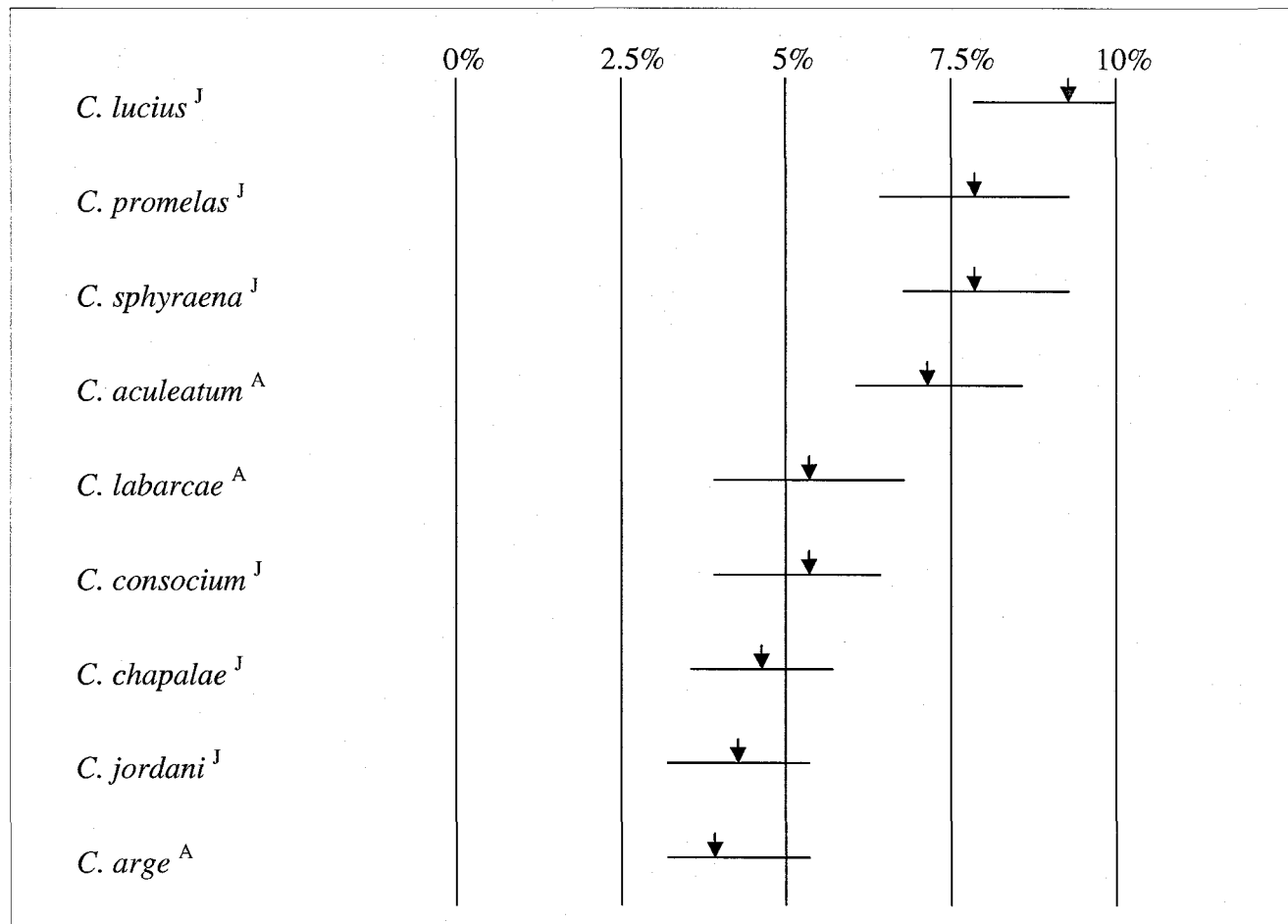


Figure 15. Comparison of mouth widths, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. J=Jordani Group, A=Arge Group.

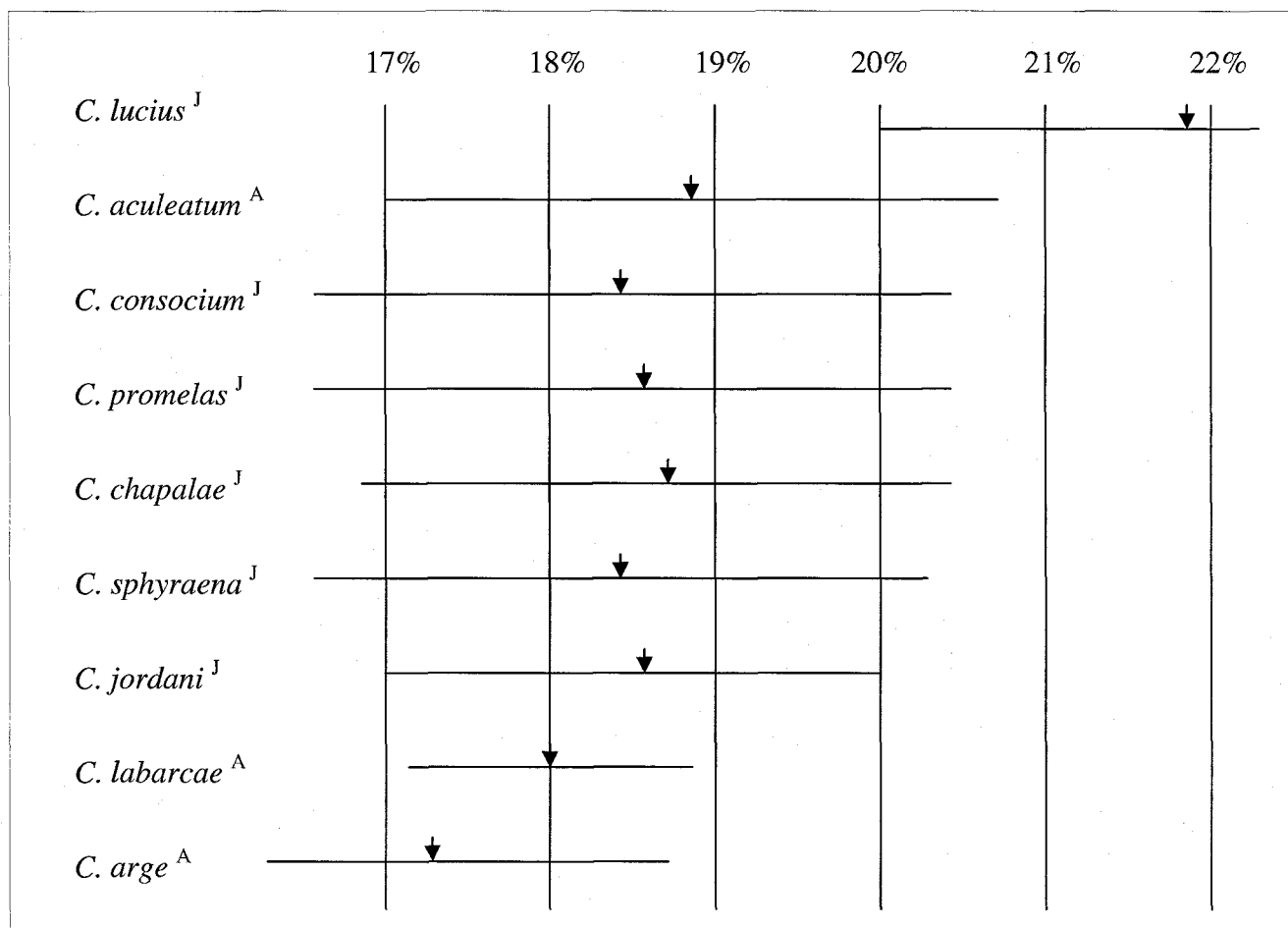


Figure 16. Comparison of body depths, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. J=Jordani Group, A=Arge Group.

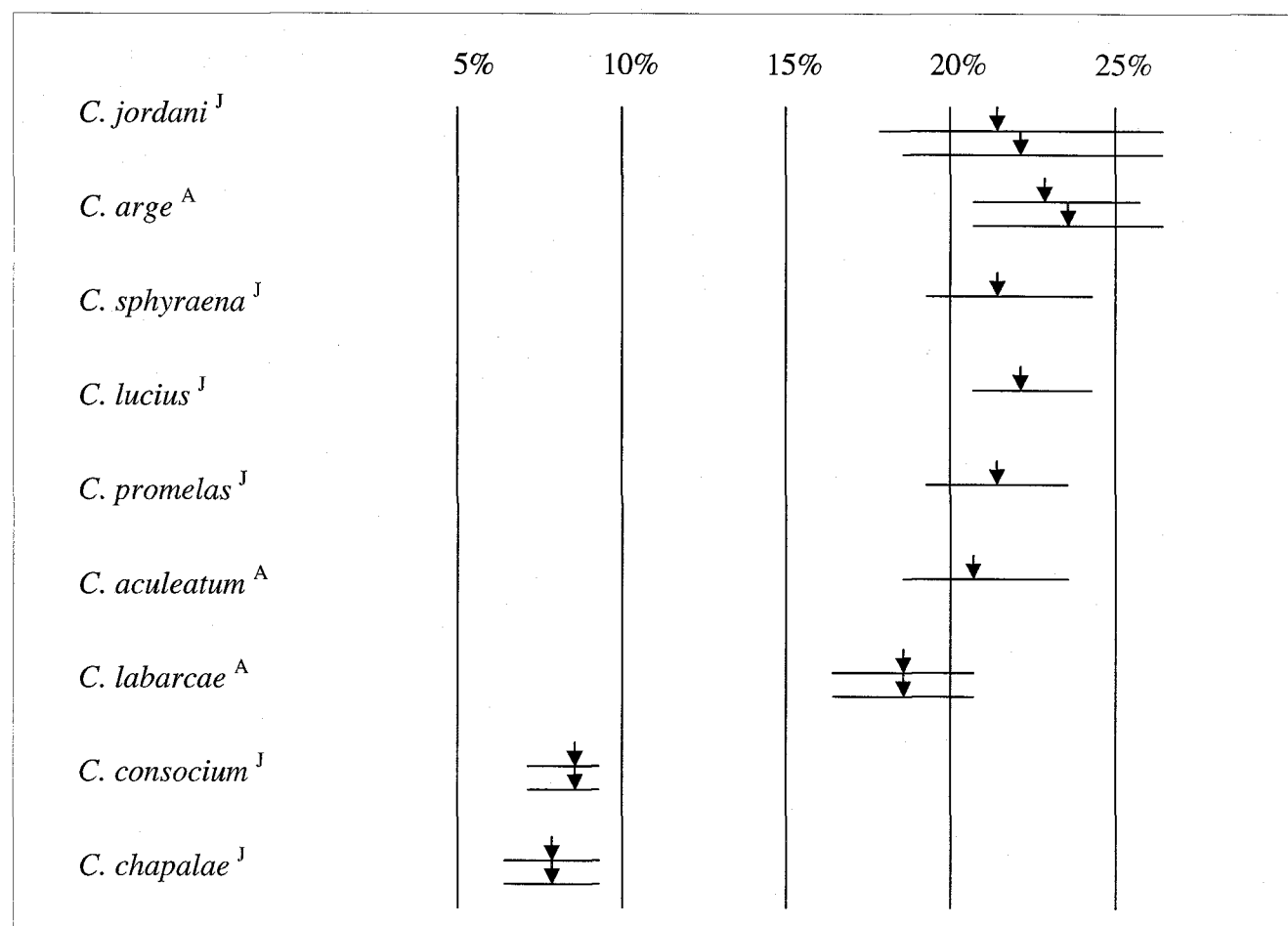


Figure 17. Comparison of caudal peduncle lengths, expressed as percentages of standard length, of nine chiostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. Red lines and arrows indicate historical comparison data from Barbour (1973). J=Jordani Group, A=Arge Group.

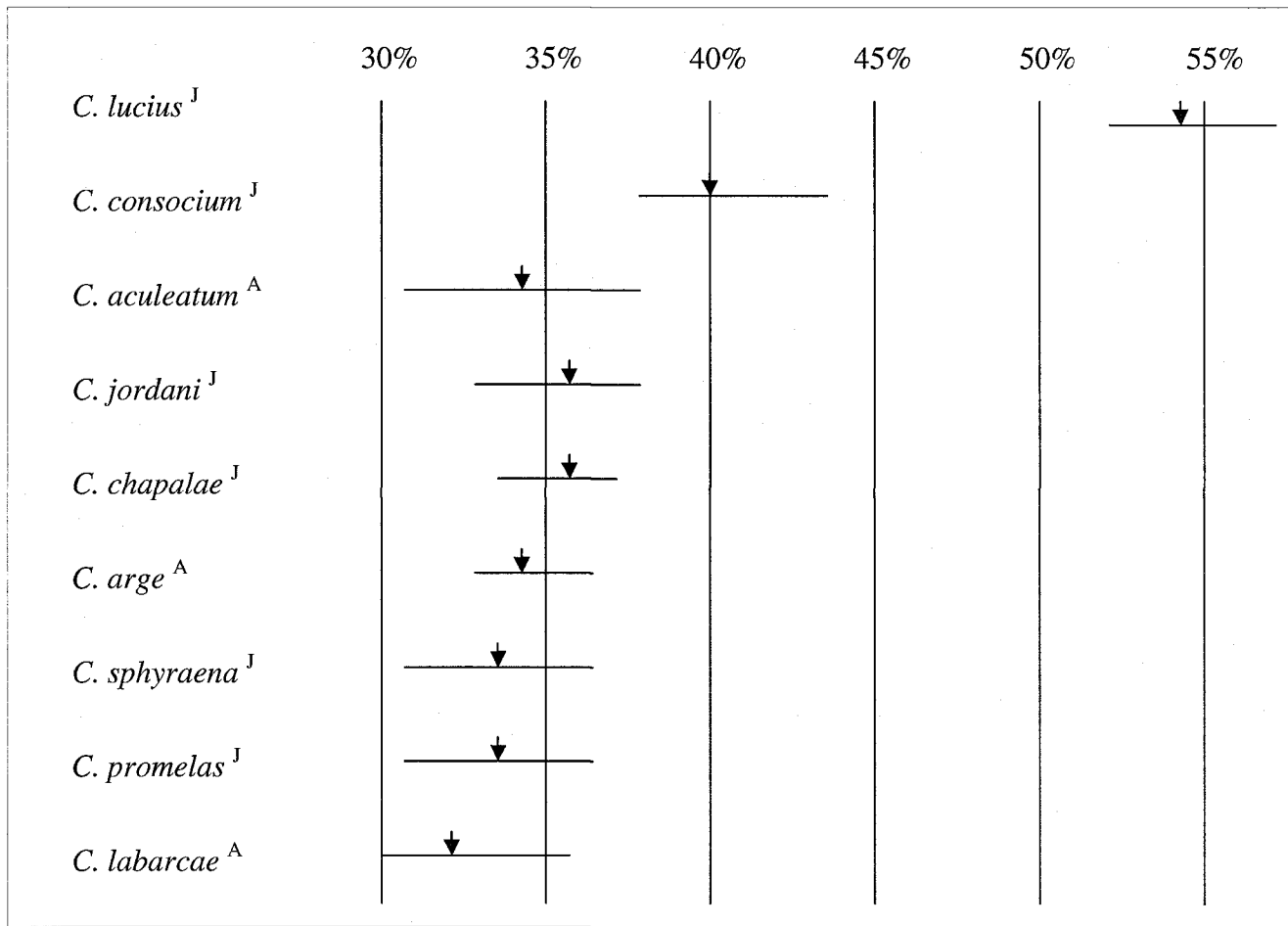


Figure 18. Comparison of Pectoral Fin Insertions, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. J=Jordani Group, A=Arge Group.

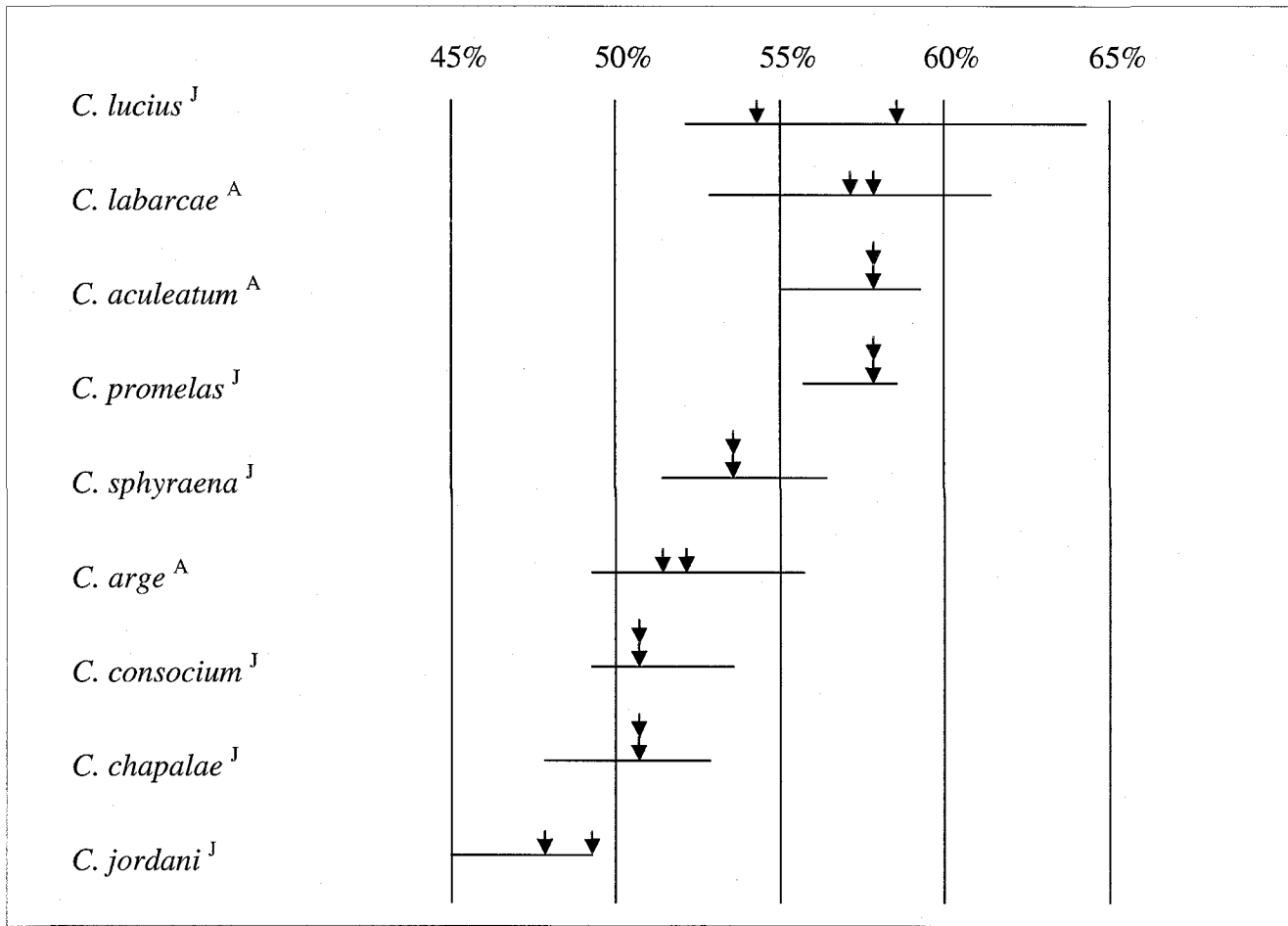


Figure 19. Comparison of dorsal fin insertions, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. Red arrows indicate historical means data from Barbour (1973). J=Jordani Group, A=Arge Group.

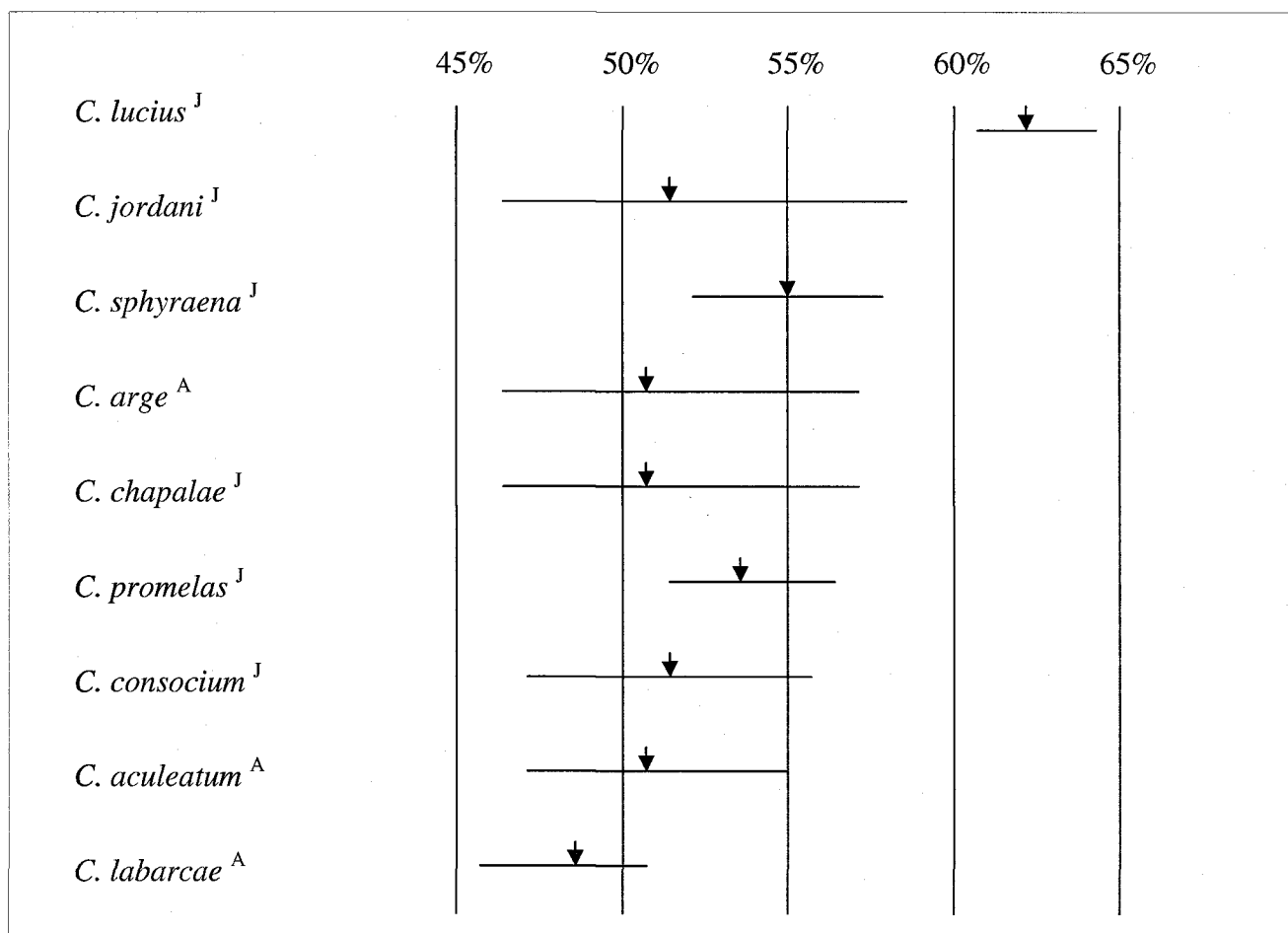


Figure 20. Comparison of Anal Fin Insertions, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. J=Jordani Group, A=Arge Group.

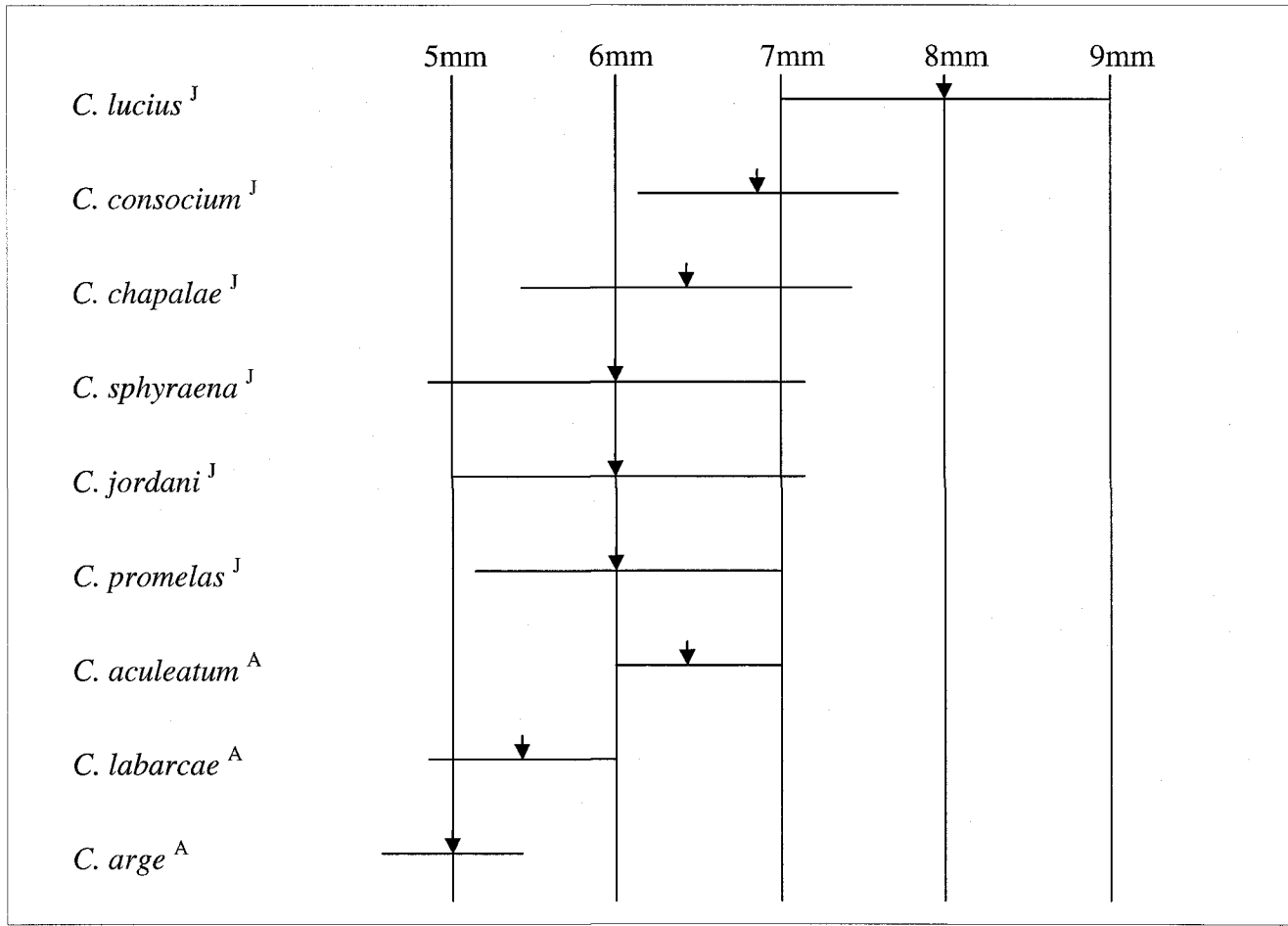


Figure 21. Comparison of Eye Sizes, in millimeters, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. J=Jordani Group, A=Arge Group.

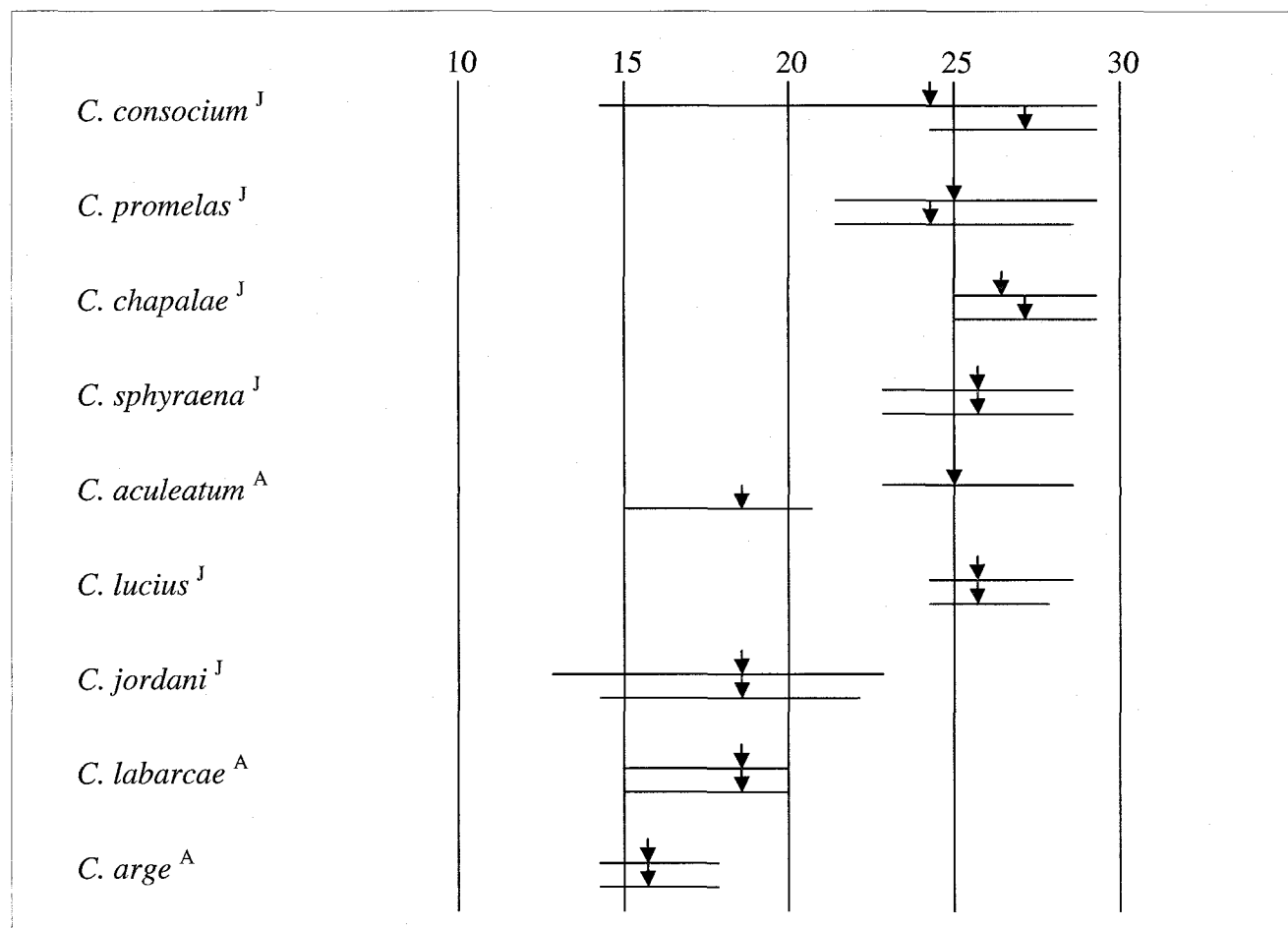


Figure 22. Comparison of Gill Raker numbers of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. Red lines and arrows indicate historical comparison data from Barbour (1973). J=Jordani Group, A=Arge Group.

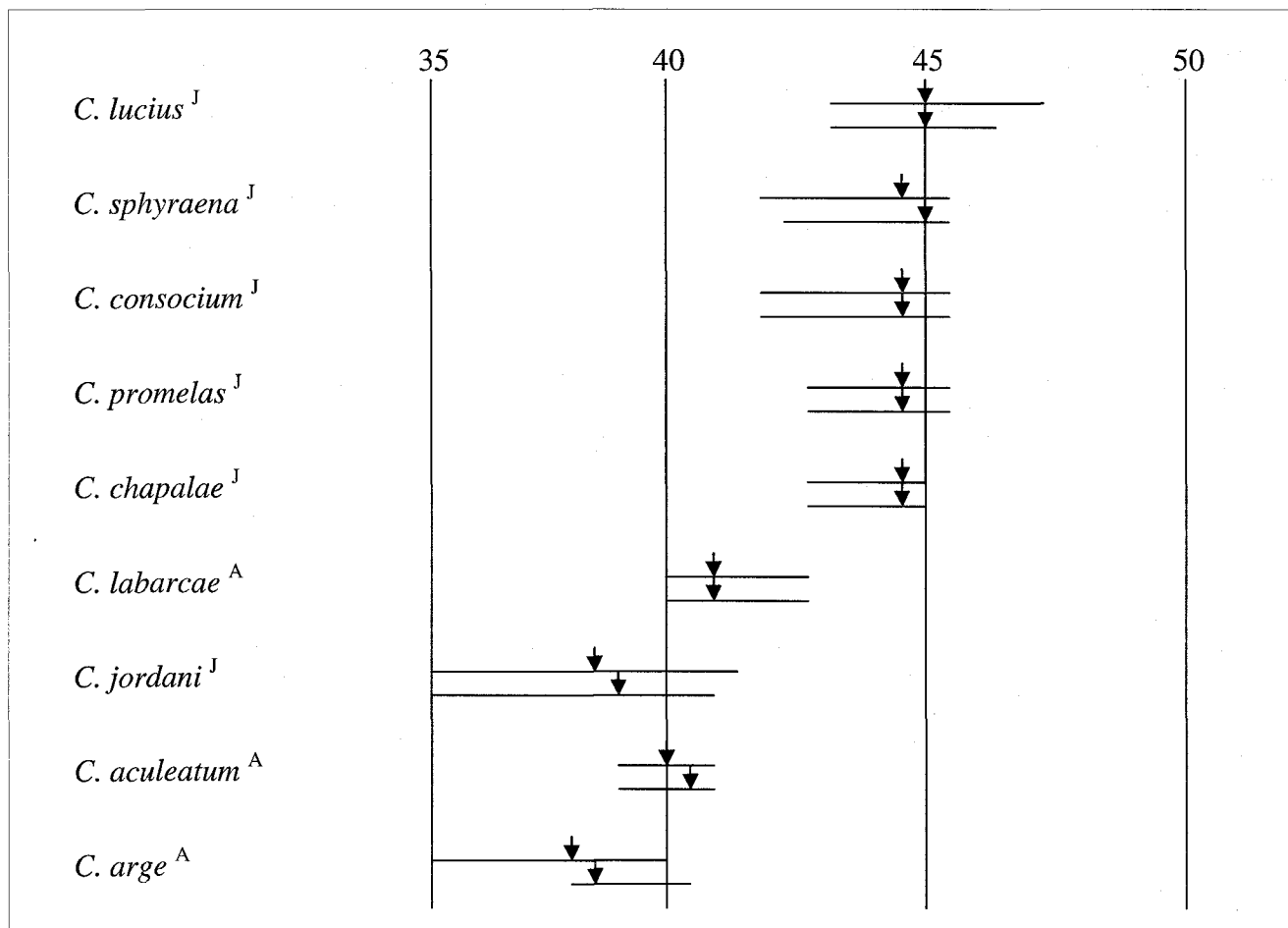


Figure 23. Comparison of vertebrae numbers of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. Red lines and arrows indicate historical comparison data from Barbour (1973). J=Jordanian Group, A=Arge Group.

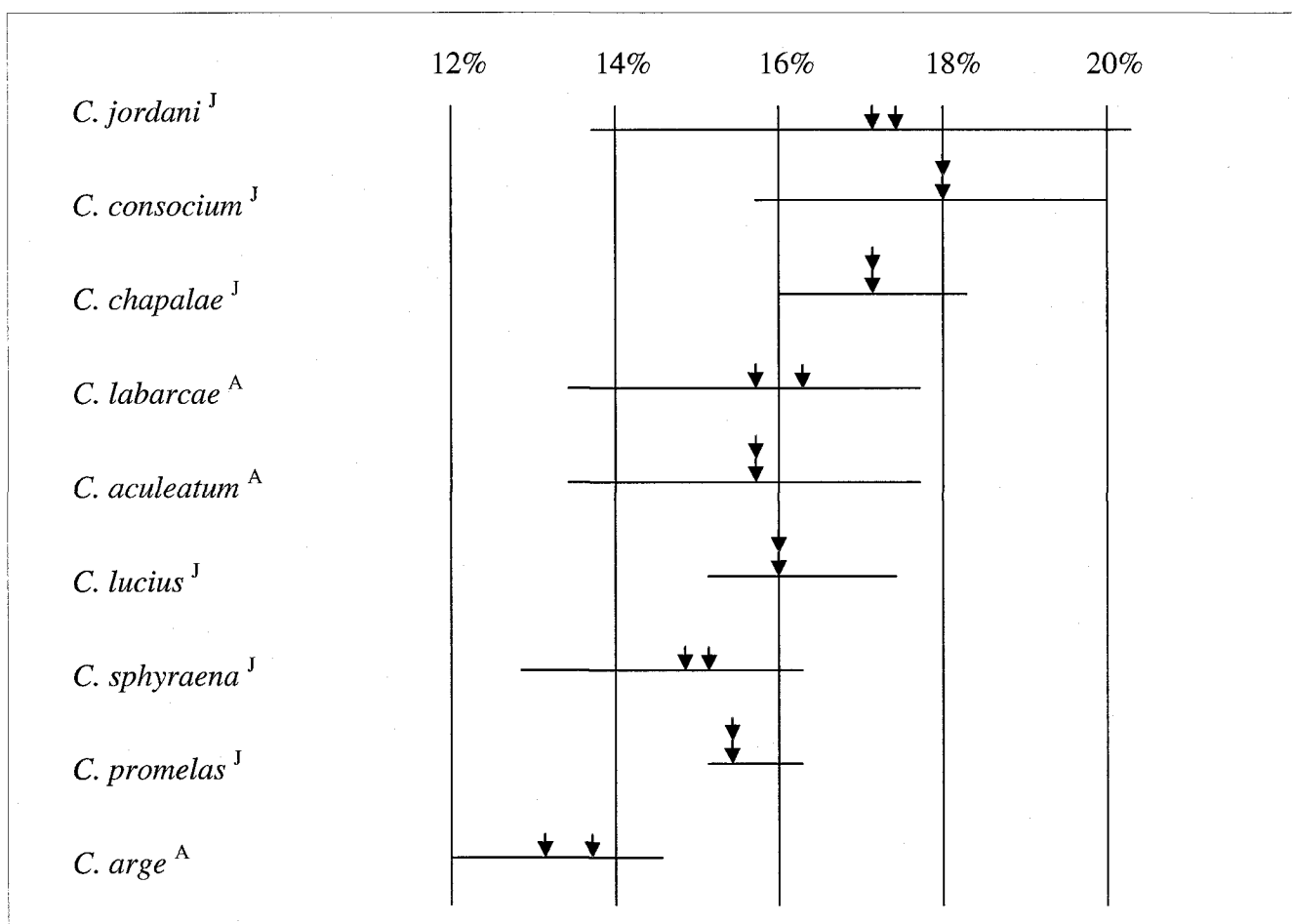


Figure 24. Comparison of anal fin heights, expressed as percentages of standard length, of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. Red arrows indicate historical means data from Barbour (1973). J=Jordani Group, A=Arge Group.

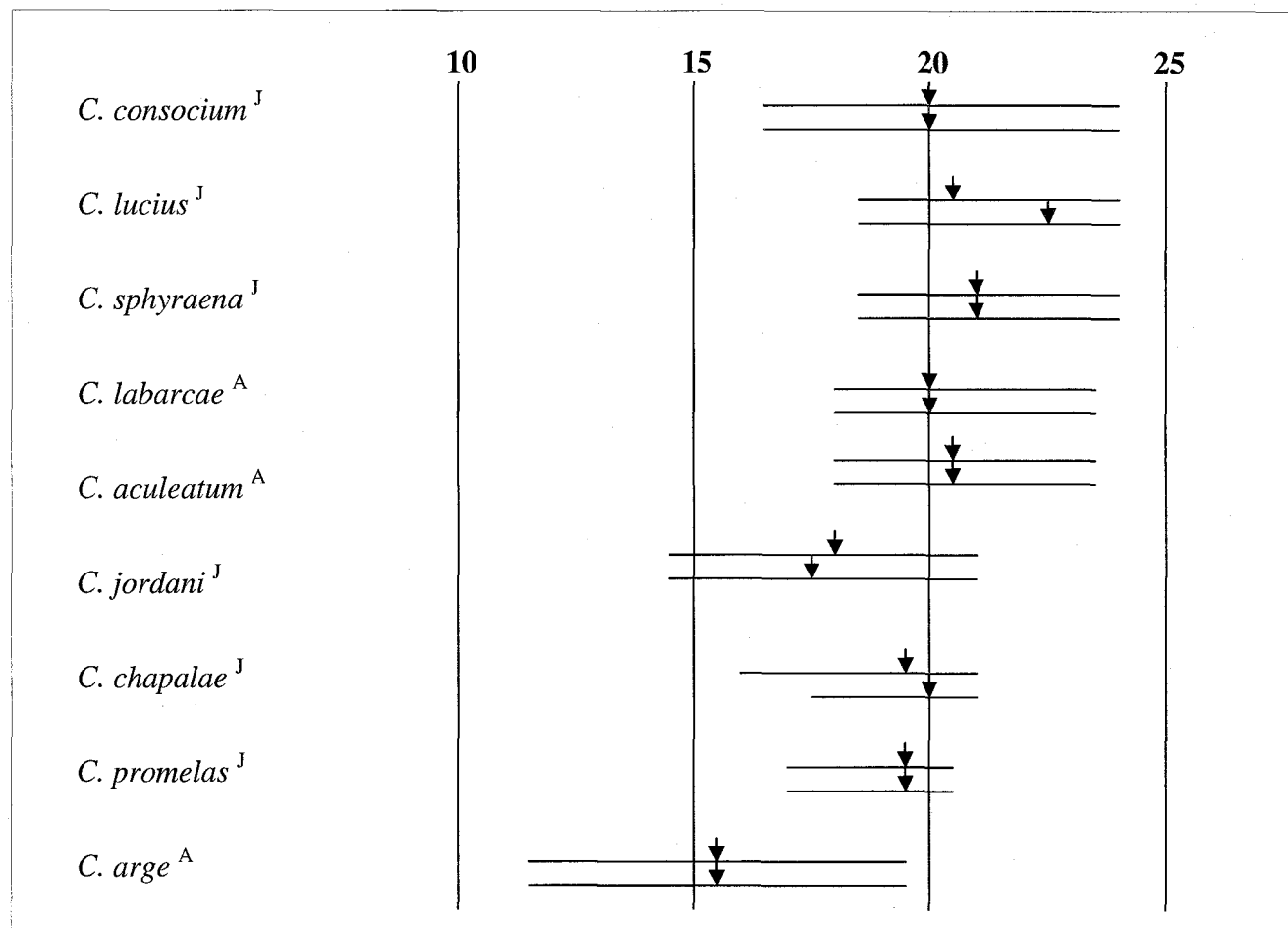


Figure 25. Comparison of anal fin rays of nine species of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. Red lines and arrows indicate historical comparison data from Barbour (1973). J=Jordani Group, A=Arge Group.

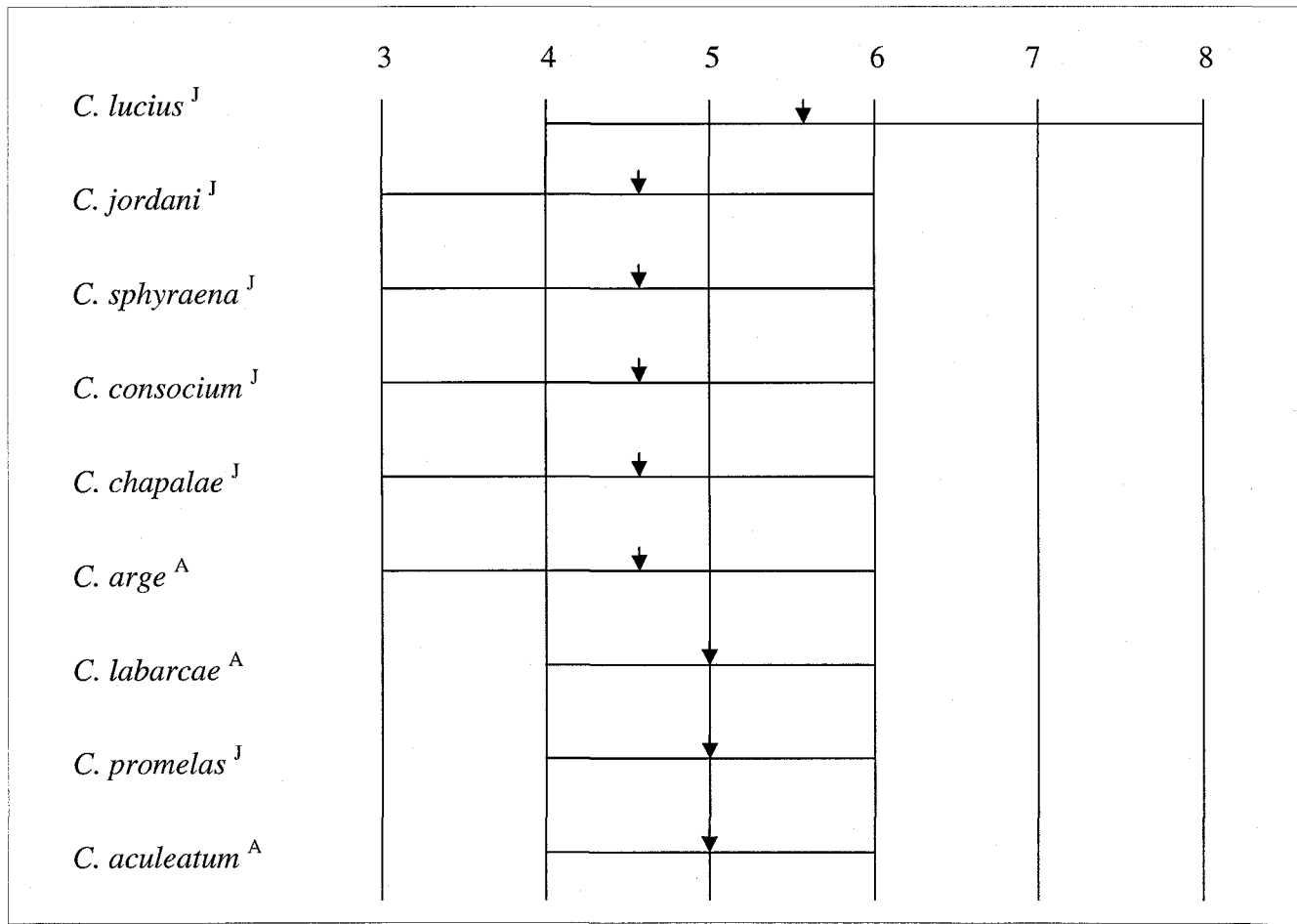


Figure 26. Comparison of the number of scales superior to the lateral of nine chiostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. J=Jordani Group, A=Arge Group.

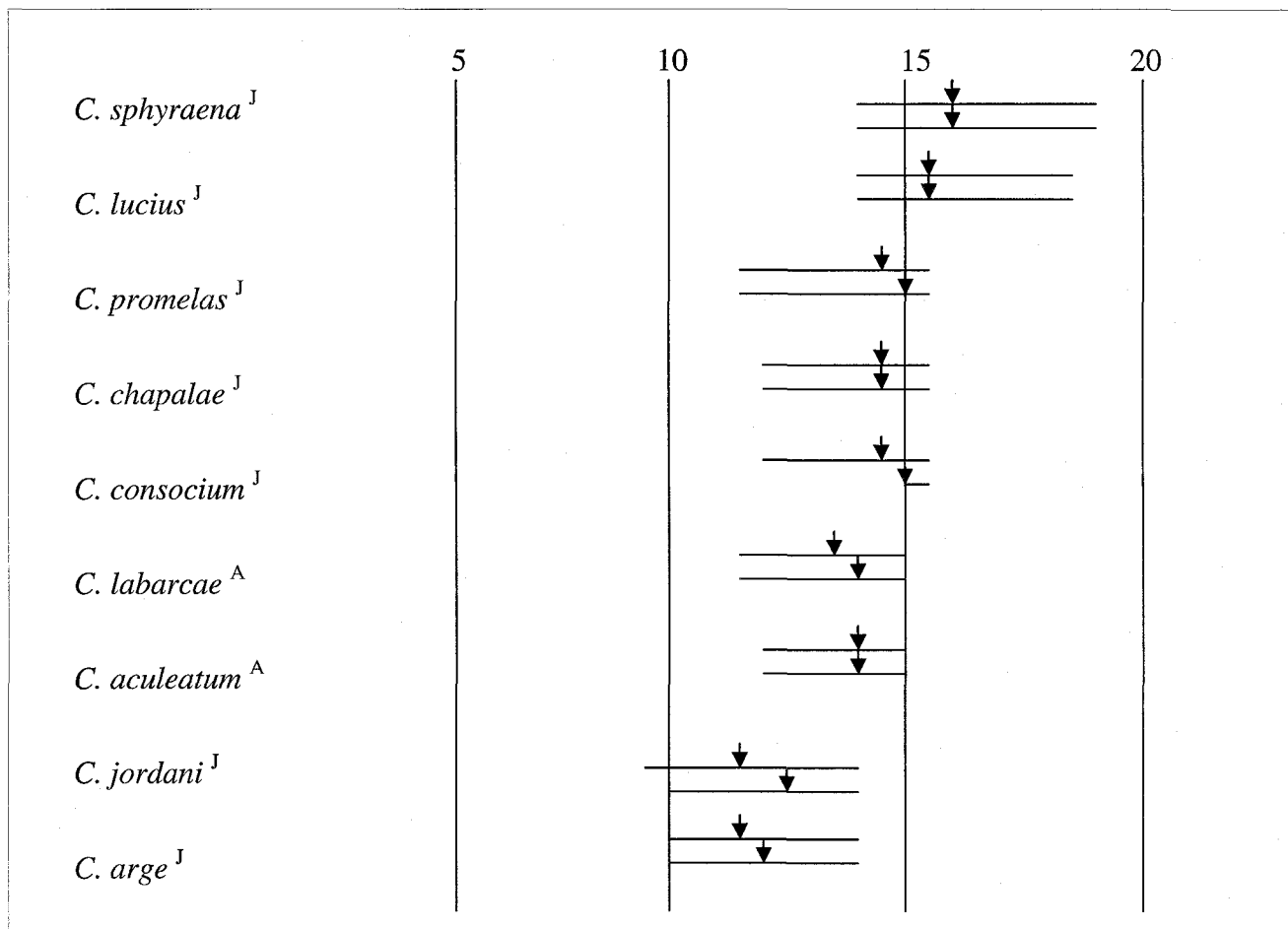


Figure 27. Comparison of the number of pectoral fin rays of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. Red lines and arrows indicate historical comparison data from Barbour (1973). J=Jordani Group, A=Arge Group.

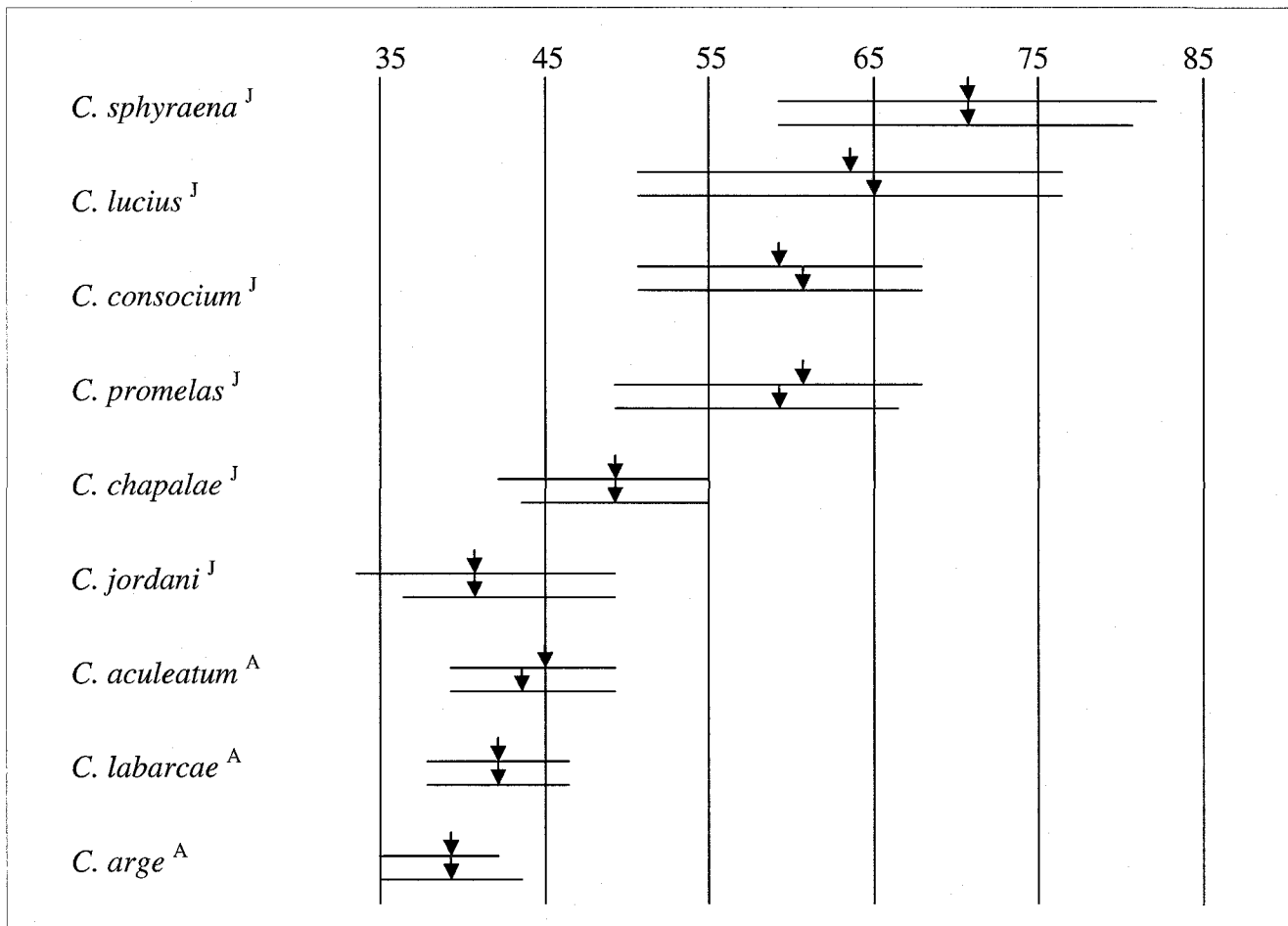


Figure 28. Comparison of median lateral line scales of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. Red lines and arrows indicate historical comparison data from Barbour (1973). J=Jordani Group, A=Arge Group.

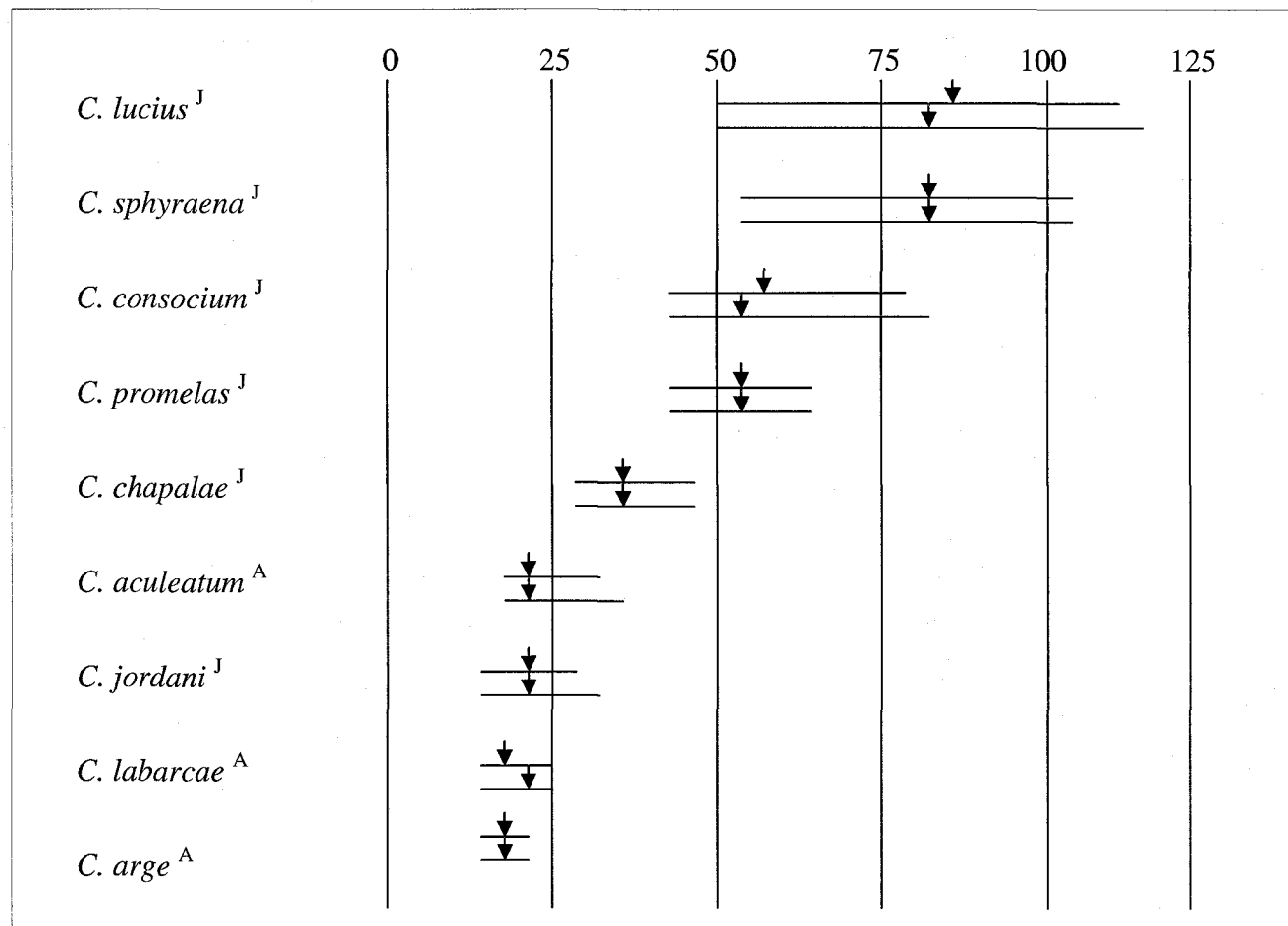


Figure 29. Comparison of predorsal scales of nine chirostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. Red lines and arrows indicate historical comparison data from Barbour (1973). J=Jordani Group, A=Arge Group.

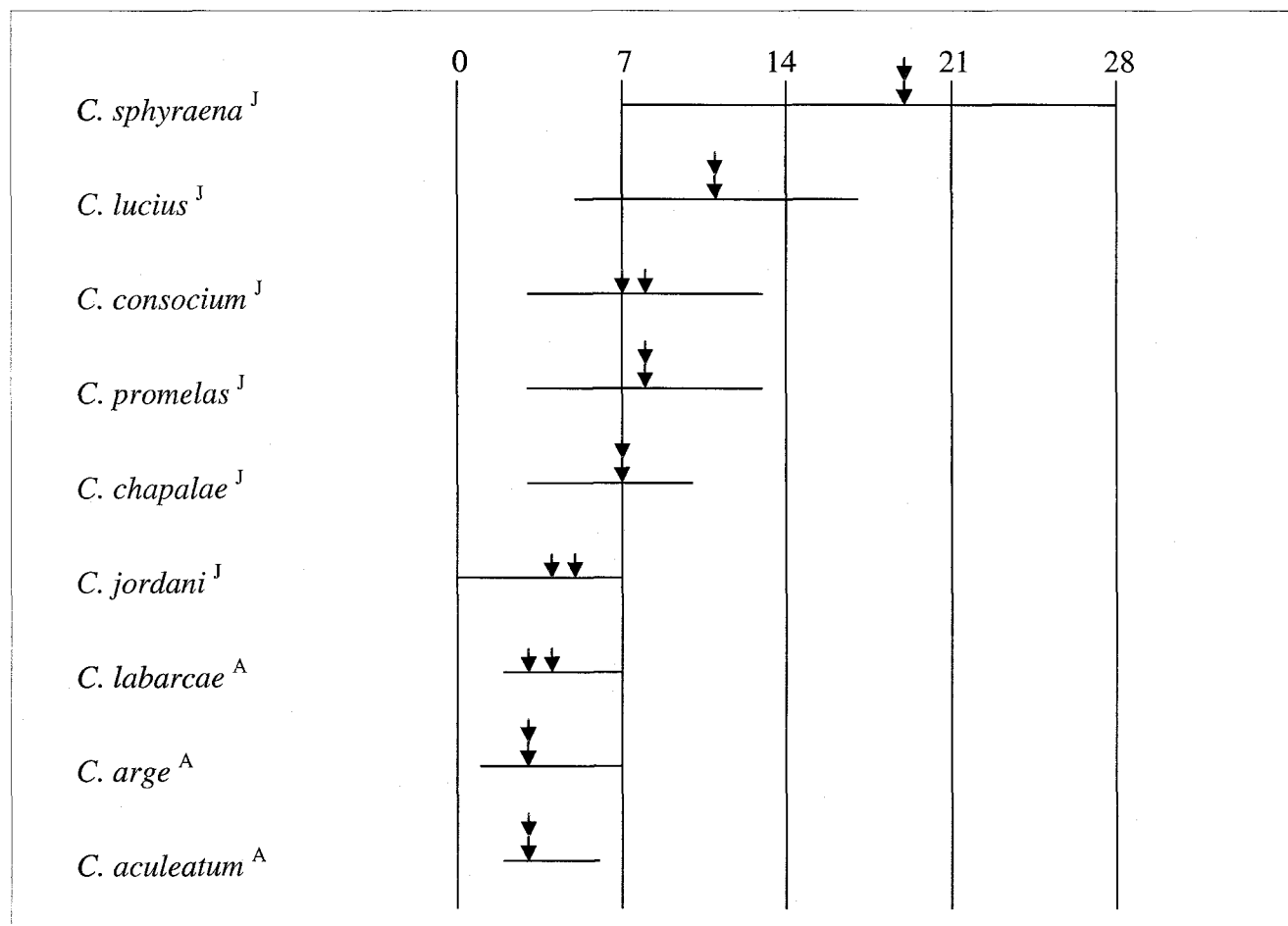


Figure 30. Comparison of interdorsal scales of nine chiostomid species from Lake Chapala, Mexico, in 1998-1999. Horizontal lines indicate the ranges and arrows indicate the means. Red arrows indicate historical means data from Barbour (1973). J=Jordani Group, A=Arge Group.

Chirostoma sphyraena (Boulenger 1900). *C. sphyraena* occurs throughout the freshwater Lerma River basin of central Mexico. This species was described by Boulenger 1900. Consistent with available taxonomic keys, the individuals of *C. sphyraena* captured during this study were characterized by the following morphological features: total length, 81.8-226.4 mm; standard length, 75.6-202.0 mm; snout length, 10.2-12.8%; head length, 28.0-32.1%; body depth, 16.5-20.3%; pectoral fin insertion, 31.1-36.0%; dorsal fin insertion, 51.9-56.3%; anal fin height, 13.0-16.3%; anal fin insertion, 52.9-57.3%; scales superior to lateral line, 3-6; median lateral line scales, 60-83; predorsal scales, 55-112; interdorsal scales, 7-28; scale type, crenulate; lateral line type, pored; anal fin rays, 19-24; pectoral fin rays, 14-18; caudal peduncle length, 19.8-24.5%; eye size, 4.9-7.1 mm; mouth width, 6.7-9.0%; mouth height, 7.5-10.4%; mandible length, 12.0-15.3%; gill rakers, 23-28; and vertebrae, 42-46 (Figures 9-30). Means and ranges are consistent with historical data cited by Barbour (1973).

Chirostoma lucius (Boulenger 1900). *C. lucius* occurs throughout the freshwater Lerma River basin of central Mexico. This species was described by Boulenger 1900. Consistent with available taxonomic keys, the individuals of *C. lucius* captured during this study were characterized by the following morphological features: total length, 85.7-253.6 mm; standard length, 77.0-227.0 mm; snout length, 10.1-12.5%; head length, 29.6-36.5%; body depth, 20.1-22.6%; pectoral fin insertion, 52.9-56.7%; dorsal fin insertion, 52.8-64.3%; anal fin height, 14.6-17.7%; anal fin insertion, 60.3-64.6%; scales superior to lateral line, 4-8; median lateral line scales, 52-76; predorsal scales, 50-116; interdorsal scales, 5-17; scale type, smooth; lateral line type, canals; anal fin rays, 19-24; pectoral fin rays, 14-17; caudal peduncle length, 20.7-24.4%; eye size, 7.0-9.0 mm; mouth width, 7.6-10.0%; mouth height,

10.0-13.0-%; mandible length, 13.0-18.1%; gill rakers, 24-28; and vertebrae, 43-47 (Figures 9-30). Means and ranges are consistent with historical data cited by Barbour (1973).

Species Diagnosis of the Arge Group

Chirostoma arge (Jordan and Snyder 1899). *C. arge* occurs throughout the freshwater Lerma River basin of central Mexico. This species was described by Jordan and Snyder in 1899. Consistent with available taxonomic keys, the individuals of *C. arge* captured during this study were characterized by the following morphological features: total length, 50.9-76.0 mm; standard length, 47.0-68.0 mm; snout length, 6.4-8.5%; head length, 23.5-26.8%; body depth, 16.1-18.7%; pectoral fin insertion, 33.0-36.1%; dorsal fin insertion, 49.7-55.3%; anal fin height, 12.0-14.6%; anal fin insertion, 46.3-56.9%; scales superior to lateral line, 3-6; median lateral line scales, 35-43; predorsal scales, 15-23; interdorsal scales, 2-7; scale type, smooth; lateral line type, pored; anal fin rays, 12-19; pectoral fin rays, 10-14; caudal peduncle length, 21.2-25.8%; eye size, 4.5-5.5 mm; mouth width, 3.6-5.1%; mouth height, 5.9-7.2%; mandible length, 8.9-10.9%; gill rakers, 14-18; and vertebrae, 35-40 (Figures 9-30). Means and ranges are consistent with historical data cited by Barbour (1973).

Chirostoma aculeatum (Barbour 1973). *C. aculeatum* occurs throughout the freshwater Lerma River basin of central Mexico. This species was described by Barbour in 1973. Consistent with available taxonomic keys, the individuals of *C. aculeatum* captured during this study were characterized by the following morphological features: total length, 98.0-151.3 mm; standard length, 89.9-136.5 mm; snout length, 10.1-12.3%; head length, 27.8-29.6%; body depth, 16.9-20.7%; pectoral fin insertion, 30.6-37.6%; dorsal fin insertion, 55.1-58.9%; anal fin height, 13.5-17.9%; anal fin insertion, 47.1-55.3%; scales superior to lateral line, 4-6; median lateral line scales, 41-49; predorsal scales, 17-30; interdorsal scales,

3-6; scale type, smooth; lateral line type, canals; anal fin rays, 18-23; pectoral fin rays, 13-15; caudal peduncle length, 18.8-23.2%; eye size, 6.0-7.0 mm; mouth width, 6.1-8.2%; mouth height, 8.9-10.1%; mandible length, 12.5-14.6%; gill rakers, 23-28; and vertebrae, 39-42 (Figures 9-30). Means and ranges are consistent with historical data cited by Barbour (1973).

Chirostoma labarcae (Meek 1902). *C. labarcae* occurs throughout the freshwater Lerma River basin of central Mexico. This species was described by Meek in 1902. Consistent with available taxonomic keys, the individuals of *C. labarcae* captured during this study were characterized by the following morphological features: total length, 74.7-96.5 mm; standard length, 69.1-85.0 mm; snout length, 8.3-9.8%; head length, 23.5-30.6%; body depth, 17.1-18.9%; pectoral fin insertion, 29.9-35.7%; dorsal fin insertion, 53.2-61.1%; anal fin height, 13.5-17.9%; anal fin insertion, 46.1-51.4%; scales superior to lateral line, 4-6; median lateral line scales, 38-47; predorsal scales, 15-25; interdorsal scales, 3-7; scale type, smooth; lateral line type, canals; anal fin rays, 18-23; pectoral fin rays, 12-15; caudal peduncle length, 16.5-21.0%; eye size, 4.9-6.0 mm; mouth width, 4.1-6.8%; mouth height, 6.5-7.4%; mandible length, 9.9-11.8%; gill rakers, 15-20; and vertebrae, 40-43 (Figures 9-30). Means and ranges are consistent with historical data cited by Barbour (1973).

The Lake Chapala Community of Chirostomids

Chirostomid fishes were most likely to occur in shallow, beach-like areas than in deeper open water, although such sampling differences were not quantified. All species of *Chirostoma* occurred throughout all sampling stations except *Chirostoma aculeatum* which was not captured at Jocotepec, the eastern most sampling site, in 1998 or 1999 (Table 3). Females (10,195) were captured more often than males (7,751). The July/August spawning

Table 4. Seasonal catch of nine species of *Chirostoma* occurring in Lake Chapala, Mexico during 1998-1999. Values in parentheses indicate the number of specimens used for morphometric and dietary analyses.

Species	Sampling Seasons			Total
	<u>March</u>	<u>July/August</u>	<u>December</u>	
Jordani Group				
<i>C. jordani</i>	1223 (997)	3332 (2000)	1144 (1000)	5699 (3997)
<i>C. consocium</i>	1344 (988)	2897 (1993)	1198 (985)	5439 (3966)
<i>C. chapalae</i>	1096 (978)	2754 (1999)	1077 (962)	4927 (3939)
<i>C. promelas</i>	953 (822)	1402 (1394)	841 (786)	3196 (3002)
<i>C. sphyraena</i>	779 (768)	1306 (1306)	747 (716)	2832 (2790)
<i>C. lucius</i>	104 (104)	162 (162)	57 (57)	323 (252)
Arge Group				
<i>C. arge</i>	361 (361)	475 (475)	107 (107)	943 (943)
<i>C. labarcae</i>	181 (181)	314 (314)	109 (109)	604 (504)
<i>C. aculeatum</i>	50 (50)	147 (147)	91 (91)	288 (288)

season provided the highest catches (Table 4). Some species were not observed at all sampling stations during each season. For example, *C. aculeatum* was not captured at the Jocotepec sampling station in either 1998 or 1999. Tables 5-9 depict the number of

specimens captured during each sampling effort at the five sampling sites and the number of specimens used for morphometric and dietary analyses.

Differences in distribution and abundance were noted between the phylogentic groups (Figure 31). Jordani Group species were relatively evenly distributed across the west-to-east gradient of Lake Chapala with the exception of *C. lucius* which steadily increased from 19 individuals at Jocotepec, the westernmost sampling area, to a high of 164 individuals at Ocatlan, the easternmost site (Figure 32). Additionally, *C. jordani* was more likely to be captured in shallow water areas than in open water samples. Arge Group species were not evenly distributed across the lake (Figure 33). Each of the three member species of the Arge Group increased in abundance along a west-to-east gradient. *C. aculeatum* was not captured at the westernmost site (Jocotepec).

For the Jordani Group, relative catch numbers indicated that *C. jordani* was the most abundant species and *C. lucius* the least abundant species (Table 10). Additionally, seasonal relative catch numbers indicated that *C. consocium* was the most abundant species in March and December, while *C. jordani* was most abundant in July/August (Table 11). *C. lucius* was the least abundant species during each season.

For the Arge Group, relative catch numbers indicated that *C. arge* was the most abundant species and *C. aculeatum* the least abundant species (Table 10). Seasonally, *C. arge* was the most abundant species in the March and July/August samples, while *C. labarcae* was most abundant in the December samples (Table 11). *C. aculeatum* was the least abundant Arge Group species during each season.

Table 5. Total catch of nine species of *Chirostoma* occurring at the Ajijic sampling site at Lake Chapala during 1998-1999. Values in parentheses are the number of specimens used for morphometric and dietary analyses.

Species	Sampling Season						Combined Seasons
	March 1998	Jul/Aug 1998	December 1998	March 1999	Jul/Aug 1999	December 1999	
Jordani Group							
<i>C. consocium</i>	99 (99)	263 (199)	109 (100)	183 (100)	291 (200)	134 (100)	1223 (799)
<i>C. jordani</i>	97 (97)	317 (200)	104 (100)	121 (100)	362 (200)	146 (100)	1147 (797)
<i>C. chapalae</i>	99 (99)	263 (199)	105 (100)	119 (100)	251 (200)	104 (100)	941 (798)
<i>C. promelas</i>	118 (100)	166 (166)	56 (56)	62 (62)	139 (139)	66 (66)	607 (589)
<i>C. sphyraena</i>	81 (81)	149 (149)	62 (62)	73 (73)	172 (172)	62 (62)	599 (599)
<i>C. lucius</i>	0 (0)	10 (10)	2 (2)	4 (4)	4 (4)	2 (2)	22 (22)
Arge Group							
<i>C. arge</i>	0 (0)	1 (1)	0 (0)	43 (43)	19 (19)	2 (2)	65 (65)
<i>C. labarcae</i>	0 (0)	0 (0)	8 (8)	19 (19)	12 (12)	11 (11)	60 (60)
<i>C. aculeatum</i>	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)	1 (1)

Table 6. Total catch of nine species of *Chirostoma* occurring at the Chapala sampling site at Lake Chapala during 1998-1999. Values in parentheses are the number of specimens used for morphometric and dietary analyses.

Species	Sampling Season						Combined Seasons
	March 1998	Jul/Aug 1998	December 1998	March 1999	Jul/Aug 1999	December 1999	
Jordani Group							
<i>C. consocium</i>	172 (100)	421 (200)	131 (100)	154 (100)	193 (193)	148 (100)	1219 (793)
<i>C. jordani</i>	132 (100)	318 (200)	120 (100)	127 (100)	403 (200)	116 (100)	1216 (800)
<i>C. chapalae</i>	128 (100)	301 (200)	109 (100)	123 (100)	354 (200)	119 (100)	1134 (800)
<i>C. promelas</i>	186 (100)	127 (134)	96 (96)	71 (71)	147 (147)	129 (100)	756 (648)
<i>C. sphyraena</i>	111 (100)	94 (94)	72 (72)	69 (69)	128 (128)	114 (100)	588 (563)
<i>C. lucius</i>	9 (9)	13 (13)	7 (7)	0 (0)	5 (5)	5 (5)	39 (39)
Arge Group							
<i>C. arge</i>	12 (12)	36 (36)	0 (0)	21 (21)	46 (46)	2 (2)	117 (117)
<i>C. labarcae</i>	2 (2)	14 (14)	7 (7)	3 (3)	36 (36)	8 (8)	70 (70)
<i>C. aculeatum</i>	0 (0)	0 (0)	0 (0)	0 (0)	8 (8)	0 (0)	8 (8)

Table 7. Total catch of nine species of *Chirostoma* occurring at the Jocotepec sampling site at Lake Chapala during 1998-1999. Values in parentheses are the number of specimens used for morphometric and dietary analyses.

Species	Sampling Season						Combined Seasons
	March 1998	Jul/Aug 1998	December 1998	March 1999	Jul/Aug 1999	December 1999	
Jordani Group							
<i>C. jordani</i>	124 (100)	306 (200)	111 (100)	122 (100)	384 (200)	113 (100)	1160 (800)
<i>C. chapalae</i>	119 (100)	274 (200)	103 (100)	116 (100)	308 (200)	121 (100)	1041 (800)
<i>C. consocium</i>	142 (100)	293 (200)	114 (100)	133 (100)	218 (200)	117 (100)	1017 (800)
<i>C. promelas</i>	78 (78)	142 (142)	103 (100)	69 (69)	156 (156)	119 (119)	667 (645)
<i>C. sphyraena</i>	99 (99)	181 (181)	33 (33)	54 (54)	125 (125)	42 (42)	534 (534)
<i>C. lucius</i>	3 (3)	0 (0)	0 (0)	7 (7)	9 (9)	0 (0)	19 (19)
Arge Group							
<i>C. labarcae</i>	0 (0)	0 (0)	0 (0)	2 (2)	27 (27)	0 (0)	29 (29)
<i>C. arge</i>	0 (0)	0 (0)	0 (0)	0 (0)	19 (19)	0 (0)	19 (19)
<i>C. aculeatum</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

Table 8. Total catch of nine species of *Chirostoma* occurring at the Mezcala sampling site at Lake Chapala during 1998-1999. Values in parentheses are the number of specimens used for morphometric and dietary analyses.

Species	Sampling Season						Combined Seasons
	March 1998	Jul/Aug 1998	December 1998	March 1999	Jul/Aug 1999	December 1999	
Jordani Group							
<i>C. jordani</i>	141 (100)	362 (200)	101 (100)	116 (100)	381 (200)	127 (100)	1228 (800)
<i>C. consocium</i>	124 (100)	316 (200)	127 (100)	89 (89)	284 (200)	98 (98)	1038 (787)
<i>C. chapalae</i>	102 (100)	251 (200)	116 (100)	104 (100)	296 (20)	112 (100)	981 (800)
<i>C. sphyraena</i>	72 (72)	101 (101)	64 (64)	81 (81)	117 (117)	108 (108)	543 (535)
<i>C. promelas</i>	83 (83)	93 (93)	71 (71)	59 (59)	142 (127)	79 (79)	527 (512)
<i>C. lucius</i>	16 (16)	27 (27)	8 (8)	11 (11)	11 (11)	6 (6)	79 (79)
Arge Group							
<i>C. arge</i>	61 (61)	11 (11)	2 (2)	76 (76)	111 (111)	11 (11)	272 (272)
<i>C. labarcae</i>	17 (17)	9 (9)	0 (0)	19 (19)	60 (60)	2 (2)	107 (107)
<i>C. aculeatum</i>	9 (9)	18 (18)	13 (13)	2 (2)	26 (26)	11 (11)	79 (79)

Table 9. Total catch of nine species of *Chirostoma* occurring at the Ocatlan sampling site at Lake Chapala during 1998-1999. Values in parentheses are the number of specimens used for morphometric and dietary analyses.

	Sampling Season						
Species	March 1998	Jul/Aug 1998	December 1998	March 1999	Jul/Aug 1999	December 1999	Combined Seasons
Jordani Group							
<i>C. jordani</i>	122 (100)	235 (200)	102 (100)	121 (100)	264 (200)	104 (100)	948 (800)
<i>C. consocium</i>	138 (100)	242 (200)	87 (87)	110 (100)	232 (200)	133 (100)	942 (787)
<i>C. chapalae</i>	79 (79)	238 (200)	62 (62)	107 (100)	218 (200)	126 (100)	830 (741)
<i>C. promelas</i>	114 (100)	148 (148)	18 (18)	113 (100)	142(142)	104 (100)	639 (608)
<i>C. sphyraena</i>	81 (81)	127 (127)	81 (81)	58 (58)	112 (112)	109 (109)	658 (557)
<i>C. lucius</i>	54 (54)	40 (40)	13 (13)	0 (0)	43 (43)	14 (14)	164 (164)
Arge Group							
<i>C. arge</i>	71 (71)	98 (98)	51 (51)	77 (77)	134 (134)	39 (39)	470 (470)
<i>C. labarcae</i>	33 (33)	44 (44)	22 (22)	86 (86)	112 (112)	51 (51)	348 (348)
<i>C. aculaetum</i>	26 (26)	47 (47)	41 (41)	13 (13)	47 (47)	26 (26)	200 (200)

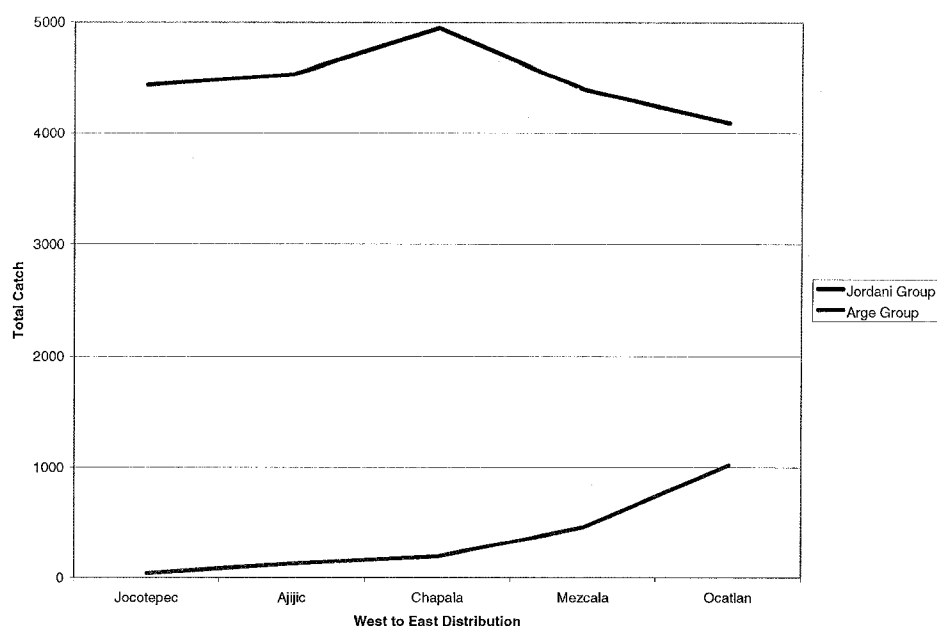


Figure 31. The distribution of Jordani Group and Arge Group chirostomids is depicted for Lake Chapala during 1998-1999.

Dietary Composition of the Chirostoma spp. of Lake Chapala

Little data are available on the dietary composition of the Lake Chapala *Chirostoma* species flock. Of the numerous chirostomid fishes examined, most guts contained readily identifiable food items. Food item identification was sometimes problematic because of digestion, but resolution to taxonomic order or family was usually possible. The nine species of chirostomids in Lake Chapala consumed a diet categorized into twelve food choices (Table 1). Food items which were found to comprise 3.0% or greater of the diet were considered to be major food choices. Those food items comprising less than 3.0% were considered to be minor food items. The pooled dietary data for all nine species was dominated by organic matter ranging from 36.95%-55.35% (mean, 48.8%)(Figure 34). Vegetation (17.7%), chironomids (10.6%), fish (9.8%), crustaceans (6.5%) and algae (4.8%)

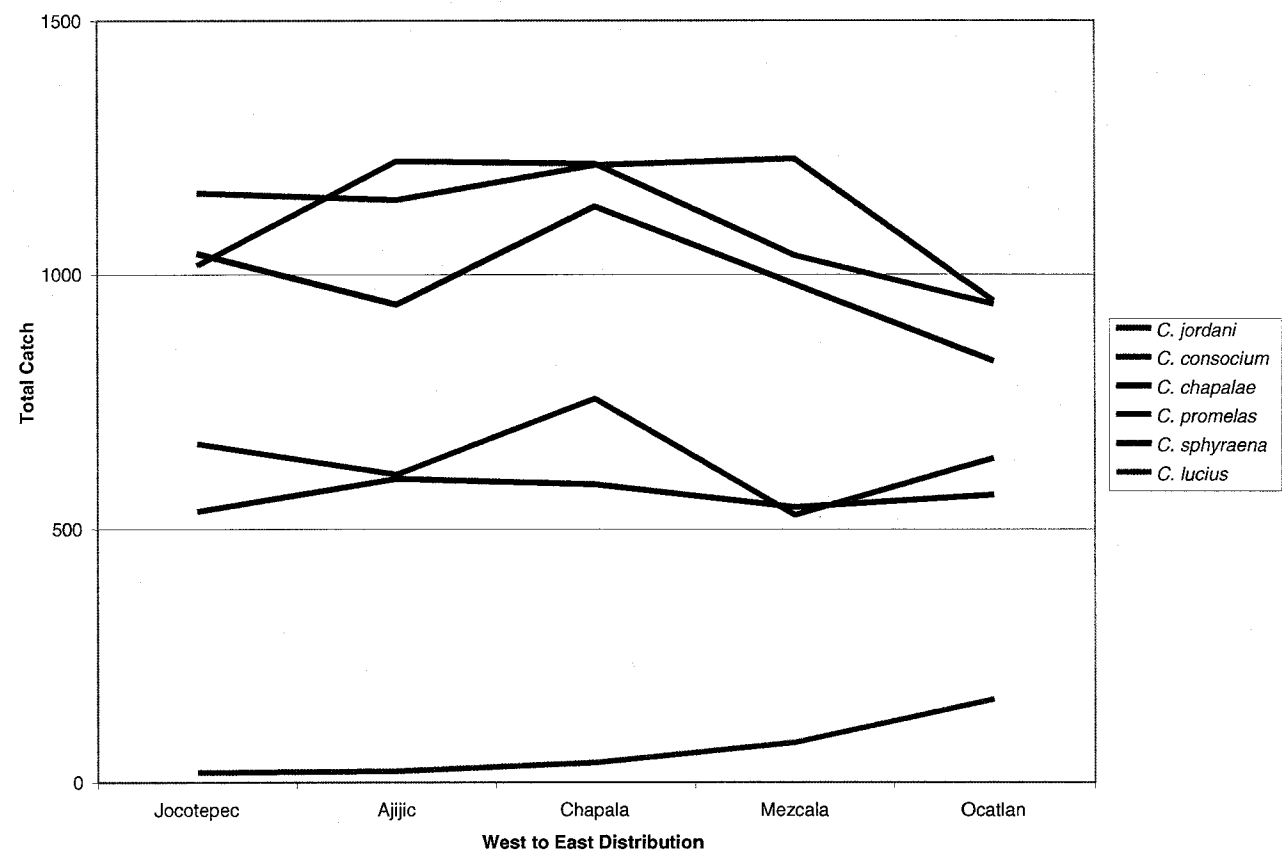


Figure 32. The distribution of six chirostomid species of the Jordani Group at Lake Chapala from 1998-1999.

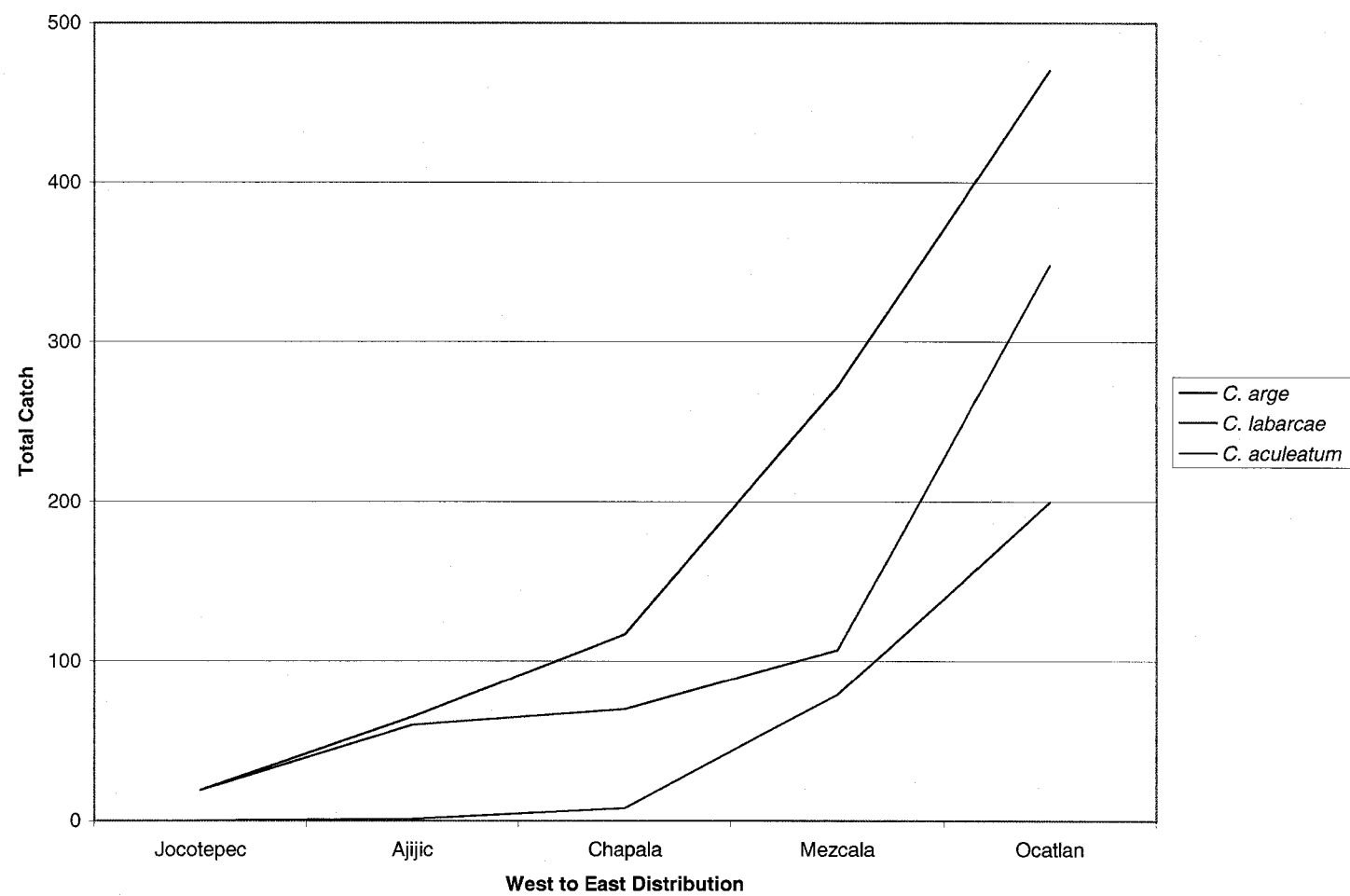


Figure 33. The cumulative distribution of three chirostomid species belonging to the Arge Group at Lake Chapala from 1998-1999.

Table 10. Relative catch of nine species of *Chirostoma* occurring at five stations in Lake Chapala, Mexico during 1998-1999.

Species	Sampling Areas					All Sites Combined
	Jocotepec	Ajijic	Chapala	Mezcala	Ocatlan	
Jordani Group						
<i>C. jordani</i>	25.86%	24.59%	23.63%	25.30%	18.56%	23.49%
<i>C. consocium</i>	22.67%	26.22%	23.68%	21.38%	18.44%	22.42%
<i>C. chapalae</i>	23.21%	20.17%	22.03%	20.21%	16.25%	20.31%
<i>C. promelas</i>	14.87%	13.01%	14.69%	10.86%	12.51%	13.17%
<i>C. sphyraena</i>	11.90%	12.84%	11.42%	11.19%	11.12%	11.67%
<i>C. lucius</i>	0.42%	0.47%	0.76%	1.63%	3.21%	1.33%
Arge Group						
<i>C. arge</i>	0.42%	1.39%	2.27%	5.60%	9.20%	3.89%
<i>C. labarcae</i>	0.42%	1.29%	1.36%	2.20%	6.81%	2.49%
<i>C. aculeatum</i>	0.00%	<0.01%	1.55%	1.63%	3.92%	1.19%

Table 11. Seasonal relative catch of nine species of *Chirostoma* occurring in Lake Chapala, Mexico during 1998-1999.

<u>Species</u>	<u>Sampling Seasons</u>			
	<u>March</u>	<u>Jul / Aug</u>	<u>December</u>	<u>All Seasons Combined</u>
Jordani Group				
<i>C. jordani</i>	20.08%	26.05%	21.30%	23.50%
<i>C. consocium</i>	22.07%	22.65%	22.30%	22.43%
<i>C. chapalae</i>	17.99%	21.53%	20.05%	20.31%
<i>C. promelas</i>	15.65%	10.96%	15.66%	13.18%
<i>C. sphyraena</i>	12.79%	10.21%	13.91%	11.68%
<i>C. lucius</i>	1.71%	1.27%	1.06%	1.33%
Arge Group				
<i>C. arge</i>	5.93%	3.71%	1.99%	3.89%
<i>C. labarcae</i>	2.97%	2.46%	2.03%	2.49%
<i>C. aculeatum</i>	0.82%	1.15%	1.69%	1.19%

comprise the bulk of the remaining diet. Minor dietary choices include amphipods (1.2%), cladocerans (0.3%), ostracods (0.1%), copepods (0.1%), rotifers (0.1%) and oligochaetes (<0.1%).

The Diet of Chirostoma aculeatum

The main components of the diet of *C. aculeatum* were organic matter (54.2%), vegetation (23.1%), chironomids (12.2%) and algae (5.0%)(Figure 35). These components accounted for 94.5% of the diet at all stations (Table 12). Organic matter, vegetation and chironomids and fish dominated dietary compositions throughout all seasons except December (Fish 2.2%)(Table 13).

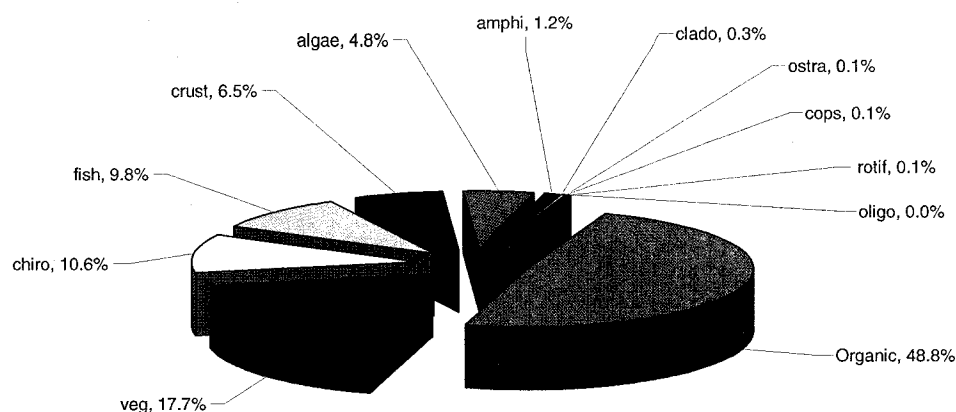


Figure 34. Dietary composition of *Chirostoma* spp. in Lake Chapala, Mexico (1998-1999).

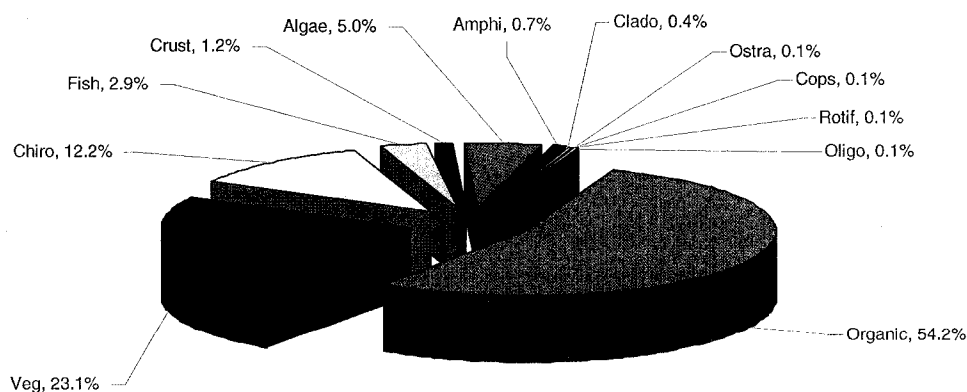


Figure 35. Dietary composition of *Chirostoma aculeatum* in Lake Chapala, Mexico (1998-1999).

Table 12. Dietary composition of *Chirostoma aculeatum* at five sampling stations in Lake Chapala, Mexico (1998-1999).

<u>Food Item</u>	<u>Sampling Areas</u>					<u>All Sites Combined</u>
	<u>Ajijic</u>	<u>Chapala</u>	<u>Jocotepec</u>	<u>Mezcala</u>	<u>Ocatlan</u>	
Organic Matter	44.9%	53.5%	N/A	48.6%	56.5%	54.2%
Vegetation	12.0%	18.1%	N/A	22.5%	23.5%	23.1%
Chironomids	38.3%	15.6%	N/A	19.2%	9.1%	12.2%
Fish	0.0%	7.3%	N/A	2.3%	3.0%	2.9%
Crustacea	0.0%	0.0%	N/A	1.8%	1.0%	1.2%
Algae	3.5%	4.1%	N/A	4.1%	5.4%	5.0%
Amphipods	0.0%	0.5%	N/A	0.5%	0.8%	0.7%
Cladocerans	0.0%	0.4%	N/A	0.7%	0.3%	0.4%
Ostracods	0.6%	0.1%	N/A	0.1%	0.1%	0.1%
Copepods	0.0%	0.2%	N/A	0.1%	0.0%	0.1%
Rotifers	0.6%	0.2%	N/A	0.1%	0.0%	0.1%
Oligochaetes	0.0%	0.0%	N/A	0.1%	0.1%	0.1%

Table 13. Seasonal dietary composition of *Chirostoma aculeatum* in Lake Chapala, Mexico (1998-1999).

<u>Food Item</u>	<u>Sampling Season</u>			<u>All Seasons Combined</u>
	<u>March</u>	<u>July / August</u>	<u>December</u>	
Organic Matter	55.7%	50.9%	58.7%	54.2%
Vegetation	18.8%	24.3%	23.4%	23.1%
Chironomids	13.6%	14.3%	8.0%	12.2%
Fish	3.3%	3.2%	2.2%	2.9%
Crustacea	2.8%	1.0%	0.6%	1.2%
Algae	3.9%	4.9%	5.8%	5.0%
Amphipods	1.0%	0.7%	0.6%	0.7%
Cladocerans	0.4%	0.3%	0.4%	0.4%
Ostracods	0.1%	0.1%	0.1%	0.1%
Copepods	0.1%	0.1%	0.0%	0.1%
Rotifers	0.1%	0.0%	0.0%	0.1%
Oligochaetes	0.2%	0.1%	0.1%	0.1%

The Diet of Chirostoma arge

The main components of the diet of *C. arge* were organic matter (51.1%), algae (14.6%), chironomids (13.1%), vegetation (12.6%), fish (3.1%) and chironomids (3.1%)(Figure 36). These components accounted for 97.6% of the diet at all stations (Table 14). Organic matter, algae, chironomids, vegetation, fish and crustaceans dominated dietary compositions throughout all seasons with two exceptions -- March (fish 2.4%) and December (crustaceans 0.1%)(Table 15).

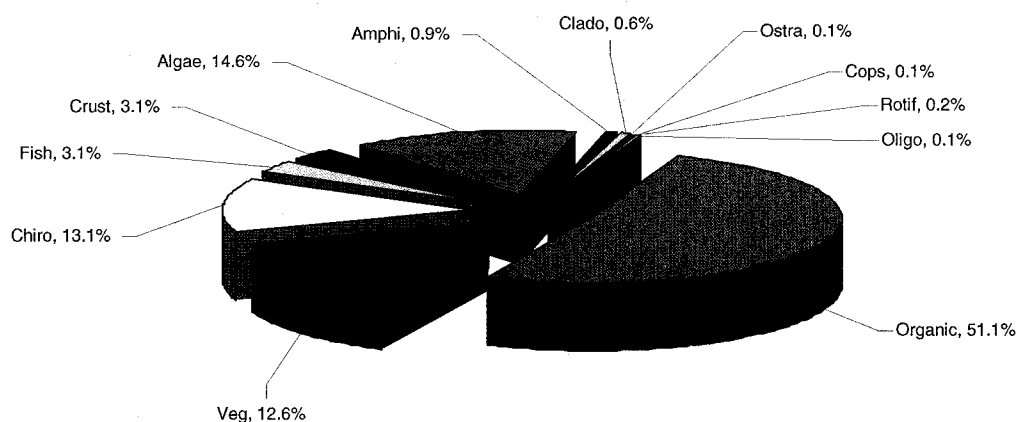


Figure 36. Dietary composition of *Chirostoma arge* in Lake Chapala, Mexico (1998-1999).

The Diet of Chirostoma chapalae

The main components of the diet of *C. chapalae* were organic matter (50.1%), vegetation (15.4%), fish (12.5%), chironomids (10.2%) and crustaceans (8.2%)(Figure 37). These components accounted for 96.4% of the diet at all stations (Table 16). Organic matter, vegetation, fish, chironomids and crustaceans dominated dietary compositions throughout all seasons. Seasonal averages (Table 17) were consistent with overall dietary percentages for

Table 14. Dietary composition of *Chirostoma arge* at five sampling stations in Lake Chapala, Mexico (1998-1999).

<u>Food Item</u>	<u>Sampling Areas</u>					<u>All Sites Combined</u>
	<u>Ajijic</u>	<u>Chapala</u>	<u>Jocotepec</u>	<u>Mezcala</u>	<u>Ocatlan</u>	
Organic Matter	39.5%	49.0%	46.9%	51.2%	53.4%	51.1%
Vegetation	10.8%	11.6%	11.8%	12.5%	13.2%	12.6%
Chironomids	22.6%	17.1%	13.3%	15.0%	9.7%	13.1%
Fish	3.5%	2.9%	6.6%	2.7%	3.1%	3.1%
Crustacea	6.9%	1.9%	1.4%	3.4%	2.7%	3.1%
Algae	10.9%	12.8%	18.8%	14.4%	15.4%	14.6%
Amphipods	0.4%	2.0%	0.5%	0.4%	0.9%	0.9%
Cladocerans	0.2%	0.4%	0.0%	0.2%	0.9%	0.6%
Ostracods	0.0%	0.2%	0.0%	0.0%	0.1%	0.1%
Copepods	0.1%	0.2%	0.0%	0.1%	0.0%	0.1%
Rotifers	2.0%	0.1%	0.5%	0.1%	0.1%	0.2%
Oligochaetes	0.0%	0.1%	0.2%	0.0%	0.1%	0.1%

Table 15. Seasonal dietary composition of *Chirostoma arge* in Lake Chapala, Mexico (1998-1999).

<u>Food Item</u>	<u>Sampling Season</u>			
	<u>March</u>	<u>July / August</u>	<u>December</u>	<u>All Seasons Combined</u>
Organic Matter	50.7%	50.6%	54.7%	51.1%
Vegetation	12.2%	12.6%	14.0%	12.6%
Chironomids	14.5%	12.5%	11.0%	13.1%
Fish	2.4%	3.5%	3.4%	3.1%
Crustacea	3.8%	3.1%	0.1%	3.1%
Algae	13.9%	15.1%	14.6%	14.6%
Amphipods	0.5%	1.1%	1.4%	0.9%
Cladocerans	0.6%	0.7%	0.1%	0.6%
Ostracods	0.0%	0.1%	0.3%	0.1%
Copepods	0.1%	0.1%	0.1%	0.1%
Rotifers	0.4%	0.1%	0.2%	0.2%
Oligochaetes	0.0%	0.1%	0.2%	0.1%

the genus (Figure 34). Copepod composition fluctuated from 0.2%-0.8% seasonally and was significantly higher than the overall genus average of 0.1%.

The Diet of Chirostoma consocium

The main components of the diet of *C. consocium* were organic matter (36.9%), vegetation (18.2%), chironomids (13.1%), fish (13.8%), crustaceans (8.6%) and algae (7.7%)(Figure 38). These components accounted for 98.3% of the diet at all stations (Table 18). Organic matter, vegetation, fish, chironomids, crustaceans and algae dominated dietary compositions throughout all seasons (Table 19).

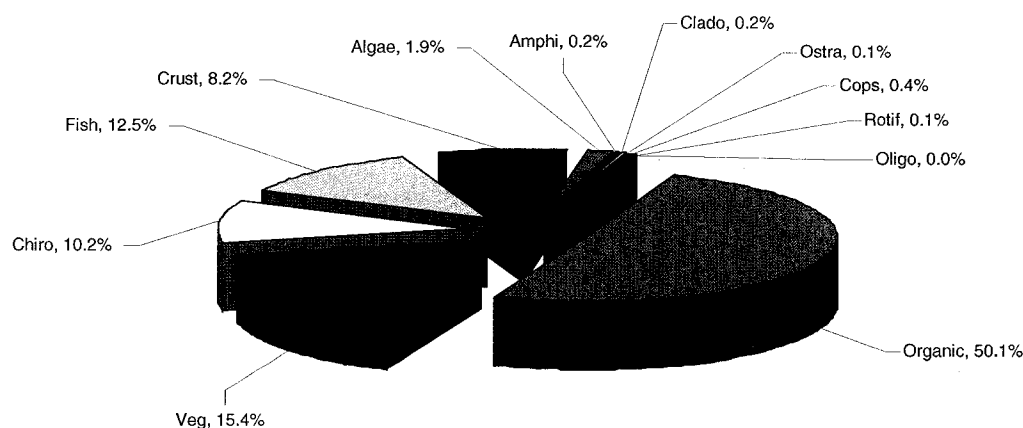


Figure 37. Dietary composition of *Chirostoma chapalae* in Lake Chapala, Mexico (1998-1999).

The Diet of Chirostoma jordani

The main components of the diet of *C. jordani* were organic matter (47.7%), vegetation (16.1%), chironomids (13.1%), fish (8.7%), crustaceans (6.6%) and algae (5.4%)(Figure 39). These components accounted for 97.6% of the diet at all stations (Table 20). Organic matter, vegetation, chironomids, fish, crustaceans and algae dominated dietary

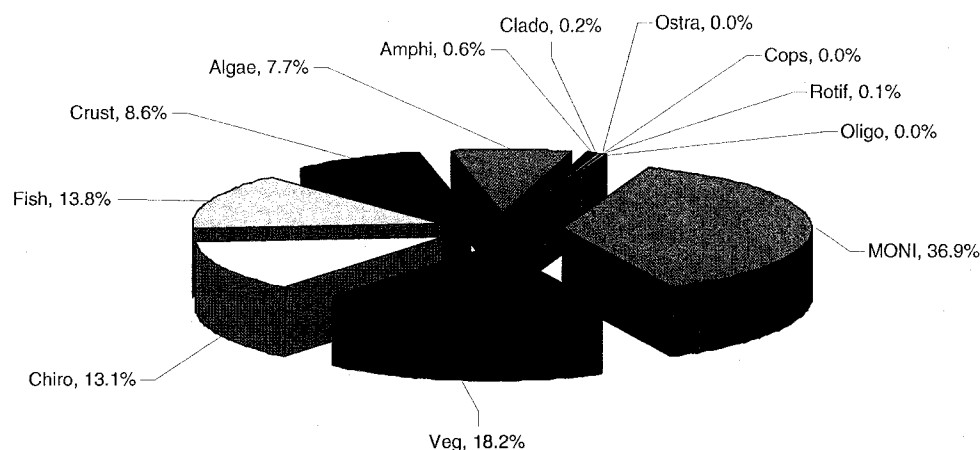


Figure 38. Dietary composition of *Chirostoma consocium* in Lake Chapala, Mexico (1998-1999).

compositions throughout all seasons (Table 21). Amphipods ranged from 0.5-0.7% of the diet seasonally which was significantly lower than the overall genus average of 1.2%

The Diet of Chirostoma labarcae

The main components of the diet of *C. labarcae* were organic matter (43.9%), chironomids (21.4%), vegetation (19.8%), algae (4.7%), fish (3.6%) and crustaceans (3.4%)(Figure 40). The only major dietary components (>3.0%) for *C. labarcae* at the Jocotepec sampling site were organic matter (40.3%), chironomids (35.9%) and vegetation (13.6%). These components accounted for 97.6% of the diet at all stations (Table 22).

The Diet of Chirostoma labarcae

Organic matter, chironomids, vegetation, algae, fish and crustaceans dominated dietary compositions throughout all seasons except December (Fish 2.1%)(Table 23).

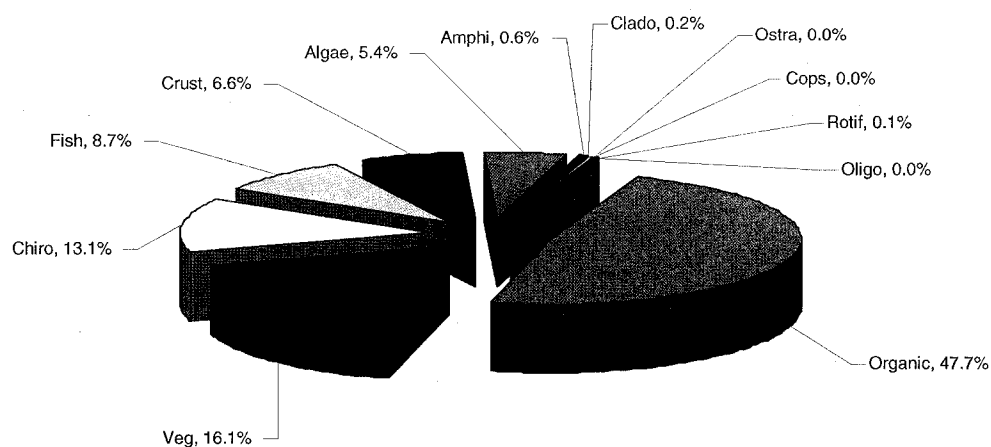


Figure 39. Dietary composition of *Chirostoma jordani* in Lake Chapala, Mexico (1998-1999).

Amphipods ranged from 1.3-2.4% of the diet seasonally which was generally higher than the overall genus average of 1.2%.

The Diet of Chirostoma lucius

The main components of the diet of *C. lucius* were organic matter (42.8%), fish (37.2%), crustaceans (6.8%) and chironomids (5.0%)(Figure 41). These components accounted for 91.8% of the diet at all stations (Table 24). *C. lucius* consumed nearly three times more fish than the genus average. Organic matter, fish, crustaceans and chironomids dominated dietary compositions throughout all seasons (Table 25).

The Diet of Chirostoma promelas

The main components of the diet of *C. promelas* were organic matter (55.3%), vegetation (21.5%), chironomids (5.4%), amphipods (5.4%), fish (4.5%) and crustaceans

Table 16. Dietary composition of *Chirostoma chapalae* at five sampling stations in Lake Chapala, Mexico (1998-1999).

<u>Food Item</u>	<u>Sampling Areas</u>					<u>All Sites Combined</u>
	<u>Ajijic</u>	<u>Chapala</u>	<u>Jocotepec</u>	<u>Mezcala</u>	<u>Ocatlan</u>	
Organic Matter	44.8%	49.8%	51.7%	51.4%	53.2%	50.1%
Vegetation	13.6%	15.1%	16.2%	15.9%	16.0%	15.4%
Chironomids	9.0%	9.9%	10.1%	11.8%	10.1%	10.2%
Fish	14.5%	12.0%	11.5%	12.9%	11.2%	12.5%
Crustacea	12.1%	9.4%	6.8%	5.9%	6.9%	8.2%
Algae	2.4%	1.9%	2.4%	1.4%	1.2%	1.9%
Amphipods	0.2%	0.3%	0.1%	0.2%	0.3%	0.2%
Cladocerans	0.2%	0.2%	0.2%	0.2%	0.3%	0.2%
Ostracods	0.1%	0.1%	0.0%	0.0%	0.1%	0.1%
Copepods	0.8%	0.4%	0.2%	0.2%	0.2%	0.4%
Rotifers	0.1%	0.1%	0.1%	0.0%	0.1%	0.1%
Oligochaetes	0.0%	0.0%	0.0%	0.0%	0.1%	0.0%

Table 17. Seasonal dietary composition of *Chirostoma chapalae* in Lake Chapala, Mexico (1998-1999).

<u>Food Item</u>	<u>Sampling Season</u>			
	<u>March</u>	<u>July / August</u>	<u>December</u>	<u>All Seasons Combined</u>
Organic Matter	52.2%	49.5%	49.2%	50.1%
Vegetation	15.3%	15.3%	15.7%	15.4%
Chironomids	9.7%	10.1%	10.8%	10.2%
Fish	11.9%	13.2%	11.5%	12.5%
Crustacea	7.1%	8.5%	8.8%	8.2%
Algae	1.6%	1.9%	2.1%	1.9%
Amphipods	0.1%	0.3%	0.2%	0.2%
Cladocerans	0.1%	0.3%	0.2%	0.2%
Ostracods	0.0%	0.1%	0.1%	0.1%
Copepods	0.4%	0.4%	0.3%	0.4%
Rotifers	0.1%	0.1%	0.1%	0.1%
Oligochaetes	0.0%	0.1%	0.0%	0.0%

Table 18. Dietary composition of *Chirostoma consocium* at five sampling stations in Lake Chapala, Mexico (1998-1999).

<u>Food Item</u>	<u>Sampling Areas</u>					<u>All Sites Combined</u>
	<u>Ajijic</u>	<u>Chapala</u>	<u>Jocotepec</u>	<u>Mezcala</u>	<u>Ocatlan</u>	
Organic Matter	33.1%	37.1%	37.8%	38.7%	37.8%	36.9%
Vegetation	13.4%	16.1%	19.8%	21.0%	20.7%	18.2%
Chironomids	10.8%	13.4%	13.0%	12.5%	15.8%	13.1%
Fish	16.4%	16.1%	12.5%	12.3%	11.4%	13.8%
Crustacea	14.0%	8.9%	8.1%	6.7%	5.0%	8.6%
Algae	9.3%	6.5%	7.4%	7.5%	7.6%	7.7%
Amphipods	0.5%	0.6%	0.3%	0.8%	0.9%	0.6%
Cladocerans	0.1%	0.3%	0.3%	0.2%	0.2%	0.2%
Ostracods	0.0%	0.2%	0.0%	0.0%	0.0%	0.0%
Copepods	0.0%	0.1%	0.0%	0.1%	0.0%	0.0%
Rotifers	0.5%	0.1%	0.1%	0.1%	0.1%	0.1%
Oligochaetes	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%

Table 19. Seasonal dietary composition of *Chirostoma consocium* in Lake Chapala, Mexico (1998-1999).

<u>Food Item</u>	<u>Sampling Season</u>			<u>All Seasons Combined</u>
	<u>March</u>	<u>July / August</u>	<u>December</u>	
Organic Matter	35.3%	36.6%	39.1%	36.9%
Vegetation	19.5%	18.2%	16.9%	18.2%
Chironomids	8.8%	14.7%	14.1%	13.1%
Fish	14.8%	13.2%	13.8%	13.8%
Crustacea	10.9%	8.1%	7.2%	8.6%
Algae	8.5%	7.3%	7.6%	7.7%
Amphipods	0.4%	0.9%	0.3%	0.6%
Cladocerans	0.1%	0.2%	0.3%	0.2%
Ostracods	0.0%	0.1%	0.0%	0.0%
Copepods	0.0%	0.0%	0.1%	0.0%
Rotifers	0.3%	0.1%	0.1%	0.1%
Oligochaetes	0.0%	0.0%	0.0%	0.0%

Table 20. Dietary composition of *Chirostoma jordani* at five sampling stations in Lake Chapala, Mexico (1998-1999).

<u>Food Item</u>	<u>Sampling Areas</u>					<u>All Sites Combined</u>
	<u>Ajijic</u>	<u>Chapala</u>	<u>Jocotepec</u>	<u>Mezcala</u>	<u>Ocatlan</u>	
Organic Matter	45.8%	47.1%	47.2%	48.3%	49.9%	47.7%
Vegetation	15.1%	16.5%	15.6%	16.3%	17.1%	16.1%
Chironomids	15.3%	13.1%	14.3%	11.7%	10.9%	13.1%
Fish	6.0%	10.2%	9.1%	10.9%	7.3%	8.7%
Crustacea	8.8%	6.5%	6.2%	4.5%	7.3%	6.6%
Algae	4.6%	4.5%	5.7%	6.0%	6.0%	5.4%
Amphipods	0.4%	0.5%	0.4%	0.5%	1.0%	0.6%
Cladocerans	0.2%	0.2%	0.1%	0.3%	0.3%	0.2%
Ostracods	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Copepods	0.0%	0.1%	0.0%	0.1%	0.1%	0.0%
Rotifers	0.1%	0.1%	0.2%	0.1%	0.0%	0.1%
Oligochaetes	0.0%	0.0%	0.0%	0.0%	0.1%	0.0%

Table 21. Seasonal dietary composition of *Chirostoma jordani* in Lake Chapala, Mexico (1998-1999).

<u>Food Item</u>	<u>Sampling Season</u>			<u>All Seasons Combined</u>
	<u>March</u>	<u>July / August</u>	<u>December</u>	
Organic Matter	49.9%	46.5%	47.9%	47.7%
Vegetation	16.5%	15.9%	16.3%	16.1%
Chironomids	14.9%	12.8%	11.8%	13.1%
Fish	3.9%	9.2%	12.6%	8.7%
Crustacea	6.0%	7.8%	4.9%	6.6%
Algae	6.0%	5.2%	5.0%	5.4%
Amphipods	0.5%	0.5%	0.7%	0.6%
Cladocerans	0.3%	0.2%	0.2%	0.2%
Ostracods	0.0%	0.0%	0.1%	0.0%
Copepods	0.0%	0.1%	0.0%	0.0%
Rotifers	0.1%	0.2%	0.1%	0.1%
Oligochaetes	0.0%	0.0%	0.0%	0.0%

Table 22. Dietary composition of *Chirostoma labarcae* at five sampling stations in Lake Chapala, Mexico (1998-1999).

<u>Food Item</u>	<u>Sampling Areas</u>					<u>All Sites Combined</u>
	<u>Ajijic</u>	<u>Chapala</u>	<u>Jocotepec</u>	<u>Mezcala</u>	<u>Ocatlan</u>	
Organic Matter	42.4%	41.2%	40.4%	44.0%	43.9%	43.3%
Vegetation	13.9%	1.4%	13.6%	22.4%	24.1%	19.8%
Chironomids	24.8%	41.9%	35.9%	13.2%	18.0%	21.4%
Fish	4.5%	0.9%	0.9%	7.4%	3.0%	3.6%
Crustacea	4.8%	2.5%	0.4%	3.0%	3.7%	3.4%
Algae	3.6%	4.9%	2.7%	4.3%	5.1%	4.7%
Amphipods	2.7%	4.6%	5.6%	2.6%	1.2%	2.2%
Cladocerans	0.9%	0.7%	0.0%	0.9%	0.3%	0.5%
Ostracods	0.0%	0.1%	0.0%	0.0%	0.1%	0.2%
Copepods	0.3%	0.2%	0.4%	0.1%	0.2%	0.1%
Rotifers	0.1%	0.2%	0.0%	0.1%	0.2%	0.1%
Oligochaetes	0.0%	0.1%	0.1%	0.2%	0.1%	0.2%

Table 23. Seasonal dietary composition of *Chirostoma labarcae* in Lake Chapala, Mexico (1998-1999).

<u>Food Item</u>	<u>Sampling Season</u>			<u>All Seasons Combined</u>
	<u>March</u>	<u>July / August</u>	<u>December</u>	
Organic Matter	44.6%	43.6%	40.3%	43.3%
Vegetation	21.9%	19.1%	18.4%	19.8%
Chironomids	17.9%	21.6%	26.6%	21.4%
Fish	3.5%	4.0%	2.1%	3.6%
Crustacea	3.8%	3.0%	3.8%	3.4%
Algae	4.6%	4.6%	5.1%	4.7%
Amphipods	2.4%	2.3%	1.3%	2.2%
Cladocerans	0.2%	0.5%	0.8%	0.5%
Ostracods	0.0%	0.1%	0.0%	0.2%
Copepods	0.3%	0.1%	0.3%	0.1%
Rotifers	0.1%	0.2%	0.2%	0.1%
Oligochaetes	0.1%	0.1%	0.0%	0.2%

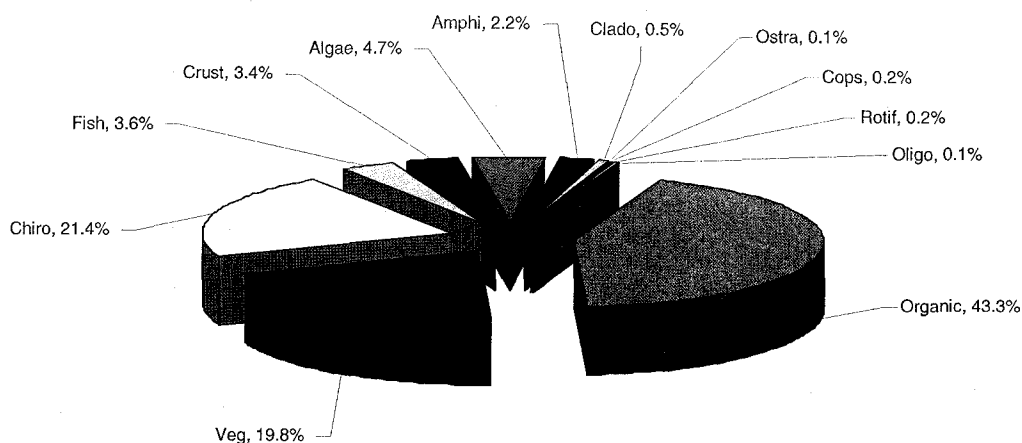


Figure 40. Dietary composition of *Chirostoma labarcae* in Lake Chapala, Mexico (1998-1999).

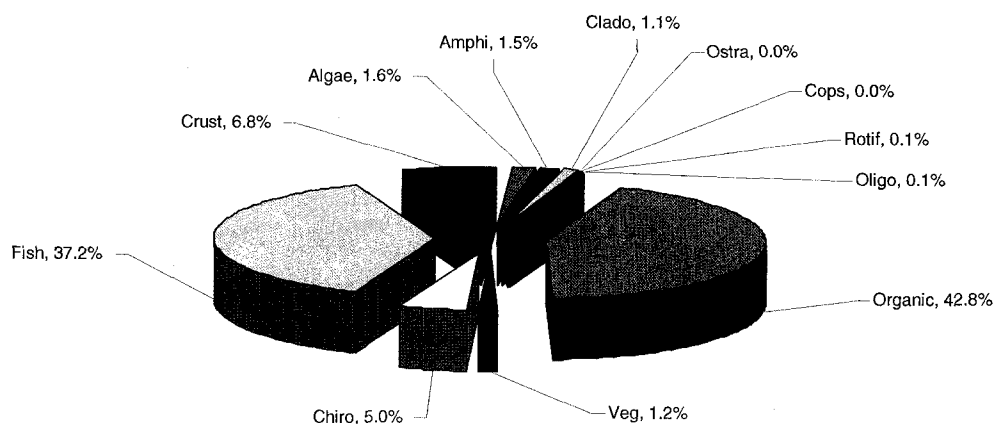


Figure 41. Dietary composition of *Chirostoma lucius* in Lake Chapala, Mexico (1998-1999).

(4.2%)(Figure 42). These components accounted for 99.2% of the diet (Table 26). Organic matter, vegetation, chironomids, amphipods, fish and crustaceans dominated dietary compositions throughout all seasons (Table 27). Amphipods ranged from 4.3-5.3% of the

diet seasonally which was approximately four to five times the overall genus average of 1.2%. *C. promelas* consumed more vegetation (mean 21.5%) than the overall genus average of 17.7%.

The Diet of Chirostoma sphyraena

The main components of the diet of *C. sphyraena* were organic matter (54.3%), vegetation (20.9%), fish (9.2%), crustaceans (5.4%), chironomids (4.9%) and algae (3.4%)(Figure 43). These components accounted for 98.1% of the diet (Table 28). Organic matter, vegetation, fish, crustaceans, chironomids and algae dominated dietary compositions throughout all seasons (Table 29). *C. sphyraena* consumed significantly fewer amphipods (0.3%) and chironomids (4.9%) than the overall genus averages (1.2%) and (10.6%) respectively.

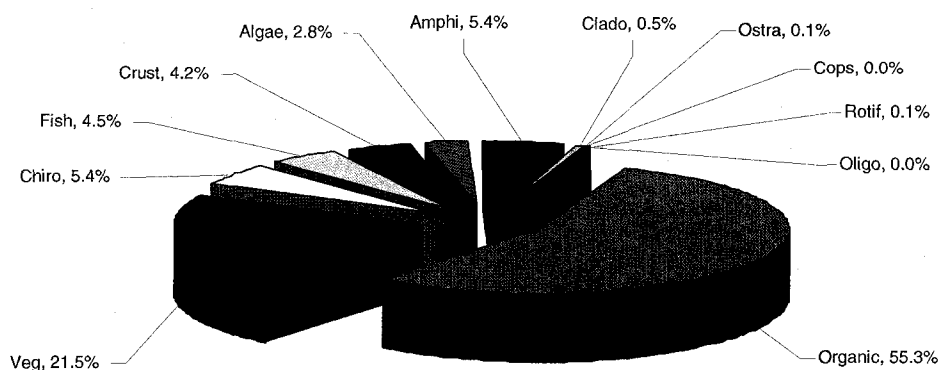


Figure 42. Dietary composition of *Chirostoma promelas* in Lake Chapala, Mexico (1998-1999).

Table 24. Dietary composition of *Chirostoma lucius* at five sampling stations in Lake Chapala, Mexico (1998-1999).

<u>Food Item</u>	<u>Sampling Areas</u>					<u>All Sites Combined</u>
	<u>Ajijic</u>	<u>Chapala</u>	<u>Jocotepec</u>	<u>Mezcala</u>	<u>Ocatlan</u>	
Organic Matter	39.7%	36.4%	45.5%	39.8%	46.4%	42.8%
Vegetation	0.3%	0.7%	0.9%	1.2%	1.5%	1.2%
Chironomids	4.4%	4.6%	7.1%	6.1%	4.3%	5.0%
Fish	43.2%	46.7%	37.0%	38.2%	33.1%	37.2%
Crustacea	9.7%	6.5%	3.7%	7.1%	6.7%	6.8%
Algae	0.9%	0.8%	1.4%	1.6%	2.0%	1.6%
Amphipods	1.2%	1.5%	2.5%	1.4%	1.5%	1.5%
Cladocerans	0.5%	2.8%	1.6%	2.0%	0.2%	1.1%
Ostracods	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Copepods	0.0%	0.0%	0.0%	0.0%	0.1%	0.0%
Rotifers	0.1%	0.0%	0.1%	0.0%	0.1%	0.1%
Oligochaetes	0.0%	0.0%	0.1%	0.0%	0.1%	0.1%

Table 25. Seasonal dietary composition of *Chirostoma lucius* in Lake Chapala, Mexico (1998-1999).

<u>Food Item</u>	<u>Sampling Season</u>			
	<u>March</u>	<u>July / August</u>	<u>December</u>	<u>All Seasons Combined</u>
Organic Matter	43.6%	40.9%	47.2%	42.8%
Vegetation	1.3%	1.0%	1.3%	1.2%
Chironomids	4.6%	3.9%	8.8%	5.0%
Fish	38.8%	38.5%	31.1%	37.2%
Crustacea	4.9%	8.0%	6.2%	6.8%
Algae	1.8%	1.5%	1.7%	1.6%
Amphipods	2.1%	1.2%	1.4%	1.5%
Cladocerans	1.6%	0.5%	2.1%	1.1%
Ostracods	0.0%	0.0%	0.0%	0.0%
Copepods	0.1%	0.0%	0.0%	0.0%
Rotifers	0.1%	0.1%	0.0%	0.1%
Oligochaetes	0.1%	0.0%	0.1%	0.1%

Table 26. Dietary composition of *Chirostoma promelas* at five sampling stations in Lake Chapala, Mexico (1998-1999).

<u>Food Item</u>	<u>Sampling Areas</u>					<u>All Sites Combined</u>
	<u>Ajijic</u>	<u>Chapala</u>	<u>Jocotepec</u>	<u>Mezcala</u>	<u>Ocatlan</u>	
Organic Matter	56.3%	52.9%	52.4%	58.1%	55.3%	55.3%
Vegetation	17.2%	22.3%	22.0%	23.4%	21.5%	21.5%
Chironomids	4.2%	6.2%	5.1%	6.4%	5.4%	5.4%
Fish	4.3%	4.9%	5.4%	2.7%	4.5%	4.5%
Crustacea	6.2%	3.7%	5.7%	2.9%	4.2%	4.2%
Algae	2.9%	2.7%	2.7%	3.0%	2.8%	2.8%
Amphipods	6.1%	6.3%	5.6%	2.9%	5.4%	5.4%
Cladocerans	0.1%	0.9%	0.1%	0.3%	0.5%	0.5%
Ostracods	0.0%	0.1%	0.1%	0.1%	0.1%	0.1%
Copepods	0.1%	0.0%	0.0%	0.1%	0.0%	0.0%
Rotifers	0.2%	0.1%	0.1%	0.1%	0.1%	0.1%
Oligochaetes	0.0%	0.0%	0.0%	0.1%	0.0%	0.0%

Table 27. Seasonal dietary composition of *Chirostoma promelas* in Lake Chapala, Mexico (1998-1999).

<u>Food Item</u>	<u>Sampling Season</u>			
	<u>March</u>	<u>July / August</u>	<u>December</u>	<u>All Seasons Combined</u>
Organic Matter	56.7%	53.8%	56.5%	55.3%
Vegetation	22.1%	21.1%	21.5%	21.5%
Chironomids	4.6%	5.8%	5.7%	5.4%
Fish	3.5%	5.2%	4.4%	4.5%
Crustacea	4.9%	4.3%	3.3%	4.2%
Algae	2.7%	2.8%	2.7%	2.8%
Amphipods	4.3%	5.3%	4.9%	5.4%
Cladocerans	0.4%	0.6%	0.2%	0.5%
Ostracods	0.1%	0.1%	0.1%	0.1%
Copepods	0.1%	0.0%	0.0%	0.0%
Rotifers	0.1%	0.1%	0.1%	0.1%
Oligochaetes	0.0%	0.0%	0.0%	0.0%

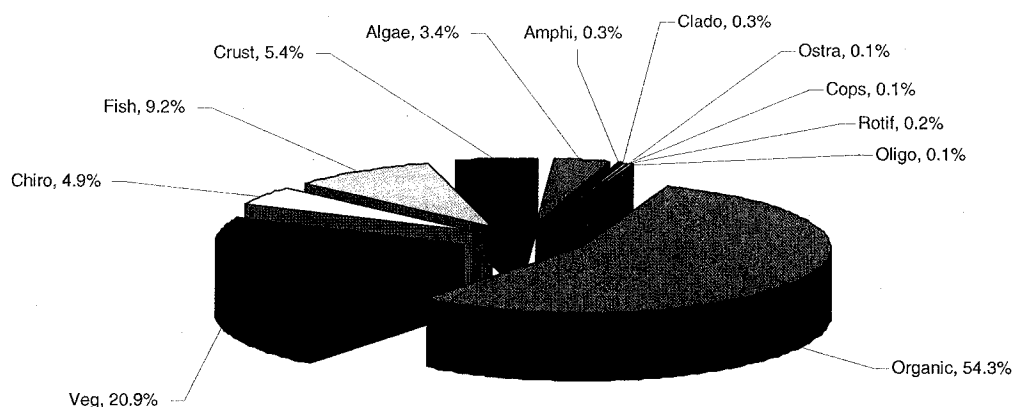


Figure 43. Dietary composition of *Chirostoma sphyraena* in Lake Chapala, Mexico (1998-1999).

Statistical Analysis of Dietary Data

Dietary analyses were designed to discern whether differences in diet would reveal any potential partitioning of dietary resources and explain how the species flock maintained species integrity. Various statistical methods were used to examine and identify any dietary trends.

Student's t Test

Student's t tests were used to evaluate whether male chirostomids consumed significantly different amounts of prey than females. These analyses failed to demonstrate differences in the amounts of prey (gut fullness) consumed by males and females. Female chirostomids did not consume significantly different amounts of prey than males during any season or for all seasons combined.

Table 28. Dietary composition of *Chirostoma sphyraena* at five sampling stations in Lake Chapala, Mexico (1998-1999).

<u>Food Item</u>	<u>Sampling Areas</u>					<u>All Sites Combined</u>
	<u>Ajijic</u>	<u>Chapala</u>	<u>Jocotepec</u>	<u>Mezcala</u>	<u>Ocatlan</u>	
Organic Matter	51.3%	57.5%	53.0%	56.5%	53.6%	54.3%
Vegetation	20.7%	15.3%	23.0%	23.7%	22.0%	20.9%
Chironomids	3.6%	6.5%	4.5%	4.4%	5.3%	4.9%
Fish	10.6%	10.4%	9.3%	7.3%	8.1%	9.2%
Crustacea	7.6%	5.0%	5.9%	3.5%	5.1%	5.4%
Algae	3.4%	3.0%	3.2%	3.7%	3.6%	3.4%
Amphipods	0.3%	0.4%	0.3%	0.2%	0.3%	0.3%
Cladocerans	0.1%	0.5%	0.0%	0.3%	0.5%	0.3%
Ostracods	0.1%	0.1%	0.0%	0.0%	0.0%	0.1%
Copepods	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%
Rotifers	0.1%	0.2%	0.1%	0.1%	0.2%	0.2%
Oligochaetes	0.0%	0.1%	0.0%	0.0%	0.1%	0.1%

Table 29. Seasonal dietary composition of *Chirostoma sphyraena* in Lake Chapala, Mexico (1998-1999).

<u>Food Item</u>	<u>Sampling Season</u>			
	<u>March</u>	<u>July / August</u>	<u>December</u>	<u>All Seasons Combined</u>
Organic Matter	55.2%	53.0%	55.7%	54.3%
Vegetation	21.5%	20.6%	20.8%	20.9%
Chironomids	5.2%	5.0%	4.2%	4.9%
Fish	8.0%	10.4%	8.2%	9.2%
Crustacea	5.1%	5.7%	5.4%	5.4%
Algae	3.4%	3.3%	3.5%	3.4%
Amphipods	0.3%	0.3%	0.3%	0.3%
Cladocerans	0.2%	0.2%	0.5%	0.3%
Ostracods	0.0%	0.1%	0.0%	0.1%
Copepods	0.1%	0.1%	0.1%	0.1%
Rotifers	0.1%	0.2%	0.2%	0.2%
Oligochaetes	0.0%	0.0%	0.1%	0.1%

Spearman's Rank Order Correlation Analyses

Spearman's Rank Order Correlation Coefficients were performed to determine whether individual morphological characters correlated to dietary preferences.

Morphological characters to be used in these analyses were identified based on reasonable biological processes. The following morphological characters were used in Spearman's calculations: mouth width, mouth height, mandible length, eye size, gill raker numbers, total length, and standard length. All dietary variables were included with the exception of organic matter since it was believed that organic matter was not a dietary variable which was thought to be affected by morphology.

No readily apparent trends were noted in the Spearman's analyses. Although rare correlations occurred (e.g., eye size versus fish percentages), the correlations were weak (0.65 for eye size - fish composition, $\alpha = 0.05$) or made little biological sense. This method of analysis failed to reveal the subtleties of dietary differences among the nine species. Single morphological characters were not useful as a predictor of dietary composition.

Spearman's rank order correlation analyses were also performed on combined data from the March, July-August, and December samples as well as the combined data from Jocotepec, Ajijic, Chapala, Mezcala, and Ocatlan. In all cases, strong negative correlations resulted which indicated that no differences in dietary composition occurred between the diets of males and females of chirostomid fishes. Sex was not useful as a predictor of dietary composition.

Discriminant Analysis

A parametric stepwise DFA was initially performed on the dietary data. This parametric test can effectively discern differences in diet among the nine chirostomid species even though the dietary data was not normally distributed. Huberty (1994) stated that analysis was appropriate as a descriptive discriminant analysis technique when the purpose of the research was to describe group differences or to predict group membership on the basis of response variable measures. Similarly, Whitaker (1997) stated that parametric DFA validly represented variables for a discriminating model and could be used cautiously to imply differences among groups, especially if follow-up corroborative analyses were employed.

Stepwise DFA produced scattergrams that allow initial visual assessments of differences among species. The parametric scattergram for chirostomid data combined from 1998-1999 gave no clear indication of separation among species and initially suggested that few differences occurred among the diets of the nine species (Figure 44). Similarly, scattergrams comparing species within each site (Figures 45-49) and within each season (Figures 50-52) failed to clearly show separation among the nine species. However, the pairwise squared distances data and Mahalanobis distances data which established the SAS scattergram indicated that dietary differences did occur among the nine species of *Chirostoma* and that further examination of the data were warranted.

Since the dietary data failed to meet the assumptions of normality but indications of further analyses were shown, a nonparametric stepwise DFA was performed. This test does not assume normality. The discriminatory ability of the statistical model underlying this nonparametric analysis is measured by Wilkes Lambda (Λ) which indicates the probability that group separation is significant.

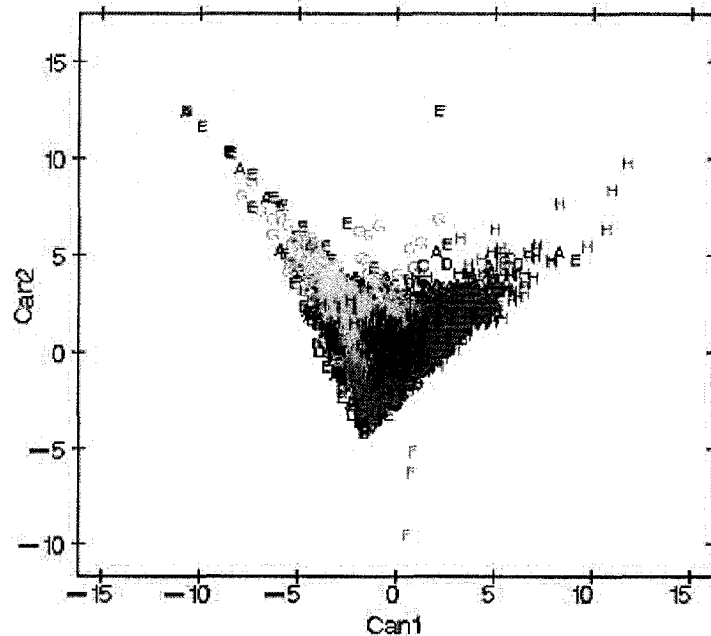


Figure 44. Parametric scattergram of the diet from the genus *Chirostoma* at Lake Chapala, Mexico during 1998-1999. The scattergram is derived from parametric DFA results of the total pooled data collected during 1998-1999. Letters indicate species.

Significant differences were indicated at each site (Table 30). Similarly, pooled diet data from all sites as well as seasonal data revealed significant differences among the nine species (Table 30).

Although the nonparametric stepwise DFA indicates significant differences in diets among species, it did not reveal which dietary components had variation most responsible for discriminating among species. Further examination of the data was required to discover which specific food items accounted for differences among the species. MANOVA was appropriate for this examination.

Table 30. Nonparametric discriminant analysis provides the Wilkes Lambda, a descriptive statistic which indicates differences in groups if significant. The probability that group separation is significant is indicated if the Wilkes Lambda is greater than the a priori probability, in this case 0.0001. All cases were found to indicate significant differences.

Sampling Area / Season	Wilkes Lambda	Probability < Lambda
Ajijic	0.367	0.0001
Chapala	0.350	0.0001
Jocotepec	0.361	0.0001
Mezcala	0.395	0.0001
Ocatlan	0.323	0.0001
All Sites Combined	0.391	0.0001
March	0.384	0.0001
July / August	0.393	0.0001
December	0.437	0.0001

MANOVA and Related Analyses

Whitaker (1997) stated MANOVA tests combined with DFA can elucidate the variables most responsible for group separation when group differences were known to occur. Whitaker further stated that DFA are statistically interdependent with MANOVA results and recommend that MANOVA be performed. He concluded that DFA should be checked and validated with MANOVA results. However, MANOVA require that the most relevant variables (e.g., food items) be identified and included in the test. I used canonical DFA to identify the most explanatory group of variables.

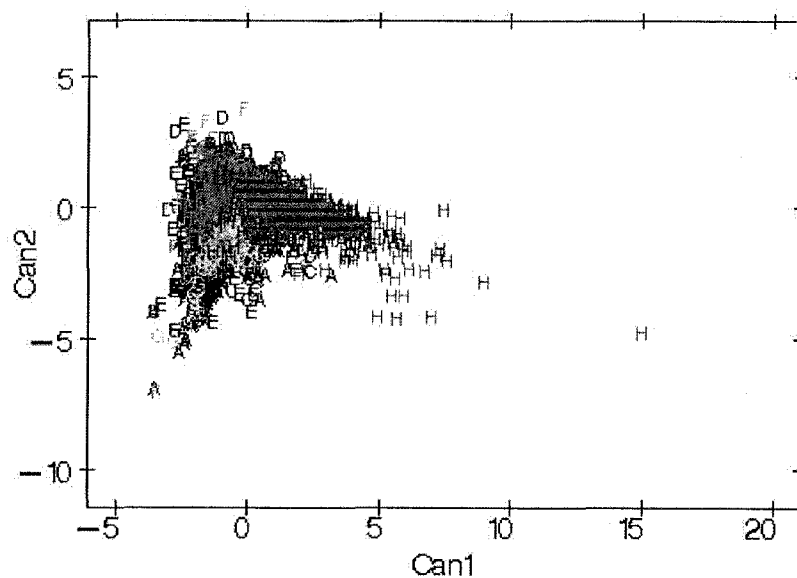


Figure 45. Parametric scattergram of the diet from the genus *Chirostoma* at the Ajijic sampling station. The scattergram is derived from parametric DFA results of the total pooled data collected at Ajijic during 1998-1999.

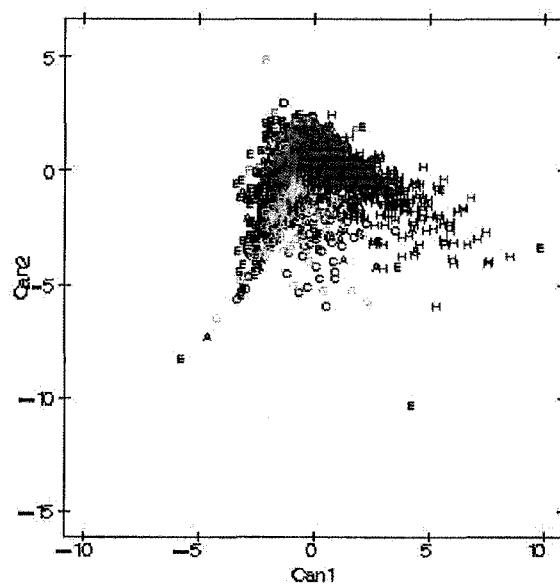


Figure 46. Parametric scattergram of the diet from the genus *Chirostoma* at the Chapala sampling station. The scattergram is derived from parametric DFA results of the total pooled data collected at Chapala during 1998-1999.

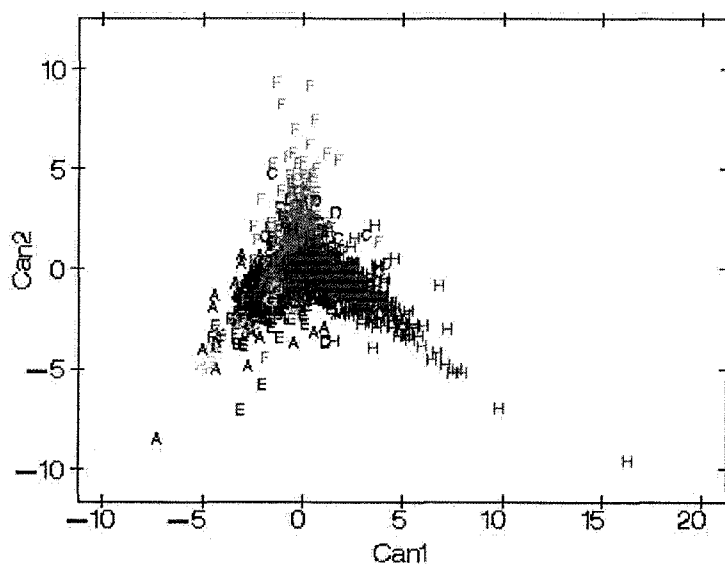


Figure 47. Parametric scattergram of the diet from the genus *Chirostoma* at the Jocotepec sampling station. The scattergram is derived from parametric DFA results of the total pooled data collected at Jocotepec during 1998-1999.

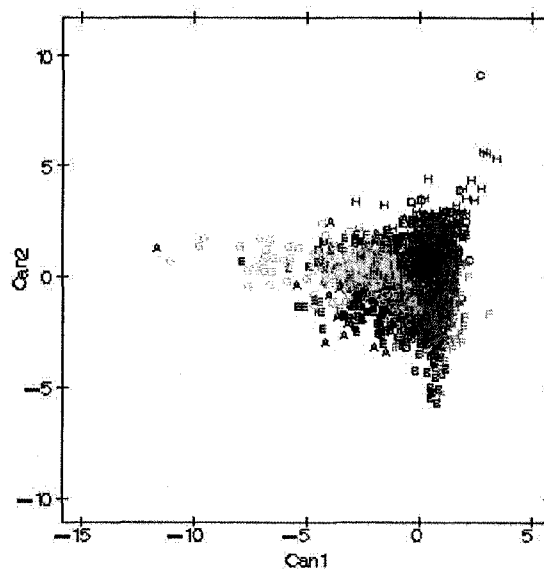


Figure 48. Parametric scattergram of the diet from the genus *Chirostoma* at the Mezcala sampling station. The scattergram is derived from parametric DFA results of the total pooled data collected at Mezcala during 1998-1999.

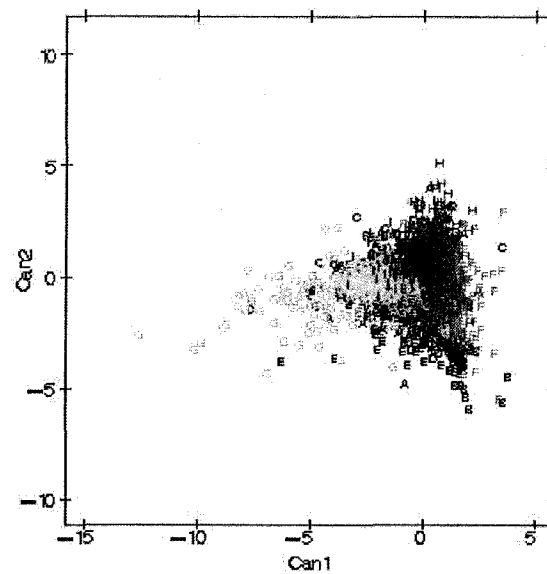


Figure 49. Parametric scattergram of the diet from the genus *Chirostoma* at the Ocatlan sampling station. The scattergram is derived from parametric DFA results of the total pooled data collected at Ocatlan during 1998-1999.

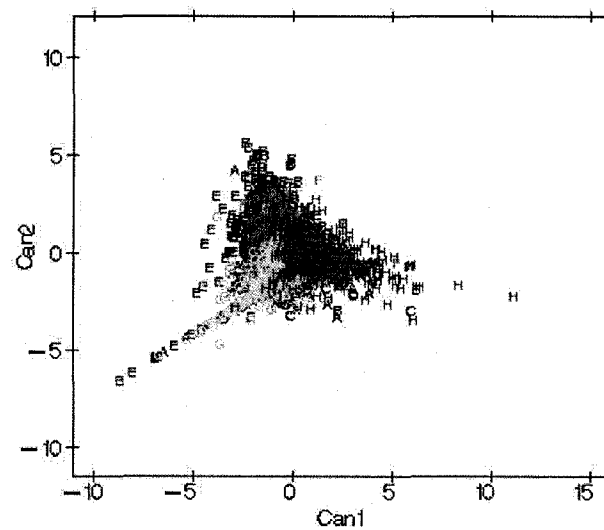


Figure 50. Parametric scattergram of the diet from the genus *Chirostoma* during the March seasonal sampling. The scattergram is derived from parametric DFA results of the total pooled data collected during the March in 1998-1999.

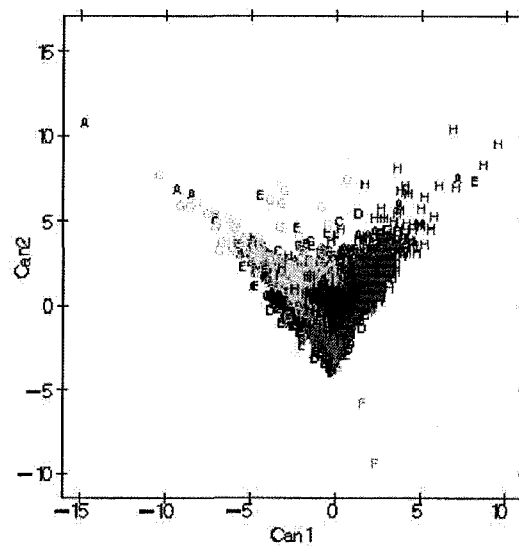


Figure 51. Parametric scattergram of the diet from the genus *Chirostoma* during the July-August seasonal sampling. The scattergram is derived from parametric DFA results of the total pooled data collected during July-August season in 1998-1999.

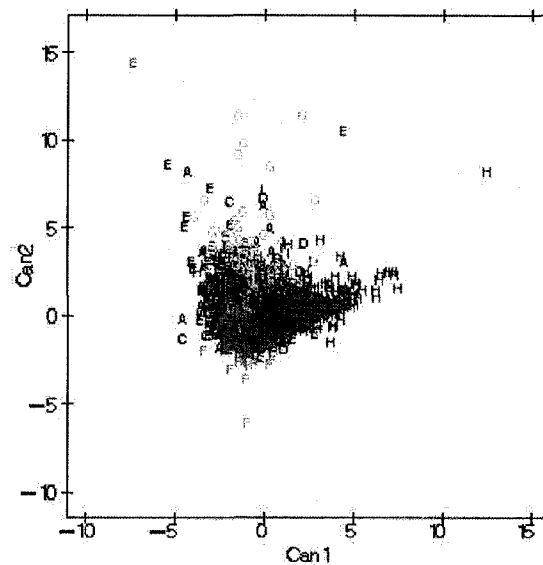


Figure 52. Parametric scattergram of the diet from the genus *Chirostoma* during the December seasonal sampling. The scattergram is derived from parametric DFA results of the total pooled data collected during the December season in 1998-1999.

Fortran-based canonical descriptive DFA were performed to determine which group of dietary variables was most discriminating in among the diets of the nine chirostomid species. The canonical DFA proceeded by first choosing the one variable (food item) that contributed the most to discriminating among the species. Then it chose the most discriminating pair of variables, then the most discriminating three variables, then the most discriminating four variables, etc.. The procedure was repeated with larger groups until the addition of another variable no longer increased the explanation of variation by less than 5%. In all cases, five variables provided optimal explanation.

This procedure provided not only the most powerfully discriminating group of dietary variables, but also provided Wilkes Lambda, the likelihood ratio criterion. The Wilkes Lambda from this test should be equal to that of the MANOVA results which indicated that no statistical errors occurred. All of the Wilkes Lambda results consistently indicated a lack of statistical error (Tables 30 and 31).

Algae, amphipods, chironomids and fish were consistently included in the most discriminating group of food items determining differences between the species diets at all sites and seasons (Table 32). Vegetation, crustaceans, organic matter and copepods occasionally were among the five most discriminating variables (Table 32).

The dietary components found to be most discriminating by canonical descriptive DFA were used to perform the MANOVA tests previously mentioned as a supplemental test to nonparametric DFA. MANOVA provided a) the Wilkes Lambda, b) the dietary variable explaining the most significant differences in diet and c) the Kruskal-Wallis Chi-Square statistic that indicated the rank order of significance for the dietary variables (Table 31). The Kruskal-Wallis Chi Square statistic was not a linear scaled value but provided a weighted ranking based on the statistical interaction.

Significant differences in diet were evident among the chirostomid species flock for each station and for each season. Significant differences were also evident in the combined data for all stations and all seasons. Data indicated that variation in the consumption of algae, amphipods, chironomids, fish and vegetation significantly discriminate among the Chirostomid species (Table 31, 32, and 33).

Interesting relationships were noted between the importance of dietary discriminatory power and the frequency of occurrence in the diet. For example, amphipods were a significant variable, yet comprised only 1.2% of the total chirostomid diet. Amphipods were the single most important dietary discriminator at the western end of Lake Chapala (Jocotepec, Ajijic, and Chapala). Algae was also a significant discriminator, yet comprised only 4.8% of the total chirostomid dietary composition. Algae was the single most important discriminator at the eastern end of the lake (Mezcala and Ocatlan). Conversely, the most abundant dietary variable (organic matter, range 33.1-58.7%, mean = 48.8%) was a significant discriminator only one time at the Mezcala sampling station.

Amphipods were the most discriminating dietary variable in the spawning and post-spawning seasons, while algae was most discriminating during the pre-spawn periods. The least abundant food items ($\leq 0.03\%$) were not significant discriminators with the exception of copepods at the Jocotepec station which may have resulted from the significant presence of high nutrient municipal discharges.

Table 31. The MANOVA results showing Wilkes Lambda values, significant dietary variables and power metric (Kruskal-Wallis Chi-square) are shown. The Kruskal-Wallis result indicates a non-linear power of significance for each dietary variable.

Sampling Area / Season	Wilkes Lambda	Dietary Variables				
Ajijic	0.367	Amphi (1625.52)	Chiro (746.76)	Fish (593.96)	Algae (528.30)	Crust (251.64)
Chapala	0.350	Amphi (1373.35)	Algae (646.48)	Chiro (552.90)	Fish (490.92)	Veg (365.79)
Jocotepec	0.361	Amphi (1523.27)	Algae (885.46)	Cops (651.65)	Chiro (583.13)	Fish (242.61)
Mezcala	0.395	Algae (1571.39)	Chiro (525.56)	Amphi (476.62)	Veg (460.45)	Organic (418.62)
Ocatlan	0.323	Algae (990.65)	Amphi (529.81)	Chiro (399.79)	Fish (378.66)	Veg (328.08)
Combined	0.391	Amphi (1105.12)	Algae (732.35)	Chiro (562.19)	Fish (401.76)	Veg (321.92)
March	0.384	Algae (1690.80)	Amphi (1355.78)	Fish (1074.50)	Chiro (845.79)	Veg (702.42)
July/August	0.393	Amphi (2651.71)	Algae (2590.21)	Chiro (1397.87)	Fish (1111.63)	Veg (702.42)
December	0.437	Amphi (1234.07)	Algae (1075.19)	Chiro (807.07)	Fish (578.93)	Crust (333.77)

Table 32. Descriptive discriminant analysis results indicate the five most significant dietary variables among the diets of the nine sympatric *Chiostoma* species at Lake Chapala, Mexico during the 1998-1999 sampling period.

Sample Area / Season	Dietary Variables					Lambda
Ajijic	Algae	Amphi	Chiro	Fish	Crust	0.367
Chapala	Algae	Amphi	Chiro	Fish	Veg	0.350
Jocotepec	Algae	Amphi	Chiro	Fish	Cops	0.361
Mezcala	Algae	Amphi	Chiro	Organic	Veg	0.395
Ocatlan	Algae	Amphi	Chiro	Fish	Veg	0.323
Combined	Algae	Amphi	Chiro	Fish	Veg	0.391
March	Algae	Amphi	Chiro	Fish	Veg	0.384
July / August	Algae	Amphi	Chiro	Fish	Veg	0.393
December	Algae	Amphi	Chiro	Fish	Crust	0.437

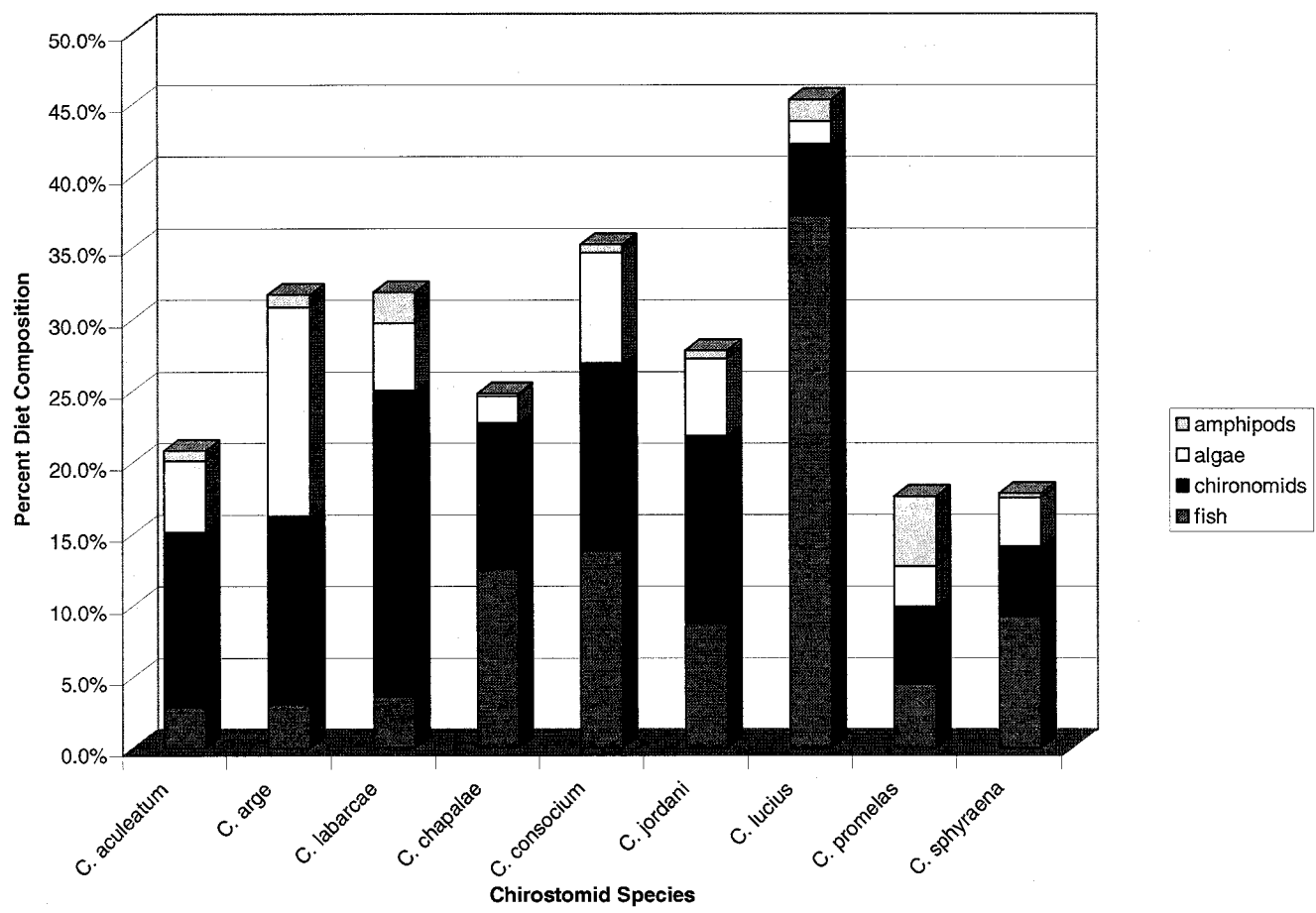


Figure 53. Composition of the four most significant food items that distinguish among diets of the Lake Chapala chirostomid species flock (1998-1999).

CHAPTER FOUR

Discussion

Lake Chapala plays a vital scientific, cultural, historical and socio-economic role in the lives of millions of people in central Mexico. The communities along the banks of the lake and throughout the region have become dependent upon Lake Chapala for water, irrigation, food, employment, recreation and more. Millions of people in Mexico depend on Lake Chapala for drinking water, and consider it to be an ancient and therefore sacred lake. It is a primary symbol of the culture and identity of the people of the surrounding areas.

Lake Chapala is the focal point of the Lerma-Chapala river basin and is a critical water resource in the central Mexico region. The Guadalajara metropolitan area is the second largest urban population concentration in Mexico with approximately 5 million people and derives its water from two primary water sources, Lake Chapala and the Tesistan-Atemajac Aquifer. Lake Chapala provides 65% of this water (Limon and Lind, 1990; Lind and Davalos-Lind, 2002). In addition, Leckie (2001) stated that the Lerma-Chapala basin accounts for approximately one-third of Mexico's economic activity, one-fifth of its commerce and one-eighth of the nation's agricultural land. Primary economic activities within the immediate Lake Chapala region include agriculture and fishing, with the exception of the industrialized City of Ocatlan.

It is no surprise that understanding the dynamics and processes of Lake Chapala is critical to the survival of not only the lake itself, but to the people who depend on it.

Unfortunately, the regional municipalities of Lake Chapala and the surrounding farm lands contribute significant amounts of polluting wastewater that is largely untreated along with agricultural runoff that is laden with nutrients and toxins. One path to understanding the dynamics of Lake Chapala, as well as the dynamics of competition within a vertebrate population is the analysis of the chirostomid fish population as both a important human resource and a model for competition among closely related species.

Relative Abundances and Distribution of Chirostomid Fishes

Although fish diversity is low for Lake Chapala compared to some of the more commonly studied tropical lakes such as Malawi and Tanganyika, it has a relatively high number of fish species for the region. Fish of Lake Chapala are represented by 39 species, 27 of which are native, including the members of the chirostomid species flock. In comparison, Lake Patzcuaro, a nearby lake of great regional importance, has only 14 fish species. The size, age and origin of Lake Chapala has contributed to its higher regional number of species. It is large and ancient, and formed as a graben of enclosed open water that landlocked the lake with an initial stock of diversity. All nine species of *Chirostoma* known to occur in Lake Chapala were sampled during this study and included representatives from both major phylogenetic groups of chirostomids, the Jordani Group (6 species) and Arge Group (3 species).

A plot of the distribution of relative abundances of the nine chirostomids showed an uneven distribution curve in two tiers (Figure 54). The Jordani Group species, *C. jordani*, *C. consocium*, and *C. chapalae*, were similar in abundance and together represented the majority of the fishes (66.8% of the total catch). Species of the Jordani Group are characteristically large, and their greater abundance corroborates Barbour's

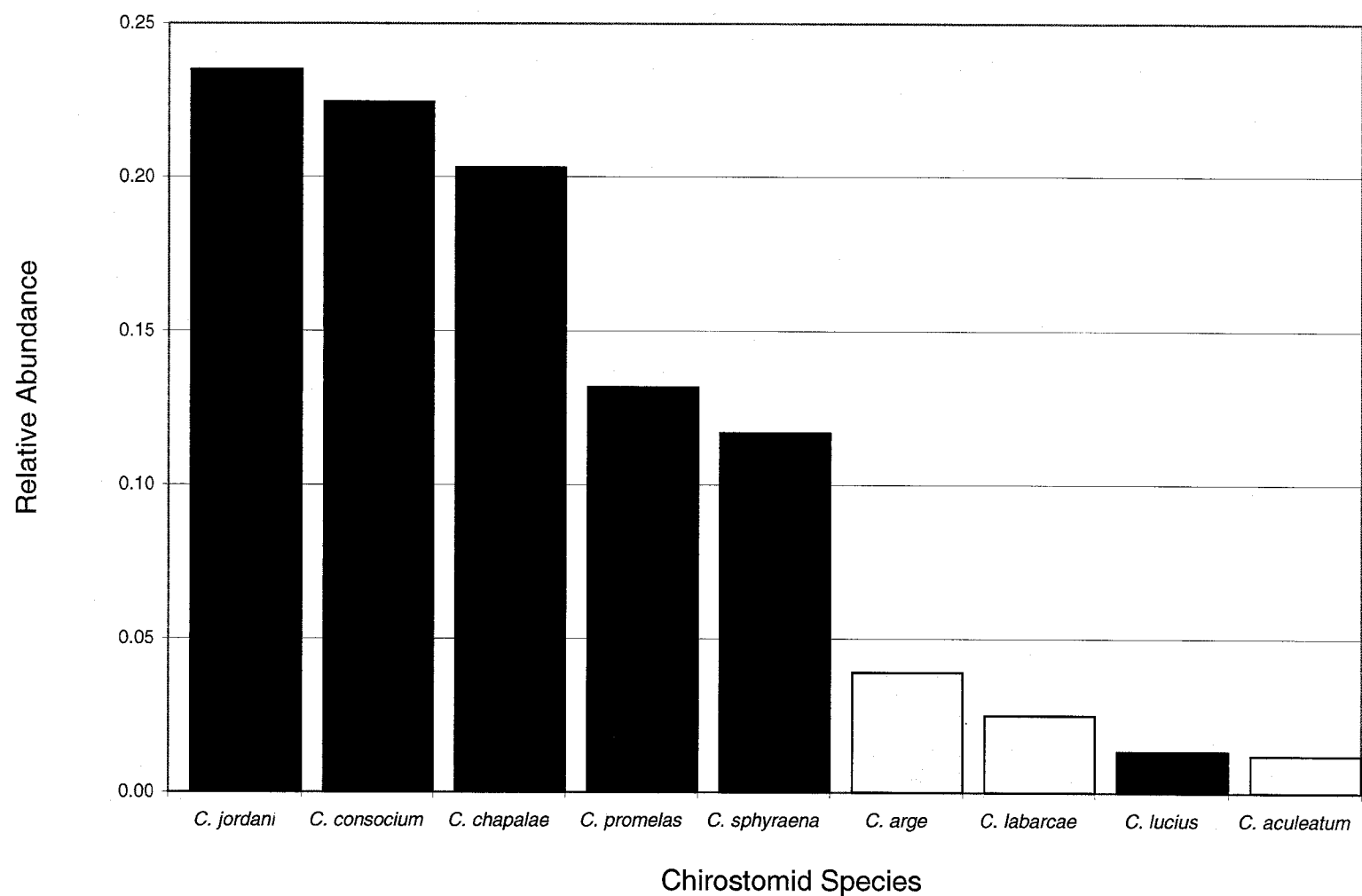


Figure 54. A plot of the relative abundances of nine chirostomid species in Lake Chapala 1998-1999 showing a two-tiered distribution. Green bars indicate species of the Jordani Group, yellow bars indicate species of the Arge Group.

comment that “Differences in body length are the most important single factors allowing the coexistence of the various species of *Chirostoma*.”

The low abundance of *C. lucius* (pescados blancos) was an exception to the distinction of Jordani Group being more abundant than the Arge Group. This may likely result from high fishing pressure on this traditionally preferred species *C. lucius*. However, *C. consocium* (Charal de Rancho) also has been preferred by fishermen and its relative abundance is not low. Unfortunately little is known about the biology of chirostomids in general and these two species in particular. The relative impacts on species abundance by fishing pressure, competitive superiority, natural fecundity rates and sensitivity to environmental stresses, all of which can vary among species, can not be readily distinguished.

Chirostomids of the Jordani Group were fairly evenly distributed across the lake in spite of a subtle, but consistent depth gradient. Relative abundance of *C. lucius*, the largest of the Jordani Group, varied from west to east (see Figure 33), with greatest abundances at the deeper eastern end and lower abundances in the more western heavily fished areas of the lake. The remaining Jordani Group species were evenly distributed along the west to east gradient.

All three Arge Group species represented the lower tier of abundance and combined for only 7.5% of the total catch. Arge Group species occurred in markedly higher numbers at the eastern end of the lake (see Figure 34). Arge Group members were most likely to occur near the City of Ocatlan and in the area of the Rio Lerma inflow. The distinction between the distributions of the Arge Group versus the Jordani Group may be related to the Jordani Group being superior competitors in the shallower

(western) areas or the Arge Group being sensitive to subtle environmental differences such as depth, water quality, and or riverine influences. Although my research cannot definitively separate the impacts of these factors on the even distribution of the Jordani Group and the skewed distribution of the Arge Group, it has been documented that all Arge Group species are classified as either “intolerant” of poor water quality or “non-classified” (California Academy of Science, www.fishbase.org). The western end of Lake Chapala has significant wastewater input. Arge Group species are also primarily riverine in habit. Although these species are commonly found in the lake, their riverine origin may be a strong influence on their distribution. I have found no documentation that the Arge Group species reproduce in the lake or that they only enter the lake via the Rio Lerma, but they are clearly more abundant near the influence of the Rio Lerma and Rio Santiago.

Ontogenetic Trends in Chirostomid Fishes

Niches may be specialized in various ways and during different life stages, including differences in diets among juvenile (subadult) versus adult fish. The diets of juvenile chirostomids were examined during preliminary sampling and indicated that juvenile chirostomids ate a consistent diet regardless of species. Distinguishing diets of juveniles among species was not possible because juvenile chirostomids could not be identified to the species level. They have virtually indistinguishable morphologies. Qualitative analysis of preliminary samples of juvenile (both young-of-the-year and fry) revealed a diet consisting of small invertebrates and diatoms. These juveniles feed high in the water column and on the submerged surfaces of aquatic vegetation. Only when the juvenile chirostomids entered the adult phases could identifications to species

be made and species diets became distinguishable. Interestingly, these juvenile chirostomids consumed consistently less organic matter than found in adult chirostomids. This noticeable lack of organic matter along with a preference for small food items by juvenile chirostomids may contribute to the partitioning of food resources between adult and juvenile chirostomids. Partitioning food into smaller items by juveniles and larger items by adults may be adaptive and promote recruitment of young chirostomids into the adult population. However, diet differences among juveniles are unlikely to play a strong role in separation of species. Only in adults can distinctive dietary compositions be explored.

Dietary Differences Between Males and Females

Preliminary sampling from 1997 indicated that females consumed more prey during periods just before and during the spawning season. This suggested an uneven allocation of resources between genders which could confer an advantage and success for gravid females. However, a t-test comparison of mean gut fullness for males versus females showed no significant difference in quantity of food resources consumed. To reveal if differences occurred in diet composition of males versus females of each species and as a genus, nonparametric Spearman's rank order analyses were used. Differences in dietary composition could not be identified by season, site or total sampling period. Preliminary observations were assumed to be an anomaly and no evidence to support partitioning of resources according to gender was found among or between species.

Morphological Evaluations of Chirostomid Fishes

Morphological and meristic measures were recorded for individual fish to aid the identification of the species and to provide data to investigate correlations of individual morphological features with the occurrence of particular food items in the diet. The tabulation of morphological data provided a current day record of the chirostomid population. For this research, data by Barbour (1973) provided a data set that could be compared to the data collected during this study.

My species identifications consistently segregated individuals into one of nine species identities. Ambiguity was rare because Barbour's taxonomic key relied on consistent sets of species-defining variables rather than single characteristics. Application of a multivariate canonical DFA further confirmed the reliability of character sets to accurately distinguish species. Huberty (1994) stated that DFA was appropriate as an analysis technique when the intent of the research was to predict membership on the basis of response variables, referring in this case to membership into a species group based on morphological response variables. The likelihood of each individual being correctly classified into its species group was significant in each case ($P < 0.001$).

Means and ranges for each morphological feature for each species were compared to values from Barbour (1973). Mean values were consistent with Barbour's synthesis in 1973 of historical records as far back as 1894. This consistency was expected because Barbour's key characteristics were the same values used to make identifications for this study. However, the ranges were also consistent with Barbour's values (see Figures 10-31) and indicated that the entire cadre of morphological measurements were consistent and definitive within a species. This also supports the conclusion that the species

integrity of all nine Lake Chapala chirostomids have remained consistent over the 25 years since Barbour's study, and that there appears to be little hybridization.

Morphological characteristics often correlate with components of the diet. For example, eye size of fish may positively correlate with feeding on a particular visually detected food item. Spearman's rank order analyses were performed to reveal correlations between selected individual morphological characters and each dietary component. Characters such as eye size, mouth width, mouth height, mandible length and others were ranked and compared to relative abundance of each dietary component for each chirostomid species and for all species combined. A few correlations were weakly positive, such as eye size versus fish intake for *C. lucius* ($r = 0.65$). All other positive correlations, such as lateral line scales with intake of amphipods, made little biological sense. The analysis failed to identify any readily apparent trends linking individual morphological characteristics to dietary preferences, and failed to reveal the subtleties of dietary differences among the nine chirostomid congeners.

Lack of correlation between selected morphological features and dietary components was unexpected. Barbour (1973) stated that "Trophic specializations have probably evolved in *Chirostoma* as the result of competition between individuals of the same size, whether congeners or not." Individual morphological adaptations should reflect finely tuned dietary preferences (Ferry-Graham et al. 2001). In a competitive environment one expects distinctive correlations of morphological features with diets specialized enough to reduce competition. Feeding can be more efficient and competitive with pronounced morphological adaptations for specialized diets. In the seemingly competitive situation of a large number of sympatric congeners in Lake Chapala, I

expected dietary specialization and feeding morphology specialization to be evident. However, correlations between morphology and diet differences were not pronounced. Even though integrated morphologies are distinctive among species, individual characters are not associated with diet specialization and partitioning. This lack of association underscores the conclusion that the chirostomid congeners are not competing intensely.

Barbour speculates that some aspects of competition analysis should include a comparison of size classes rather than species identifications. Future studies of such functional groups of competitors would well include species of carp, tilapia, and especially goodeids. Comparisons based on size rather than species membership would be of interest.

Dietary Differences Among Chirostomid Fishes

Differences in diets among species were difficult to discern from initial inspection of the data. All food items were consumed by each of the nine species, and all food items appeared to be consumed in roughly the same proportions. More scrutiny was warranted. Parametric DFA were performed on the dietary data to discern differences in diet among the nine chirostomid species and to provide greater resolution and robustness to the overall analysis. Although the data failed to meet the assumption of normality, a parametric DFA can be useful as a predictor of group membership based on diet. Plots of the canonical values derived by the DFA gave no visual indication of dietary differences. However, the Mahalanobis distances between the central points (centroids) of each species cluster indicated that the clusters were significantly separated, i.e., significant differences existed in the diets. Further analyses with nonparametric techniques were warranted.

Observational field data from complex natural systems oftentimes deviate from normality and require nonparametric analyses. This data set's large size enhanced the power and robustness of appropriate and robust nonparametric analyses. Nonparametric DFA indicated that significant differences in diets occurred among the nine species. Indeed, variation in the relative proportions consumed rather than selection of different food items was enough to significantly separate the diets. However, these analyses could not reveal which dietary components most clearly described these differences. To identify which set of dietary variables described the most variation in the diets canonical nonparametric DFA were performed. In all cases canonical nonparametric DFA found that five of the 12 food items best described variation among diets. A sixth variable added less than 5% to the explanation of the variance among diets. Algae, amphipods, chironomids, and fish were always among the five most discriminating dietary variables. Vegetation, crustacea, organic matter and copepods also were discriminating among fish diets at some sites for some seasons (see Table 32).

The relative contributions of each of the most significant five items could be distinguished by further analysis. MANOVA ranked each significant dietary variable according to its discriminating power. Amphipods were the singular most important discriminator among diets at the western end of the lake (see Table 31) despite the fact that amphipods were never more than 6.4% of a fish species diet (*C. promelas* at the Chapala sampling area). Algae was the most discriminating food item for the two eastern most sampling areas. The maximum relative consumption was 18.6% (*C. arge* at the Jocotopec sampling area). Notably, highly consumed food items (e.g., fish, chironomids, vegetation) discriminated little between the diets of each fish species. Research on

amphipod, algal, fish, and chironomid densities at various sampling areas and seasons is needed to explain their prominence in diet variation among chirostomid species.

What Factors Shape Competitive Interactions of Chirostomids in Lake Chapala?

The approach of this research investigating coexistence of chirostomids relied on assumptions that competition among sympatric congeners is pronounced and partitions niches among spatial, temporal, and trophic resources. Because Lake Chapala has little spatial, structural or morphometric diversity, and because it experiences reduced seasonal and temporal variation typical of the tropics, my research emphasized trophic resource partitioning and associated morphological characteristics as the mechanisms allowing nine congeners to maintain their species integrity. The results and answers to the immediate questions posed in this research are summarized in the conclusions.

Based on these results, I conclude that competition among chirostomid fishes in Lake Chapala is not intense. Two potential forces may have dampened any observable niche specialization at Lake Chapala during this study. Productivity rates and system stress may have reduced competitive interactions in the chirostomid species flock by lowering and stressing the population to a point where competitive interactions had lessened or had become too subtle to distinguish.

Overfishing

Have reductions in the fish population eased competitive pressures among chirostomids and blurred those forces driving resource partitioning in Lake Chapala? Reduced fish densities ease the rate at which trophic resources are consumed, and Lake Chapala's fish populations are declining. Overfishing, increased pollution, sediment

loading, declining water levels, and increased water demand have all played major roles in the decline of the native fishery (Moncayo-Estrada and Buelna-Osben, 2001).

Historically, one of the most common resources from Lake Chapala has been the “pescados blancos” (white fish) fishery. The white fish of Lake Chapala consist of the nine species from the atherinid genus *Chirostoma*. Approximately 1700 registered fishermen from 80-90 fisheries cooperatives use Lake Chapala for their primary economic income. Thousands of people rely on these fishermen for their primary source of protein. The lake is filled with various fishing instruments including gill nets and fish traps of various constructions. One fishermen advised me that gill nets are found every five meters in certain areas of the lake. There is little to no seasonal enforcement of fishing practices designed to protect the fishery. As a result, over-fishing has likely induced marked declines in yields of the chirostomid fishery (SEMANARP, 1999).

Historically, large-sized chirostomids (>200 mm) commonly occurred in the lake. These were likely members of the two larger chirostomid species, *C. lucius* and *C. aculeatum*. Tremendous rates of over-fishing have significantly reduced the catch rates of these two species. The white fish fishery now harvests mid-size adults (60-200 mm) of the nine known chirostomid species. The capture of larger chirostomids is very rare. In this study, I captured only 82 large *C. lucius* and no large *C. aculeatum*, representing only 0.34% of my total catch (n=24,251)

Although Lyons et al. (1998) concluded that the lake’s fishery is not in a state of decline due to the increase in exotic species, historic fish yields have declined steadily over the years falling from 13,710 tons per year in 1990 to less than 3,500 tons during this study period (SEMANARP, 1999; Moncayo-Estrada and Osben, 2001) with

approximately 2000 tons coming from the chirostomid fishery (Ford et. al., 2000).

Declines in fish yields are likely to accelerate as not all fish captures are being reported (J. Ruiz, personal communication). If this trend continues, the fishery will continue to decline rapidly. This sharp decline in fish production in Lake Chapala may be partially attributed to overfishing. Severe reductions at the top of an ecosystem's food web such as this can have devastating effects on the entire system (McClanahan, 2000), in this case, a potentially collapsed fishery.

Productivity

High rates of productivity dampen competition. However, Lake Chapala's traditional algal productivity rates fall in the oligotrophic range, indicating low rates of primary production. Wouldn't lower productivity rates demand more rigid competition among the species? Lind and Davalos-Lind (2001) found that bacterial production was significant and that an entire trophic level (e.g., primary consumers) could be skipped. Zooplankton may not be significantly involved in the typical food chain. Chirostomids may exploit organic matter and bacterial aggregates directly. This is highly efficient. The predominance of organic matter, such as bacterial aggregates in the fishes diets support the contention that bacterial productivity supplements primary productivity and constitutes a significant trophic component for chirostomids.

System Stressors – Water Quantity and Water Quality

System stress plays a role in competition in a variety of ways. For instance, stress on available prey items can trigger a reduction of available prey resulting in increased competitive forces being placed upon the consumers of that pool of prey items. In Lake

Chapala, system stress seems to play a different role by acting upon the consumers themselves. Stressors such as the input of raw wastewater and the reduction of water quantity may reduce chirostomid population densities. By reducing the chirostomid population numbers while not necessarily affecting prey densities, system stressors such as those noted above can dampen competitive forces by lessening competition for food, space, etc.

Declines in water quantity and quality are linked to reduced fishery yields. Since the 1970's, the lake has experienced a steady decline in water levels. Approximately one half of the lake's annual water loss can be attributed to the removal of water by the Guadalajara metropolitan pumping station which delivers drinking water to the Guadalajara metropolitan area. Evaporation also accounts for significant annual water loss. Historically, the Rio Lerma was a significant source of water for Lake Chapala, however, the removal of water for agricultural and municipal purposes up river from the lake has severely restricted the flow of water into Lake Chapala. The Rio Lerma is no longer a reliable or significant source of inflow. Rains provide less water annually than evaporative losses. As a result, water levels were close to historic lows during this study. Such low levels concentrate contaminants and reduce water quality as well.

Lake Chapala is the primary wastewater receiving water body in Central Mexico. Significant amounts of untreated wastewater flow into the lake. Municipal discharges have been shown to significantly reduce chirostomid populations by allowing the more tolerant goodeids to gain a competitive advantage and to thrive (Becerra-Munoz et al., 2003).

Declining water quality is believed to be responsible for a shift in the fish population of Lake Chapala towards exotic species (*Tilapia* and carp) and more tolerant species such as goodeids at the expense of the preferable chirostomids (Becerra-Munoz et al., 2003). Species diversity will decline as water quality declines. Declines in water quality often result in the recruitment of tolerant and exotic fish species and the displacement of native fish fauna.

The flow of mainly untreated wastewater into Lake Chapala alters not only the potential biotic composition of the fish community, but stresses the micro environments available to the lake's fish communities. Toxic loading, organic loading and nutrient loading related to wastewater disposal all contribute to the decline of habitat quality. As a result, chirostomid populations may be reduced due to the effects of wastewater input.

Wastewater carries numerous heavy metals and toxins into Lake Chapala daily. Toxins freely enter Lake Chapala via wastewater and concentrate in the organic substrate. Our study showed that chirostomid fishes consume significant amounts of organic material. It is safe to assume that bioaccumulation of toxins occurs at a high rate. The addition of large amounts of toxins into Lake Chapala likely stresses the chirostomid population, contributes to a reduction of the total population of chirostomids and reduces competition for food. It also reduces intolerant species populations and increases populations of tolerant species which may reduce competitive forces on the remaining population.

Organic and nutrient loading from wastewater plays a similar role in the decline of the chirostomid fishery. Increased turbidities are obvious at all major wastewater outflows into the lake. As a result, bacterial communities thrive and prey composition

and trophic structure shifts. The influx of organic materials and nutrients results in an increase of total productivity in both the traditional algal pathway and the bacterial pathway. This effect results in a higher potential food supply and likely dampens competitive forces among chirostomid fishes.

Summary and Conclusions

1. Species members of the Jordani Group are evenly distributed in Lake Chapala. Arge Group species increase along a west-to-east gradient and are more likely to occur at the eastern part of the lake. Jordani Group species show no apparent sensitivity to depth or riverine influences. Arge Group species at Lake Chapala are riverine species and are concentrated near the Rio Lerma outfall.
2. Jordani Group species are more abundant in Lake Chapala than Arge Group species. Arge Group members are notably intolerant of the environmental stresses common to Lake Chapala.
3. As chirostomids develop through their ontogeny, they utilize food resources differently. Diets of juvenile chirostomids are indistinguishable among the nine species. However, dietary composition diverges according to species in adult chirostomids. Differences in diets among juveniles are unlikely to play a strong role in species separation.
4. Dietary differences between males and females are not pronounced. Females do not appear to have a competitive advantage over males in spite of the fact that energy demands of gravid females are typically higher than the energy demands of males. Gut fullness and dietary composition are similar for males and females.

5. Morphological characteristics are clearly distinguishable among the nine chirostomid species and are consistent with historical data. Sets of morphological characteristics are highly definitive among species and indicate little or no hybridization.
6. Individual morphological characters were not reliable predictors of dietary composition. Individual morphological characters failed to correlate with diet.
7. Significant differences occur among the diets of Lake Chapala's chirostomid population. Revealing subtle differences in dietary composition requires close statistical examination. Algae, amphipod, chironomid and fish percentages accounted for the most distinctive variation among the species diets.
8. Competition for food resources by Lake Chapala's chirostomids is not intense. Stressors such as poor water quality, water quantity, overfishing, raw wastewater input, and other anthropogenic perturbations dampen competitive interactions among the chirostomid flock. Lake Chapala's high overall productivity, both primary and bacterial, reduces competition in the chirostomid populations.

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