THE ROLE OF *CERCOPAGIS PENGOI* IN NEARSHORE AREAS OF LAKE

ONTARIO

A Dissertation

Presented to the Faculty of the Graduate School

of Cornell University

In Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

by

David Michael Warner

May 2004

THE ROLE OF *CERCOPAGIS PENGOI* IN NEARHSORE AREAS OF LAKE ONTARIO

David Michael Warner, Ph. D.

Cornell University 2004

Exotic species introduced to Lake Ontario in the past 100 years have had varied effects on the food web. The exotic cladoceran *Cercopagis pengoi* is a zooplankton predator, and the effects of its establishment (in 1998) were difficult to predict without research conducted years since its introduction. Little to no work has been conducted at spatial scales necessary to examine the role of *C. pengoi* on a lakewide basis. This study was conducted to assess the relative importance of *C. pengoi* as prey and predator by examining its abundance, distribution, and potential impacts based on these variables and its trophic interactions with zooplankton and fish.

Data from a number of field studies were used to develop equations relating acoustic size (target strength) to length and mass, which allowed estimation of abundance using acoustic surveys. Target strength varied significantly with length and mass. Target strength equations were significantly different from previously published equations.

Field collections revealed that *C. pengoi* was an important prey item for only for juvenile and adult alewives > 66 mm total length. Due to the planktivorous nature of *C. pengoi* and similar distributions of these organisms, alewives and rainbow smelt also compete with *C. pengoi*. The relative importance of *C. pengoi* as prey and competitor depended on fish size and habitat use; habitat use determined the degree of spatial overlap, while fish size and the defensive spine of *C. pengoi* influenced the

degree to which these fish were able to utilize *C. pengoi* during periods of spatial overlap.

Late summer abundance of bosminids, *Diacyclops thomasi*, and copepod nauplii was significantly lower in 1998-2000 than 1995-1997, while abundance of *Daphnia retrocurva* did not vary significantly. Other factors that may have contributed to this decline were excluded by examination of their seasonal patterns. I concluded that predation by *C. pengoi* caused the observed declines. The relative magnitude of consumption by *C. pengoi* and alewives indicated that they were important predators and competitors and both were capable of structuring zooplankton community structure through predation.

BIOGRAPHICAL SKETCH

David Warner was born on 18 February 1968 in Alton, Illinois. After a move to Brockport, New York, he graduated from Brockport High School in 1986. He worked at several manufacturing plants and as a painter until enrolling at the State University of New York (SUNY) at Cobleskill in 1987. He obtained an Associates degree in Fisheries and Wildlife Technology as well as a Bachelor's of Technology in Fisheries and Aquaculture between 1987 and 1992. Between 1992 and 1996, he worked as Fish Hatchery Manager at SUNY Cobleskill and as a Fishery Technician for the New York State Department of Environmental Conservation. In 1996 he enrolled in the Master of Arts in Biology program at SUNY Oneonta. While a student at SUNY Oneonta, he worked as an interpretive guide for students on field trips to the SUNY Oneonta Biological Field Station in Cooperstown, New York. In 1997 he took a job as a high school science teacher. While at Cornell, David enjoyed the many opportunities to meet and work with a number of acousticians/scientists in the U.S. and abroad, especially Mike Jech, John Horne, Thomas Axenrot, and Tomas Didrikas. He was a member of the Great Lakes Fishery Commission Acoustic Working Group, was a Sea Grant Scholar for three of his five years at Cornell, and contributed to research published in journals including Journal of Great Lakes Research, ICES Journal of Marine Science, Lake and Reservoir Management, Limnology and Oceanography, and Transactions of the American Fisheries Society. David presented his research at four national level scientific conferences. David is employed as a research fishery biologist at the U.S. Geological Survey Great Lakes Science in Ann Arbor, Michigan. David enjoys music, reading, kayaking, making beer, architecture, and home renovation.

This manuscript is dedicated to my wife, Emily Grace Warner and my parents, David

and Dorothy Warner.

A number of wonderful people made Cornell a great place to be. The oddities and difficulties of graduate school loom large at times, but they were minimized thanks to interactions with a number of people including: Robert Klumb, Jeremy Coleman, Nate Smith, Brian Weidel, Sandy Parker Stetter and Brian Irwin.

TABLE OF CONTENTS

LIST OF FIGURES

number of fish whose stomachs contained *C. pengoi* spines and the unshaded portion the number that did not contain *C. pengoi* spines. The total number of alewife stomachs examined = 167 (empty stomachs =4).

LIST OF APPENDICES

PREFACE

The Great Lakes have undergone significant changes in the past few decades. Anthropogenic influences of positive, negative, and uncertain nature have included management of water quality, control of sea lamprey (*Petromyzon marinus*) abundance, and both intentional and unintentional introductions of exotic species. Nutrient loading and nutrient concentrations have declined and stabilized at levels lower than in the 1970s (Millard et al. 2003; Johengen 1991). In Lake Ontario, nutrient reductions were accompanied by declines in zooplankton abundance and production (Johannsson 2003) as well as alewife biomass (Mills et al. 2003), suggesting that nutrient management efforts have had a bottom-up effect on the standing stock of forage fish. In 1998, the planktivorous cladoceran *Cercopagis pengoi* became established in Lake Ontario, and given the already reduced levels of zooplankton production and alewife biomass, additional predation pressure exerted by *C. pengoi* may negatively affect alewives if *C. pengoi* does not replace other organisms in the diet of alewives. Because alewife form the major portion of salmonid diets and alewife abundance is related to predation pressure by salmonids, factors that limit alewife abundance and production likely may also affect the carrying capacity of salmonids. Therefore, understanding the role of *C. pengoi* (predator, prey, energy source or sink) is an important contribution to management of alewives and salmonids in the currently more oligotrophic environment of Lake Ontario.

As a small predatory cladoceran (Ojaveer 2000), *C. pengoi* was expected to prey on zooplankton and compete with alewives and rainbow smelt while at the same time serve as prey for these fish species. These expectations were based on observed relationship between *C. pengoi* and Baltic herring (Ojaveer and Lumberg 1995). The relative importance of these roles in the food web was expected to be complicated because invertebrate predators like the similar *Bythotrephes longimanus* (and by

extension *C. pengoi*) may utilize multiple antipredator defenses including migratory behavior, limited habitat use, and defensive spines (Straille and Hälbich 2000). Without significant temporal and spatial overlap between *C. pengoi* and dominant zooplankton (bosminids and cyclopoids), the predatory effect of *C. pengoi* on the zooplankton community will be minimal. Habitat use may also influence the amount of spatial and temporal overlap between *C. pengoi* and alewives while defensive spines may limit their availability as prey during periods overlapping distribution.

This study was focused on assessing the trophic role of *C. pengoi* by 1) examining its distribution and seasonal patterns in abundance, and hence its overlap in habitat use with zooplankton and alewives, 2) determining if alewives and rainbow smelt (*Osmerus mordax*) prey on *C. pengoi*, 3) determining whether the seasonal patterns in nearshore zooplankton abundance and size changed in a predictable way reflective of *C. pengoi* predation following establishment of *C. pengoi*, and 4) comparing the relative magnitude of consumption by *C. pengoi* and alewives with zooplankton production.

Estimates of zooplankton consumption by alewives required alewife density estimates. Acoustic surveys offered a significant advantage over other gears because of the ability to survey large areas quickly. One weakness of acoustic surveys was the lack of a published equations relating alewife target strength to length or mass (necessary for accurate estimation of abundance). Without these equations I would have relied on those published for marine clupeids (Foote 1987), a mixed-species assemblage of Lake Michigan fish (Fleischer et al. 1997), or a mixed-species equation previously used in the Great Lakes (Love 1977) by Brandt et al. (1991) and others. To improve accuracy of surveys, a methodological study was undertaken to develop these equations specifically for freshwater alewives. Data from a number of field studies were used to develop equations relating acoustic size (target strength) to length and

mass observed in trawl and gill net catches. I found that alewife target strength varied significantly among size or age classes. Alewife target strength predicted from length or mass was significantly higher than values published for Atlantic herring, and values predicted for small alewives (<10 cm) were significantly higher than those predicted by the equations of Fleischer et al. (1997). Differences between Atlantic herring and alewives may have been the result of differences in buoyancy demands on the swimbladder being mitigated in saltwater by the higher lipid content of Atlantic herring and the specific gravity of seawater.

In order to determine if alewives and rainbow smelt consumed *C. pengoi*, field collections of these fish by midwater trawl provided stomach content data throughout Lake Ontario in 1997-1999. I hypothesized that *C. pengoi* would not be important in the diet of young-of-the-year alewives and rainbow smelt because of limited spatial overlap and the defensive tail spine possessed by *C. pengoi*. I also hypothesized that *C. pengoi* would be more important in the diet of adult alewives than adult rainbow smelt because of a more hypolimnetic distribution of rainbow smelt than *C. pengoi*. Examination of these data revealed that *C. pengoi* was an important prey item for juvenile and adult alewives > 66 mm total length, but was not an important prey item in the diet of rainbow smelt. Due to the planktivorous nature of *C. pengoi* and the absence of *C. pengoi* in the diet of alewives <66 mm, I concluded that although *C. pengoi*, alewives, and rainbow smelt were competitors, the relative importance of this competition was mediated by the ability of these fish to consume *C. pengoi*. Whether *C. pengoi* is most important to alewives and rainbow smelt as a prey item or competitor remains unclear.

In order to determine if there was evidence for restructuring of the zooplankton community after establishment of *C. pengoi*, I tested hypotheses related to seasonal abundance patterns in density and mean length using a data set consisting of

fortnightly zooplankton samples collected at seven nearshore locations from May-October 1995-2000. Seasonal patterns in zooplankton density and length were examined along with water temperature, total phosphorus, and chlorophyll *a* (as potential explanatory variables). Because of the seasonal abundance pattern of *C. pengoi* observed in Lake Ontario (population peak in late July-September, Laxson et al. 2003; Benoît et al. 2002), I hypothesized that late summer abundance of bosminids, *Diacyclops thomasi*, and copepod nauplii would be significantly lower only in late summer 1998-2000 (during the seasonal peak in *C. pengoi* abundance) than during the same seasonal period of 1995-1997 and that early summer densities would be similar in both groups of years (epochs). I considered abundance and mean length of *Daphnia retrocurva* as an indicator of fish predation intensity; had decreases observed in zooplankton density occurred concurrent with decreases in mean length, I would have concluded the changes were the result of fish predation. Decreased density concurrent with increased length was interpreted as indicating that the observed changes were the result of invertebrate predation. The data supported the hypothesis that abundance of bosminids, *D. thomasi*, and nauplii in late summer 1998-2000 would be significantly lower than late summer 1995-1997 while early summer abundance remained unchanged; these organisms were all significantly less abundant in late summer 1998-2000 than in 1995-1997, while early summer abundance was similar in both groups of years. Mean length of bosminids was lower in early summer 1998-2000 than in 1995-1997, but late summer length was similar. Early and late summer abundance of *D. retrocurva* was similar in both groups of years, suggesting changes in other taxa were not the result of fish predation. Mean length of *D. retrocurva* was significantly lower in early summer and similar in late summer. Mean length of *D. thomasi* and nauplii were similar in all seasons and years. Other factors (water temperature, TP, and chlorophyll *a*) that may have contributed to declines in

density were excluded by examination of their seasonal patterns. Exclusion of these factors as well as fish predation led me to conclude that predation by *C. pengoi* caused the observed declines.

Although changes in the zooplankton community (decreased late summer abundance of bosminids, *D. thomasi*, and nauplii) were likely attributable to predation by *C. pengoi*, it was unclear how consumption by *C. pengoi* compared to consumption by alewives and zooplankton production in the nearshore. Using hydroacoustic alewife abundance estimates (including the target strength-size relationship from this study) and a bioenergetics model, consumption for yearling-and-older fish was estimated fortnightly between May and late July 2000 at one nearshore location in western Lake Ontario. Consumption by *C. pengoi* was estimated fortnightly at six nearshore locations throughout eastern and southern Lake Ontario using biomass and a mass-specific consumption rate of 100% of body weight per day. Production of location at the same six locations was estimated from water temperature, biomass, and allometric equations (Shuter and Ing 1997) for predicting production/biomass ratios. The relative magnitude of consumption by *C. pengoi* (9-50% of growing season production) indicated that it was an important predator with low early summer consumption and high late summer consumption (late July-September). Consumption by yearling-and-older alewives was significant relative to zooplankton production (52% of growing season production in 2000). However, alewife abundance and consumption peaked much earlier in the season. Seasonal patterns of crustacean zooplankton production were significantly different (lower in late summer) following establishment of *C. pengoi* than in the three years prior to its establishment.

One important result of this study was the improved understanding of the acoustic size of alewives. I learned that one equation commonly used in early acoustic surveys of the Great Lakes (Love 1977, used in Brandt et al. 1991) was very similar to

the one I developed for alewives, while another more recently published equation was significantly different for small fish (<10 cm) and likely produced biased density or biomass estimates given the lower predicted TS at length. This study also provided several important insights regarding the role of *C. pengoi* in nearshore areas of Lake Ontario. *Cercopagis pengoi* abundance and predatory impact appear to peak later in the summer than that of yearling-and-older alewives but is likely similar to seasonal patterns in YOY alewife abundance. Consumption by *C. pengoi* and yearling-and-older alewives was of similar magnitude. It is unclear where in the lake peak densities of YOY alewives occur in August-September, but given similar seasonal patterns in abundance of *C. pengoi and* YOY alewives, similarities in the magnitude and seasonal pattern of *C. pengoi* density in both nearshore and offshore areas (Makarewicz et al. 2001), and widespread distribution of YOY alewives throughout the offshore waters in 1997-1999 (Bushnoe et al. 2003), it does not matter. Due to the planktivorous nature of *C. pengoi* and similar distributions of these organisms, I concluded that alewives and rainbow smelt face competition that they did not face prior to establishment of *C. pengoi*. The only factor that could reduce competition between alewives, rainbow smelt, and *C. pengoi* is a difference in vertical distribution.

REFERENCES

Benoît, H. P., O. E. Johannsson, D. M. Warner, W. G. Sprules, and L. G. Rudstam. 2002. Assessing the impact of a recent predatory invader: The population dynamics, vertical distribution and potential prey of *Cercopagis pengoi* in Lake Ontario. Limnology and Oceanography 47:626-635.

Brandt, S. B., D. M. Mason, E. V. Patrick, R. L. Argyle, L. Wells, P. A. Unger, and D. J. Stewart. 1991. Acoustic measures of the abundance and size of pelagic planktivores in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 48:894–908.

Bushnoe, T. M., D. M. Warner, L. G. Rudstam, and E. L. Mills. 2003. *Cercopagis pengoi* as a new prey item for alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) in Lake Ontario. Journal of Great Lakes Research 29:205-212.

Fleischer, G. W., R. L. Argyle, and G. L. Curtis. 1997. *In situ* relations of target strength to fish size for Great Lakes pelagic planktivores. Transactions of the American Fisheries Society 126:786–794.

Foote, K. G. 1987. Fish target strengths for use in echo integrator surveys. Journal of the Acoustical Society of America 82:981–987.

Johannsson, O. E.. 2003. A history of changes in zooplankton community structure and function in Lake Ontario: responses to whole-lake remediation and exotic invasions. State of Lake Ontario (SOLO): Past Present and Future. Ed. M. Munawar. Leiden, The Netherlands, Backhuys Publishers Leiden, The Netherlands (in press).

Johengen, T. H., O. E. Johannsson, G. L. Pernie, and E.S. Millard. 1994. Temporal and seasonal trends in nutrient dynamics and biomass measures in Lakes

Michigan and Ontario in response to phosphorus control. Canadian Journal of Fisheries and Aquatic Sciences 51: 2570-2578.

Laxson, C. L., K. N. McPhedran, J. C. Makarewicz, and I. V. Telesh. 2003. Effects of Cercopagis pengoi on the lower food web of Lake Ontario. Freshwater Biology 48:2094-2106.

Love, R. H. 1977. Target strength of a fish at any aspect. Journal of the Acoustical Society of America 62:1397–1403.

Makarewicz, J.C., Grigorovich, I.A., Mills, E.L., Damaske, E., Cristescu, M.E., Pearsall, W., LaVoie, M.J., Keats, R., Rudstam, L., Herbert, P., Halbritter, H., Kelly, T., Matkovich, C., and MacIsaac, H.J. 2001. Distribution, fecundity, and genetics of *Cercopagis pengoi* (Ostroumov) (Crustacea, Cladocera) in lake Ontario. J. Great Lakes Res. 27:19-32.

Millard, E. E., O. E. Johannsson, M. A. Neilson, and A. H. El-Shaarawi. 2003. Long -term, seasonal and spatial trends in nutrients, chlorophyll *a*, and light attenuation in Lake Ontario. In: *The State of Lake Ontario Ecosystem (SOLO) – past, present, and future*. Ed. M. Munawar. Backhuys Publishers, Leiden, The Netherlands (in press).

Mills, E. L., and 17 co-authors. 2003. Lake Ontario: Food web dynamics in a changing ecosystem (1970-2000). Canadian Journal of Fisheries and Aquatic Science 60:471-490.

Ojaveer, H., M. Simm, A. Lankov, and A. Lumberg. 2000. Consequences of invasion of a predatory cladoceran. ICES C. M. 2000/U:16.

Ojaveer, H., and Lumberg, A. 1995. On the role of *Cercopagis pengoi* (Ostroumov) in Pärnu Bay and the NE part of the Gulf of Riga ecosystem. Proc. Estonian Acad. Sci. Ecol. 5:20-25.

Shuter, B. J., and K. K. Ing. 1997. Factors affecting the production of zooplankton in

lakes. Canadian Journal of Fisheries and Aquatic Sciences 54: 359-377.

Straille, D., and A. Hälbich. 2000. Life history and multiple antipredator defenses of an invertebrate pelagic predator, *Bythothrephes longimanus*. Ecology 81:150-163.

CHAPTER 1

In Situ Target Strength of Alewives in Freshwater

ABSTRACT

Acoustic estimation of absolute fish abundance depends on knowledge of the relationship between target strength (TS) and size for the species of interest. We have derived a relationship between in situ TS and both length (L, cm) and mass (W, g) for alewives *Alosa pseudoharengus* in Lake Ontario and eight inland lakes in New York to provide equations for predicting one variable from the other. The pelagic fish community in these lakes was dominated by alewives (>80% numerically). Target strength distributions from fish populations investigated in 25 surveys were multimodal, whereas those for individual fish were unimodal, indicating that each mode for the populations corresponded to a size-group of alewives (range, 2.5–15.2 cm). The positive relationship between mean TS and mean length was highly significant (TS = 20.53 $\log_{10} L_{cm}$ -64.25), as was the relationship between mean TS and mean mass (TS = 6.98 $\log_{10} W_g$ -50.07). These equations are similar to one often-used TS–length relationship but differ substantially from other relationships in the literature. Predictions of TS from our equations were 8.2 decibels greater than those from commonly used equations for marine clupeids. Our equations also differ for fish smaller than 10 cm compared with the equations available for mixed species of Great Lakes forage fish (alewives, rainbow smelt *Osmerus mordax*, and bloater *Coregonus hoyi*).

INTRODUCTION

Acoustics are increasingly used in freshwater lakes for measuring abundance and distribution of open-water fish populations and can greatly improve our ability to sample fish on a lakewide scale. However, acoustic surveys require knowledge of the acoustic reflectivity of the fish species present for the echoes to be translated into length stratified absolute fish abundance (MacLennan and Simmonds 1992; Brandt 1996). Therefore, acoustic target strength (TS) measurements are a necessary step for acoustic surveys. The acoustic reflectivity is given by the backscattering cross-section (σ_{bs}) or its logarithm, TS. For fish with swimbladders, the swim bladder scatters the majority of the sound. Thus biological, physical, and behavioral factors that affect the swim bladder will directly influence the TS (Ehrenberg 1972; Foote 1979, 1980; Ona 1990). Because backscattering at frequencies used for fisheries studies is typically in the geometric region (MacLennan and Simmonds 1992), backscattering strength is dependent on the dorsal swim bladder surface area (Horne and Clay 1998). The TS also depends on the fish's orientation in the sound beam (Ona 1990; MacLennan and Simmonds 1992).

Target strength–length relationships are required for each species in each environment for effective use of acoustics in abundance estimates. When in situ target information is unreliable or unavailable, knowledge of TS–length relationships allows measurement of absolute fish abundance acoustically. The TS–length relationships can also be used to derive acoustically based length-frequency distributions. Several studies in the Laurentian Great Lakes have estimated pelagic planktivore biomass by translating individual TS to fish weight (Brandt et al. 1991; Goyke and Brandt 1993; Mason et al. 2000) with use of a general equation for the relationship between TS and fish length from Love (1971). However, even though a considerable body of literature

exists on TS as a function of fish size (reviews by MacLennan and Simmonds 1992;
McClatchie et al. 1996), only two studies have reported a relationship between TS and
fish size for Great Lakes pelagic planktivores, both of which described mixed
assemblages of alewives *Alosa pseudoharengus*, rainbow smelt *Osmerus mordax*, and
bloaters *Coregonus hoyi* (Argyle 1992; Fleischer et al. 1997). Fleischer et al. (1997)
suggested that the equation used previously for Great Lakes forage fishes (Love 1971)
was not appropriate and could potentially lead to underestimation of forage fish
biomass. However, alewives were a minor component of the catch in both studies,
even though this species is a major forage fish in many Great Lakes (Brandt et al.
1991).

Ideal conditions for in situ studies of TS are found when the study area
contains only one size class of a single species (MacLennan and Simmonds 1992).
Although in practice these conditions are rare, the pelagic fish communities in many
of the New York Finger Lakes are dominated by alewives, which comprise 80–95% of
gill-net catches (L. G. Rudstam, unpublished data). Lake Ontario is also dominated by
alewives (O'Gormanet al. 1997). Therefore, these lakes offer good conditions for
estimation of the in situ TS–size relationship for this species. Objectives of the present
study were to (1) determine in situ the TS–size relationship for alewives in freshwater
lakes dominated by this species and (2) assess the applicability of three existing
equations to estimate freshwater alewife size from TS (Love 1971; Foote 1987;
Fleischer et al. 1997). These objectives led to an investigation and results that are
widely applicable to other species or environments.

METHODS

Acoustic and catch data were collected between July and November in the
following eight inland New York lakes: Canadice (2000), Cayuga (1998), Cayuta
(1995–1996, 2000), Conesus (1996–1998, 2000), Otisco (2000), Otsego (1996, 1997,

1999, 2000), Seneca (2000), and Owasco (1997). Lake Ontario embayment and
nearshore areas were also sampled in 1997–1998. Surface areas of the inland lakes
that were sampled ranged from 3.4 to 172 km2 and maximum depths ranged from 7 to
190 m.

Fish were collected with vertical gill nets, larval trawl, and an Isaacs–Kidd
midwater trawl. In all lakes, we used six 3-m long 3 12-m deep or 3-m long 3 20-m
deep vertical monofilament gill nets, each with a different mesh size (bar mesh of
6.25, 8, 10, 12.5, 15, and 18.75 mm). Gill nets were set with the upper end at the water
surface. In most cases, netting and acoustic sampling took place concurrently. Gill nets
were set immediately preceding acoustic sampling and then retrieved immediately
after the sampling was completed. In two cases gill-net catches were obtained as much
as a week before or after acoustic sampling. Because weekly growth of alewives in
New York lakes is about 0.5 cm (Cornell Biological Field Station, unpublished data)
the time difference in netting and acoustic sampling was unlikely to introduce a
significant bias. Gill nets were typically within a few hundred meters of the acoustic
transect used for TS estimation. Selectivity for each mesh of the gill nets was
calculated from the size distribution for 733 alewives caught with these nets during
1994–1996 by using the method of Wulff (1986). Following Hansson and Rudstam's
(1995) work on Atlantic herring *Clupea harengus* in the Baltic Sea, we assumed
skewed normal selectivity curves, with each mesh size having the same maximum
selectivity. The equations are as follows:

(1) $S_{(L,m)} = \exp(-1/2\ K^2)\ [(1 - K/2)\ (S_{(m)}^{3/2}\ (K - 1/3\ K^3)]$

(2) $K = (L - L_0(m))/\ S_{(m)}$

(3) $L_0(m) = a(m - 1),$

(4) $S_{(m)} = bm,$

where $S_{(L,m)}$ is the selectivity for a fish of length L in a net with bar mesh size m (both

in cm), $L_0(m)$ is the modal length of the selectivity curve, $S_{(m)}$ is the standard deviation of the selectivity curve, and K is the skewness constant. Maximum likelihood estimates for $a, b,$ and k were 1.1, 0.12, and 0.3, respectively. The average sizes of fish caught in the gill nets were calculated on the basis of the catch and were corrected for the size selectivity of the nets. In Cayuta, Conesus, Otisco, and Otsego lakes, we also used a larval fish trawl (2-m frame, 0.1-cm stretch mesh cod end). In Otsego we also used a modified Isaacs–Kidd midwater trawl (3-m frame, 0.063-cm stretch mesh cod end). Trawls were towed for either 5 or 10 min at a single depth per tow (surface, 3, 6, and 9 m deep), with trawl depth estimated from cable angle. Because all fishing gears are selective, it is important to consider the potential bias of correlating TS with fish sizes that may not be representative of the mean size in the lake. The gill nets used were are not efficient at capturing alewives shorter than 5 cm (Figure 1.1). This selectivity was confirmed with concurrent gill netting and trawling. As a result, we decided not to include young-of-year in the regression for surveys when trawl samples were not available (see method for excluding targets for this age–size-class below). We calculated mean length and mass for young-of-year from the trawl catches, whereas adult alewife length and mass was determined from gill-net catches. If no young-of-year shorter than 5 cm was captured in the trawl (which happened only in the fall), we calculated mean length and mass from pooled gill-net and trawl data. Differences in fall young-of-year lengths between gill nets and trawls were less than 0.5 cm during fall. Alewives hatched during June and July in our study lakes and grew to maximum of 10 cm by fall. Age-1 fish (determined from otoliths) during June in Otsego Lake were 7–9 cm long (D. Warner, unpublished data). Therefore, we distinguished young-of-year alewives as fish shorter than 7.0 cm in summer and shorter than 10 cm in fall.
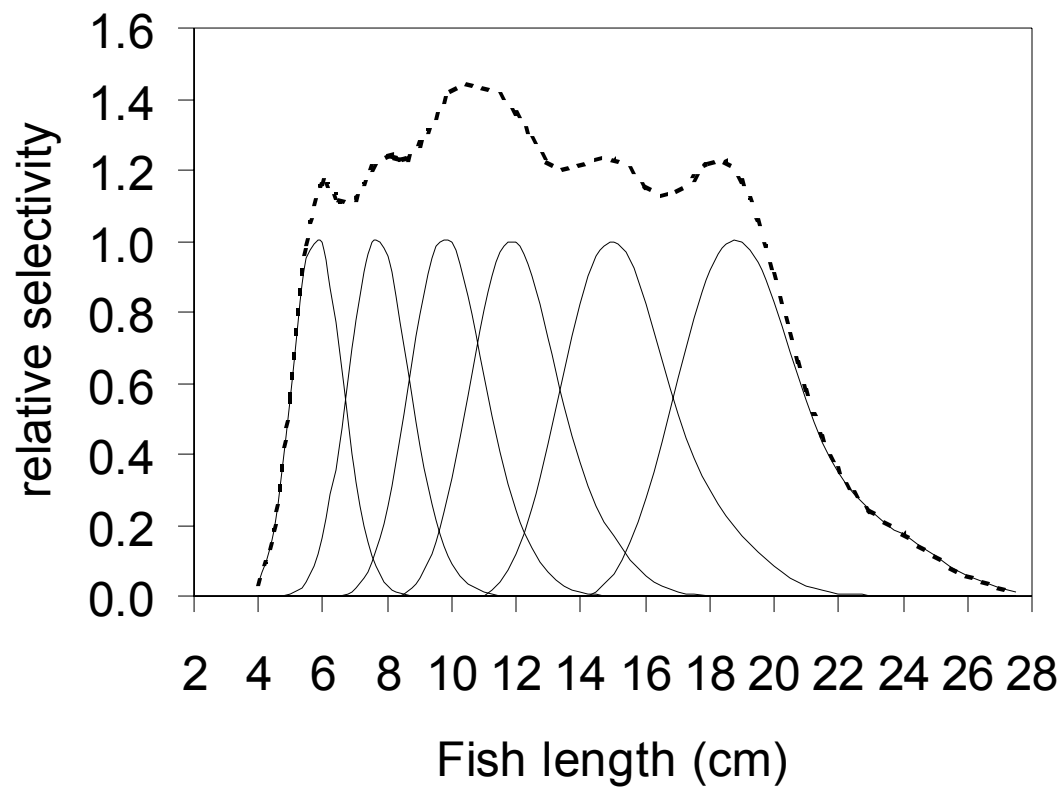
Figure 1.1. Relative selectivity curves of the gill nets utilized in this study. Each unbroken line represents a net with mesh size (from left to right) 6.25, 8, 10, 12.5, 15, and 18.5 mm. The broken line represents the summed selectivity at each size.

Acoustic data were collected at night by using a 70-kHz split-beam echosounder (Simrad EY500; 0.6- or 0.2-ms pulse length, 11.1° half-power beam width). Transects ranged from 0.5 to 5 km in length and surveyed areas within 300 m of the gill-net sets. The acoustic system was calibrated with a standard copper sphere (32 mm diameter, TS =39.1 dB) either immediately after each survey or within 1 month after the survey. Simrad EY500 and EP500 software were used for data collection and analysis. This software provides the depth and TS (corrected for the location in the acoustic beam) to the nearest 0.1 m and 0.1 dB of each target that passes the criteria for recognition of single fish. Single-fish criteria were set to accept targets with echo length between 0.8 and 1.8 times the pulse length and a phase deviation of four steps. We accepted targets with a maximum gain compensation of 4 or 6 dB (Simrad 1996). Calibrations indicated that the effect of the beam angle on a standard target was well described by the beam pattern function applied (typical maximum deviation of 0.6 dB from calculated targets after accounting for the beam pattern within the 6 dB compensation angle). Averages were calculated in the linear domain (backscattering cross-section) and back-transformed to decibels. Targets between -61 dB and -37 dB from surveys that met the single-target criteria were included in the analysis of TS distributions. The upper echo threshold was necessary because larger fish were present throughout the year in all study lakes. We based the upper threshold (–37 dB) on the observed TS distributions; targets in the depth strata occupied by alewives were extremely rare above this TS level. We chose –61 dB as the lower threshold, based on an ongoing study in Oneida Lake, New York. This study shows good agreement between abundance for fish 1.5–2.0 cm long and abundance of targets between –61 and -55 dB (Rudstam et al. 2002). As a measure of risk for including multiple echoes as single fish, we calculated the N_v index of Sawada et al. (1993) for each acoustic survey using the following equation:

$$(5) \quad N_v = 0.5 \, c \, \tau \, \psi \, r^2 \, n,$$

where c is the speed of sound underwater (m/s), τ is the effective pulse width (s), ψ is the equivalent beam angle (sr), r is the range of the layer (m) to the transducer, and n is fish density (defined as mean volume backscattering, Sv/σ_{bs}, for the layer of interest). We calculated this index for a single depth stratum (from 2 m to the maximum depth fished with nets) for each transect used in TS estimation. Values less than 0.1 indicate suitable densities for measurement of in situ TS with splitbeam echo sounders (Sawada et al. 1993). Because we included all targets of -70 dB or more in the Nv calculations, this is a conservative measure of the incidence of including multiple targets of –61 dB or more. To calculate the mean TS for the different modes in the TS distributions, we had to separate the distributions into two- or three-component distributions that represented the contribution from young-of-year, yearling, and adult alewives. This step was necessary because of the selectivity of the gill nets. Inclusion of all targets between -61 and -37 dB would not be appropriate for regression analysis when individual fish within the full size range of alewives present were not captured with equal efficiency. The TS modes were separated by using the nonlinear curve-fitting feature in S-PLUS 2000 (Mathsoft 1999). A similar approach has been used to separate the contribution of different size-classes from TS distributions for lake herring (cisco) *C. artedi* (Rudstam et al. 1987), sockeye salmon *Oncorhynchus nerka* (Parkinson et al. 1994), and in marine systems Atlantic herring (Lassen and Stæhr 1985). Peaks in TS distributions have also been used to separate species in a mixture of different sized species (Barange et al. 1994).

Our method assumed that a given size-class of fish has a unimodal and approximately normal TS distribution. To assess this assumption, we examined acoustic data for individual fish collected from stationary vessels in Lake Ontario (August 1996, July 2000) and Otsego Lake (July 1997). Mean TS and the deviations

from that mean were determined for each fish. These data were then separated into

two groups, according to whether the mean TS was less than or greater than-49 dB.

We assumed that if a given size-class of fish exhibited a bimodal TS distribution, this

characteristic would appear in a histogram of the pooled deviations from all fish in the

stationary data. Pooled data from 48 fish of less than -49 dB (317 TS measurements)

and 36 fish of more than –49 dB (754 TS measurements) indicated that the deviations

were unimodal and approximately normally distributed (Figure 1.2). Therefore, we

used the sum of multiple normal distributions to represent the overall TS distribution,

with each distribution representing a TS mode. The fitted probability density function

(f) of targets within the -61 to -37 dB range is as follows:

$$(6) \ f = [p_1 \ (N_1(\mu_1, v_1)) + p_2 \ (N_2(\mu_2, v_2)) + p_i \ (N_i(\mu_i, v_i))....],$$

$$\text{where } \Sigma p_i = 1$$

where $Ep_i = 1$ and $N(m,v)$ is the normal distribution with mean m and standard

deviation v. In cases where two or three TS modes were evident, the modes were

identified from catch data (and from the seasonal change in TS for a mode in lakes

with more than one survey per year). In summer (June through August), three TS

modes were evident, corresponding to young-of-year, yearling, and adult alewives. In

the fall, the largest TS mode was considered to be yearling and older alewives, and the

mode with the smallest TS was considered to be young-of-year. This interpretation is

based on the catches, observed seasonal growth, and the fact that alewives have a

protracted spawning period (Smith 1985). The mean backscattering cross-section was

calculated in the linear domain from each component distribution and was back-

transformed to TS. We correlated mean TS from the transect nearest the gill-net set or

trawl location with the mean size (length or mass) except in Otsego Lake, where we

used TS data from all transects trawl catch data were representative of the entire lake.

The relationship between TS and fish size was determined by simple linear regression

with SPLUS 2000. We derived equations with TS as the dependent and independent variable, because error associated with TS and fish size invalidates the inverse property of the equations. Some studies of in situ TS have used functional regression techniques (Gal et al. 1999) to address concerns over the errors in both variables or assumed that errors were insignificant (e.g., Argyle 1992). Even though error is present in both fish size (length and weight) and TS, we used simple linear regression to provide an unbiased predictive model (Jensen 1986; Sokal and Rohlf 1995; Fleischer et al. 1997). To assess the model fit and potential biases due to influential points, we compared the leverage coefficients (diagonal elements of the hat matrix) with the high leverage threshold of $2p/N$, where p = the number of parameters to be estimated (Belsley et al. 1980; Neter et al. 1996). We also examined the Cook's distance values and the amount by which the model coefficients changed (DFBETAS) for each data point excluded (Neter et al. 1996).

RESULTS

We observed a wide range of lengths and weights of alewives (Table 1.1). The widest range of lengths (0.8–16 cm) was observed in July, when the larval trawl was used in conjunction with gill nets. In general, fish were separable into two or three size-classes corresponding to young-of-year, yearling, and older fish (Figure 1.3). In September the young-of-year size range contained two modes. In July two groups of older alewives could be distinguished, corresponding to yearling and older fish; the separation of these two groups was not possible in the fall. From July to September, young-of-year alewives increased in size and their overall size distribution broadened. Mean lengths and weights for young-of-year alewives included in our model ranged from 2.5 to 8.9 cm and 0.2 to 6.0 g, respectively (Table 1.1). Mean lengths and weights observed for yearlings ranged from 8.7 to 10.3 cm and 5.2 to 8.8 g,
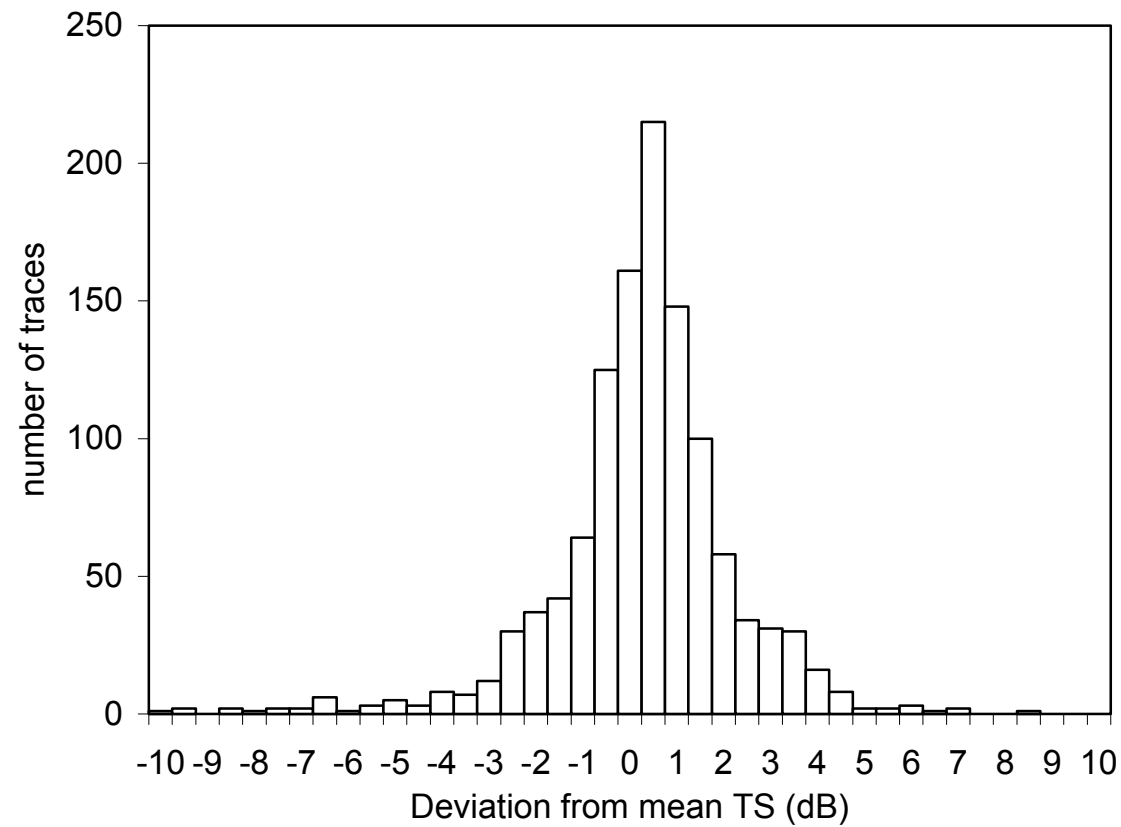
Figure 1.2. Distribution of deviations from mean target strength for young-of-year (upper panel) and older (lower panel) alewife in Lake Ontario collected during stationary surveys on 26 August 1996 and Otsego Lake on 24 July 2000 and 16 September 1996. Bars depict the observed deviations from mean target strength (TS) for all individual fish in each age group. The lines depict a normal distribution with the mean and SD of the observed distributions of deviations from mean TS.

respectively. Yearlings were separable only in surveys conducted from June through August (four surveys). Mean lengths and weights for older alewives ranged from 10.1 to 15.2 cm and 9.5 to 25.7 g, respectively (Table 1.2).

Acoustic estimates of fish density were sufficiently low to allow us to distinguish individual fish targets. All of the surveys included in this study exhibited Nv values less than 0.1, indicating suitable conditions for in situ TS measurements (Table 1.2; Sawada et al. 1992). Mean TS values derived from the nonlinear fitting procedure ranged from -56.1 to -48.0 dB for the smallest size-group (young-of-year alewife), from -45.1 to -43.3 dB for yearlings, and from -43.4 to -39.0 dB for the largest size-group (adult alewife). As with length, the average TS of the young-of-year fish groups increased and the TS distribution broadened from July through September. In nearly all fall surveys, we observed two modes in the TS distribution for the small targets that had also been apparent in the length distributions (Figure 1.3).

The correlations between TS and all fish size (length in centimeters and weight in grams) were highly significant. The predictive equations (± SE of coefficients) were as follows:

$$TS = 20.53(\pm0.78) \log_{10} L_{cm} - 64.25(\pm0.80) \quad (7)$$

$$r = 0.98, P < 0.001, N = 37$$

$$TS = 20 \log_{10} L_{cm} - 63.61(\pm0.18) \quad\quad (8)$$

$$N = 37$$

$$\text{Log}_{10} L = 3.03(\pm0.077) + 0.046(\pm0.002) \text{ TS} \quad (9)$$

$$r = 0.98, P < 0.001, N = 37$$

$$TS = 6.98(\pm0.30) \log_{10} W_{g} - 50.07(\pm0.33) \quad (10)$$

$$r = 0.97, P <0.001, N = 37$$
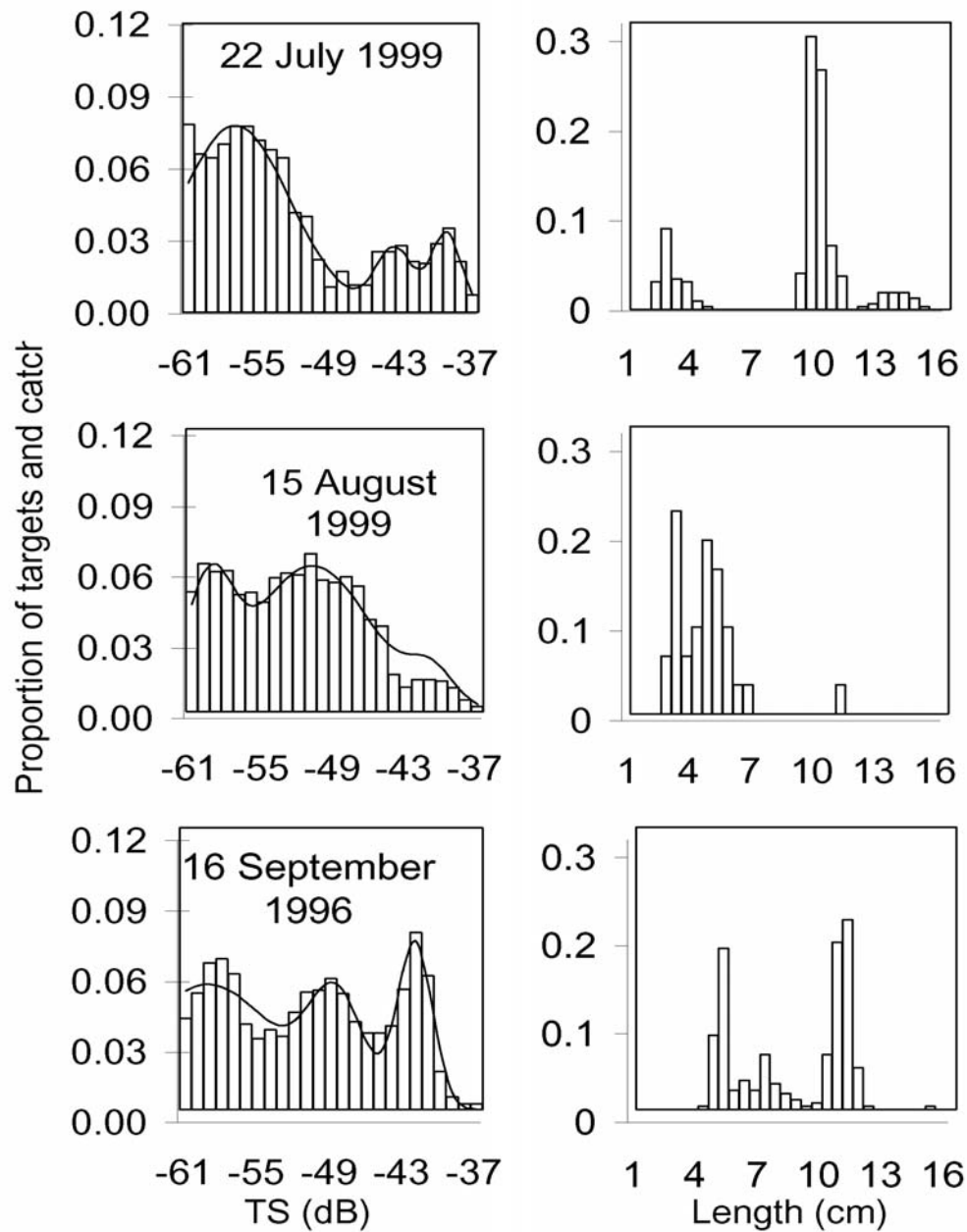
Figure 1.3. Target strength (TS) and length-frequency distributions for surveys on 20-21 July 1999, 12 August 1999, and 16 September 1996 in Otsego Lake. The curve super-imposed on the TS histograms represents the non-linear fit for the TS distribution.

Table 1.1. Mean length (cm; ± 2 SE), mean weight (g; ± 2 SE), and sample size (in parentheses) for young-of-year and yearling alewives in four New York lakes. Cases where young of year were not sampled effectively are noted accordingly.

Date	Lake	Mean length (YOY)	Mean weight (YOY)	Mean length (yearling)	Mean weight (yearling)
05 August 1996	Cayuta	ineffectively sampled	ineffectively sampled	10.3±0.1 (61)	8.8 (61)
16 September 1996	Otsego	5.8±0.2 (132)	1.5±0.2 (140)	Not separable	Not separable
21 July 1999	Otsego	3.0±0.2 (63)	0.3±0.1 (63)	10.0±0.06 (236)	8.6±0.2 (26)
12 August 1999	Otsego	4.4 ±0.4 (30)	0.5±0.1 (30)[b]	Not separable	Not separable
03 June 2000	Otsego	Not present	Not present	8.7±0.2 (40)	5.2±0.3 (40)
23 July 2000	Otsego	2.5±0.2 (76)	0.2±0.1 (76) [b]	9.7±0.2 (28)	8.1±0.3 (28)
08 September 2000	Conesus	6.8±0.2 (121)	2.6±0.3 (121)	Not separable	Not separable
14 September 2000	Otisco	8.9±0.2 (41)	6.0±0.4 (41)	Not separable	Not separable
16 September 2000	Cayuta	7.2±0.2 (279)	3.0±0.2 (279)	Not separable	Not separable

[a] Lengths and weights of fish collected on 20–21 July were used for the surveys on 21

[b] Weight estimated using a weight-length relationship determined from fish captured 21-22 July 1999

Table 1.2. Mean length (cm; ± 2 SE), mean weight (g; ± 2 SE), and sample size (in parentheses) for adult alewives captured in eight inland New York lakes and Lake Ontario. The index of suitability for in situ target strength (Nv; Sawada et al. 1992) is shown as well.

Date	Lake	Mean length	Mean weight	N_v
10 October 1995	Cayuta	13.3±0.5 (60)	16.8±0.1 (60)[a]	0.04
05 August 1996	Cayuta	11.7±0.4 (103)	11.7±0.1 (103)[a]	0.01
16 September 1996	Otsego	10.9±0.1 (146)	10.1± 0.3 (146)	0.02
24 September 1996	Conesus	10.7±0.5 (95)	10.4±0.1 (95)[a]	0.03
01 July 1997	Ontario	15.1±0.4 (72)	25.7±1.6 (72)	0.02
06 July 1997	Otsego	11.7±0.2 (214)	11.6±0.2 (214)	0.03
16 August 1997	Owasco	13.3±0.1 (258)	18.0±0.1 (258)	0.03
17 September 1997	Ontario	10.1±0.2 (4)	14.0±1.0 (4)	0.05
22 September 1997	Conesus	13.4±0.9 (101)	20.2±0.1 (101)[a]	0.03
06 November 1997	Owasco	13.4±0.3 (101)	18.5±0.1 (101)[a]	0.02
06 July 1998	Ontario	14.8±0.2 (180)	23.7±0.6 (180)	0.04
07 July 1998	Ontario	15.2±0.3 (85)	25.4±0.9 (85)	0.02
23 July 1998	Ontario	10.4±0.8 (24)	14.1± 2.0 (24)	0.02
17 September 1998	Conesus	12.0±0.4 (118)	15.3±1.1 (118)	0.02
14 October 1998	Cayuga	12.8±0.2 (67)	17.5±0.6 (67)	0.05
21 July 1999	Otsego	13.8±3.0 (26)	19.1±1.2 (7)	0.07
22 July 1999	Otsego	13.8±3.0 (26)	19.1±1.2 (7)	0.04

[a] Estimated using a weight–length equation determined from the lake in question.

Table 1.2. (Continued).

Date	Lake	Mean length	Mean weight	N_v
03 June 2000	Otsego	12.7±0.2 (22)	9.5±1.5 (22)	0.03
23 July 2000	Otsego	12.2±0.2 (27)	12.5±0.5 (27)	0.02
4 September 2000	Seneca	12.9±0.2 (47)	17.5±1.6 (47)	0.01
5 September 2000	Canadice	13.1±0.2 (37)	18.4±1.4 (37)	0.02
8 September 2000	Conesus	11.9±0.1 (79)	14.0±0.9 (79)	0.05
14 September 2000	Otisco	13.6±0.1 (152)	24.6±0.9 (152)	0.01
16 September 2000	Cayuta	14.5±0.2 (93)	24.4±2.0 (93)	0.01

[a] Weight estimated using a weight-length equation determined from the respective lake.

$$\text{Log}_{10}\,L = 3.03(\pm 0.077) + 0.046(\pm 0.002)\,\text{TS} \quad (9)$$

$$r = 0.98,\, P < 0.001,\, N = 37$$

$$\text{TS} = 6.98(\pm 0.30)\,\log_{10} W_g - 50.07(\pm 0.33) \quad (10)$$

$$r = 0.97,\, P < 0.001,\, N = 37$$

$$\log_{10} W_g = 6.79(\pm 0.26) + 0.13(\pm 0.005)\text{TS} \quad (11)$$

$$r = 0.97,\, P < 0.001,\, N = 37$$

Regression diagnostics revealed two unusual characteristics of the models. The residual variation increased with increasing alewife TS, length, and weight. Leverage coefficients indicated that there were three high-leverage data points (leverage >0.11; Figure 4). Values for DFBETAS were < 0.5, while Cook's distance values were < 0.15.

DISCUSSION

Target strength–fish size relationships that are derived in situ have the advantage of including the effects of physiology and natural behavior (gut fullness, gonad development, and tilt angle) in the TS measurements (MacLennan and Simmonds 1992). However, several areas of potential error exist, associated with (1) obtaining a representative sample of the fish species and sizes present, (2) acoustic detection and discrimination of individual targets, and (3) the statistical techniques used. If we can assume these potential errors were minimized here, the results we present provide an important first step in developing a robust TS–length relationship for alewives in freshwater lakes.

We minimized the potential bias associated with fish sampling by accounting for size selectivity of gill nets. We used knowledge of seasonal changes in size distributions of inland lake alewife populations to help determine the expected sizes of alewives in a given lake during sampling (which allowed us to determine whether we
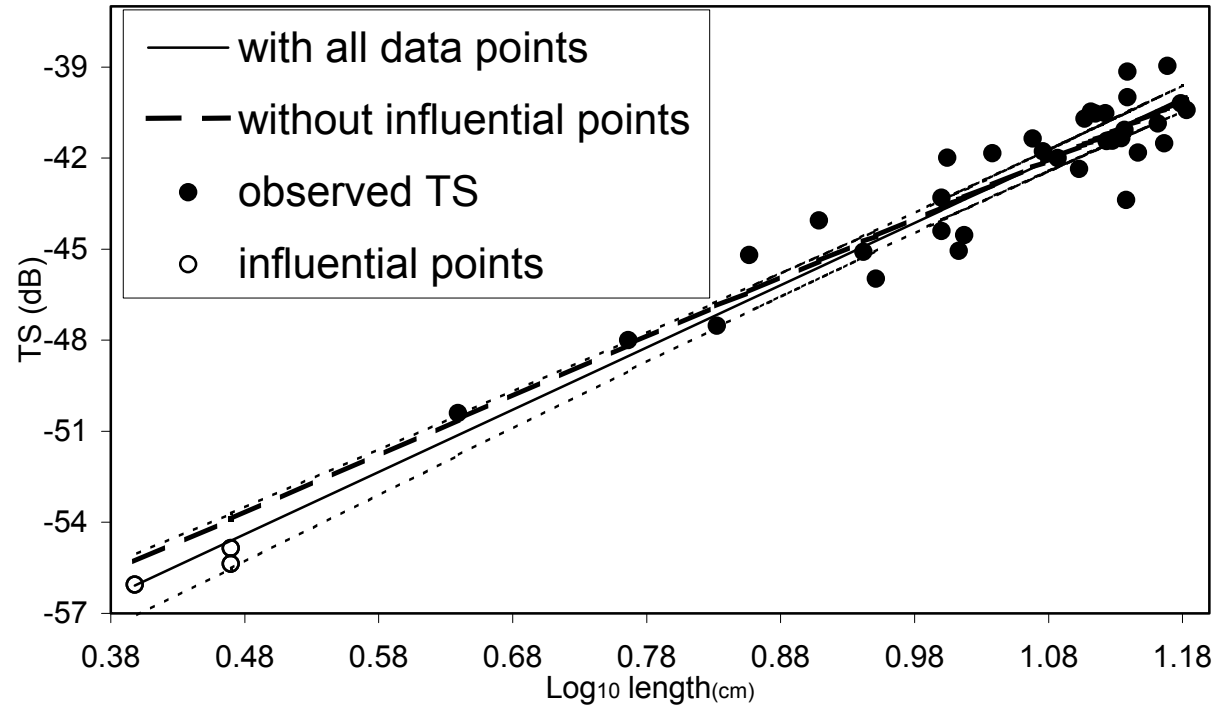
Figure 1.4. Comparison of regression lines for predicting alewife target strength (TS) from length. The solid line represents the regression with all 37 data points. The heavy broken line represents the regression without three high-leverage points identified as young-of-year alewives (open symbols). Both closed and open symbols represent the observed data. The light broken lines represent the 95% confidence interval for the regression line. Differences in regression parameters were insignificant (P>0.1).

had captured all sizes effectively). In addition, we included only young-of-year data for the lakes where we collected midwater trawl catch data because our gill nets do not adequately sample fish smaller than 5 cm (Figure 1.1).

There are several possible sources of bias in acoustic target recognition and discrimination. In situ studies may include non-target species, for example, but contamination was reduced in this study because we sampled in lakes with pelagic fish communities dominated by alewives. In situ studies also carry the risk of including multiple echoes as single-fish TS data. However, the risk of multiple echoes is minimal in situations where the *Nv* index of Sawada et al. (1992) is less than 0.1. Another potential acoustical problem was the possibility of one size-class of fish exhibiting more than one TS mode. Traynor and Williamson (1983) and Williamson and Traynor (1984) observed multimodal TS distributions for single size-classes of walleye pollock *Theragra chalcogramma* and Pacific whiting *Merluccius productus*. If multiple TS modes exist for individual size-classes, our approach to identifying and separating modes in the TS distribution would be invalid. However, our analysis of stationary acoustic data indicated that individual alewives do not have bimodal TS distributions at 70 kHz. Lastly, different acoustic pulse widths can influence TS measurements and the rate at which single targets are accepted (Soule et al. 1997). However, the differences observed in the number and distribution of targets larger than −61 dB in Oneida Lake during June 2000 were very small at the pulse lengths used in this study (0.2 and 0.6 ms; L. G. Rudstam, unpublished data).

The statistical issues faced in TS studies include model choice and the distribution/dispersion of data points. Model choice depends on the study objective (Jensen 1986; Sokal and Rohlf 1995). Because we were primarily interested in deriving predictive equations, a simple linear regression model was most appropriate, despite errors associated with measures of both TS and alewife size (Jensen 1986;

Sokal and Rohlf 1995). We observed a pattern that suggested increased residual variability with increasing TS and alewife size. This pattern was most likely a result of the fact that most of the smaller fish were collected during the summer in one lake, whereas the larger fish were collected during summer and fall in multiple lakes. Estimation of the leverage of individual points in our models revealed three influential points (corresponding to young-of-year alewives), but none of these points appeared to have excessive influence on the estimated parameters (DFBETAS < 0.5 for all data; Neter et al. 1996) or on the predictions (Cook's distance values <0.15 for all data; Neter et al. 1996).

The slope of our equation for the TS–length regression was similar to several published equations, but the intercept was higher (Figure 1.5). The Lindem and Sandlund (1984) regression, also supported by 70 kHz data in freshwater lakes (Bjerkeng et al. 1991), is based on the Craig and Forbes (1969) algorithm for removing the beam pattern effect from single-beam acoustic data. The Lindem and Sandlund (1984) method may have resulted in TS values that are biased low for two reasons. First, Rudstam et al. (1999a) showed that the modified Craig and Forbes (1969) algorithm is biased low by 0.8 dB. Second, Lindem and Sandlund (1984) compared the modes in length and TS distributions, which may allow for correct identification of size groups but will result in TS that is biased low because the mode of a TS distribution is lower than the average calculated in the linear domain as a result of the logarithmic scale of TS. Our equation had a slightly steeper slope than Love's (1971) dorsal aspect equation used by Brandt et al. (1991) and a greater intercept (2.5 dB) than Love's (1977) average 0–45º tilt angle equation. Predictions with our equations were quite different from those based on existing equations for Great Lakes planktivores (Argyle 1992; Fleischer et al. 1997). Predicting TS from our observed alewife lengths and using Argyle's (1992) equation resulted in TS values
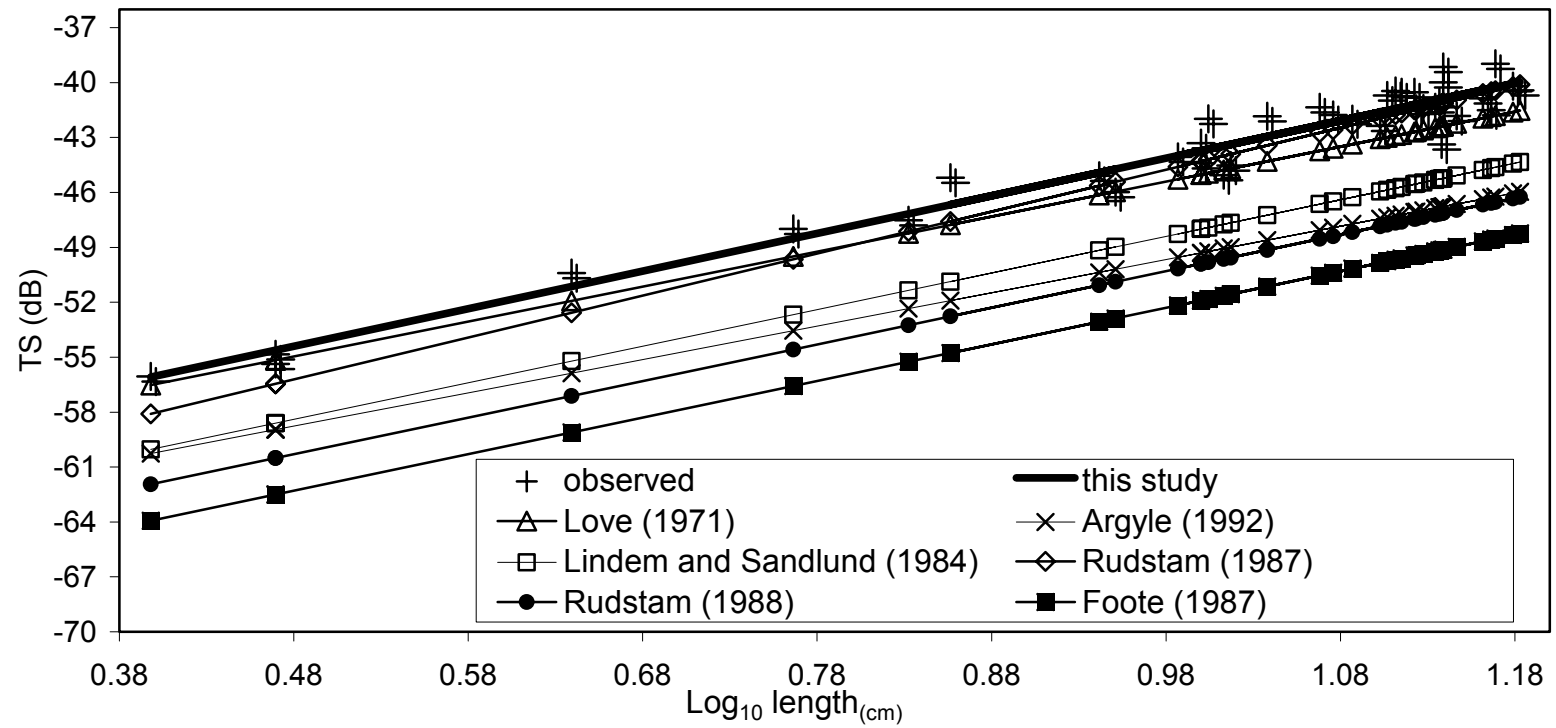
Figure 1.5. Comparison of the TS-length regression from this study with regression lines for Atlantic herring (Foote 1987) and Rudstam et al. (1988). Also shown for comparison are regression lines for cisco (Rudstam et al. 1987), two lines from laboratory work with data pooled from several orders/species (Love 1971; Love 1977), *Osmerus* *eperlanus* (Lindem and Sandlund 1984), and a mixture of alewives, rainbow smelt, and bloater (Argyle 1992). Both marine equations are shown in 20 log L – b form.

4.2 to 6.0 dB lower than those predicted from our equation. Fleischer et al.'s. (1997) equations had a shallower slope and greater intercept than ours. Although this study and the study by Fleischer et al. (1997) predicted similar fish sizes for TS of -41 dB, our equations predicted smaller fish sizes for targets of less than -41 dB and larger fish sizes for targets of greater than -41 dB (Figure 1.6). One possible explanation for the difference observed between our results and those of Argyle (1992) and Fleischer et al. (1997) is fish community composition. Argyle (1992) and Fleischer et al. (1997) caught primarily rainbow smelt in Lake Michigan. Alewives were a minor portion of the fish they sampled, suggesting that their equations may be more representative of smelt TS–size relations. Rudstam et al. (1999b) and Burczynski et al. (1987) found the TS for smelt to be 3–4 dB lower than our values for alewives of the same length. Also, the trawl used by Fleischer et al. (1997) had a 13-mm bar mesh cod end that probably limited the capture of small fish. Lastly, Horne and Jech (1999) found major differences in backscattering strength of threadfin shad *Dorosoma petenense* at different frequencies, which suggests that differences between our equations and those of Argyle (1992), Fleischer et al. (1997), and Burczynski et al. (1987) could be frequency-induced. However, Rudstam et al. (1999a) compared mean in situ TS from concurrent sampling with 70 and 120 kHz split-beam echosounders and found that the 120 kHz system provided TS values only 1dB lower than the 70 kHz echosounder. Differences between dual and split-beam methods should be minor, as should differences in calibration methods (Foote 1987).

An alternative to using the equations of Fleischer et al. (1997) for alewives is to use the standard TS–length relationship for marine clupeids (based on Atlantic herring; Foote 1987). However, use of a marine equation for freshwater alewives may not be appropriate because TS of Atlantic herring has been shown to vary 2–3 dB with salinity (Lassen and Stæhr 1985; Rudstam et al. 1988) and lipid content (Ona 1990).
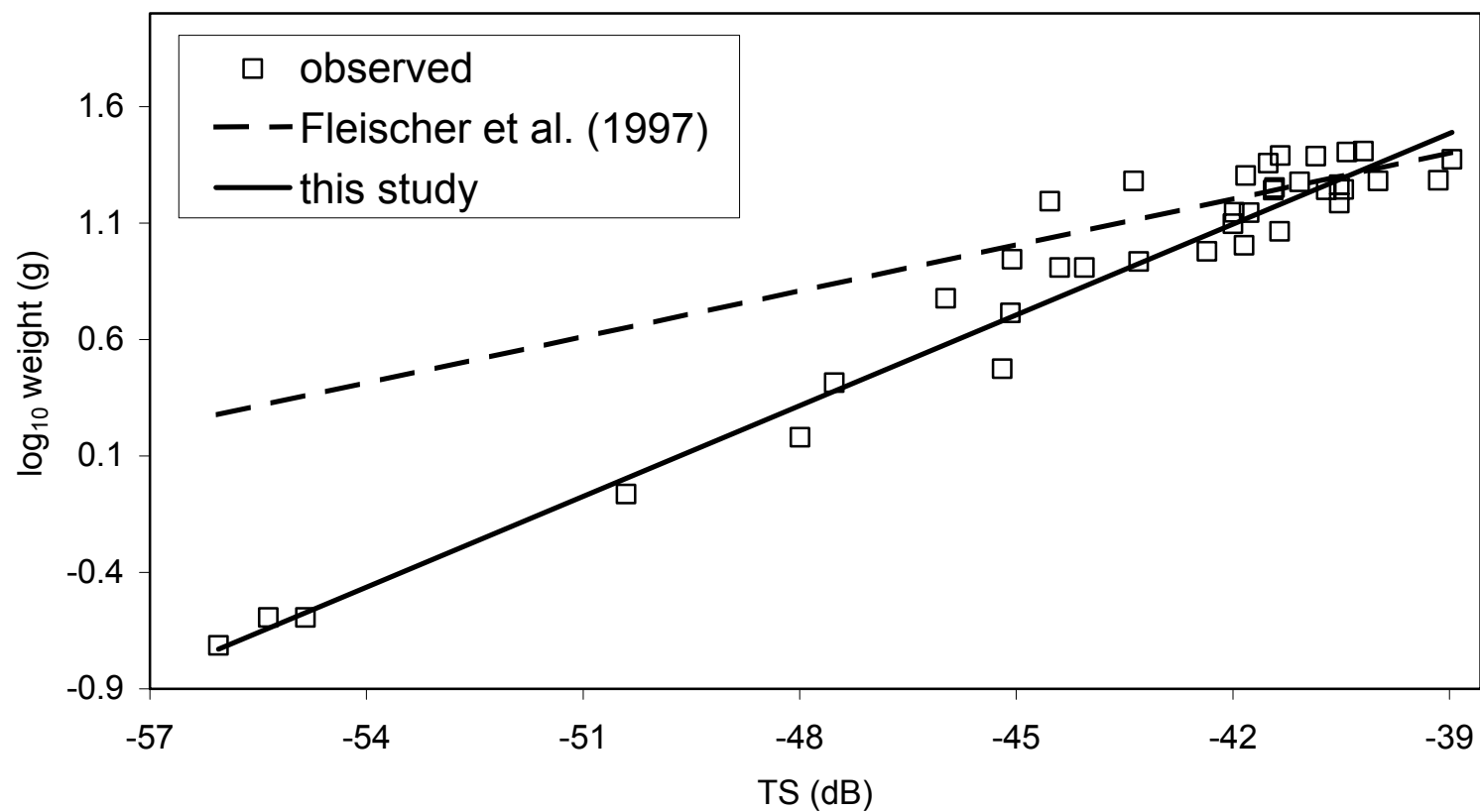
Figure 1.6. Comparison of the length-TS and weight-TS regression lines determined for alewives in this study with those from a recent study of Great Lakes planktivores (rainbow smelt, bloaters, and alewives, Fleischer et al. 1997).

Lipid content has been shown by Machias and Tsimenides (1996) to influence swim bladder surface area (and therefore TS) in the sardine *Sardina pilchardus*. In addition to the obvious difference in salinity of the two environments, the lipid content of Atlantic herring (16.8% of wet weight; Ona 1990) is greater than the lipid content of freshwater alewives (9.1% of wet weight; Flath and Diana 1985). These differences in salinity and lipid content suggest that freshwater alewives may have a greater TS for a given fish length than do Atlantic herring. The effect of both lower salinity and lower lipid content is a decrease in buoyancy, which may necessitate a larger swim bladder to achieve a given buoyancy level in freshwater alewives.

We observed considerably greater TS for alewives than have been observed in situ by others for marine clupeids of similar size. The standard clupeid regression proposed by Foote (1987) predicts TS values that are about 8 dB lower than those obtained from our equation. Although both Lassen and Stæhr (1985) and Rudstam et al. (1988) observed lower TS for Atlantic herring than we observed for alewives of a similar size, they observed greater in situ TS (2–3 dB) for Atlantic herring in brackish water (Baltic Sea) than was measured in seawater. Differences in specific gravity of the occupied water, differences in lipid content, different tilt angle distributions, different echosounder frequencies, and differences in depth distribution all may have contributed to the observed differences between marine and freshwater clupeids. Differences in reproductive state may have been a factor as well (Machias and Tsimenides 1996). The greater TS measured here for a freshwater clupeid may be the result of the lower specific gravity of freshwater or the lower lipid content of alewives relative to Atlantic herring, both of which decrease buoyancy and may necessitate a larger swim bladder volume (Ona 1990). Whether increased swim bladder volume results increased TS in alewives is unclear. Although fish anatomy (the spinal column and rib cage) may prevent an increase in swim bladder volume from increasing the

dorsal swim bladder surface area, Blaxter et al. (1979) found that pressure-induced decreases in herring swim bladder volume were accompanied by decreases in dorsal surface area. This response suggests that changes in TS may be correlated with changes in swim bladder volume. Fleischer and TeWinkel (1998) and Mukai and Iida (1996) suggested that this pattern was present in bloater and sockeye salmon as well. Fish tilt angle can have a major influence on TS (Foote 1980), and perhaps the tilt angle distribution of Atlantic herring is different; a greater mean tilt angle for these fish could result in lower TS values than we observed for freshwater alewives. Lastly, the marine studies described above used 38-kHz echosounders. It remains unclear whether the observed differences result from different frequencies. Our results suggest that salinity may influence TS enough to complicate acoustic estimates of fish abundance/biomass along salinity gradients such as the Chesapeake Bay (Luo and Brandt 1993) or the Baltic Sea (Orlowski 1998).

The slope of our TS–length equation was similar to those of other published equations (Love 1971, 1977; Foote 1987). In particular, our equation and Love's (1971) predicted similar TS and length values over most of the observed range for freshwater alewives. Our results do not support the contention by Fleischer et al. (1997) that use of Love's equation (1971) for Great Lakes planktivores (e.g., Brandt et al. 1991; Goyke and Brandt 1993; Mason et al. 2000) will lead to underestimation of biomass when alewives are the dominant pelagic fish species.

In summary, our results support several conclusions. First, there was a strong positive relationship between TS and both length and weight of alewives, the young-of-year and older fish having significantly different TS values. The TS differences between size-classes allowed acoustic separation of these groups and indicated that in some cases length frequency distributions can be derived from acoustics. Second, the methods used to acoustically separate size-classes of alewives could be used for other

species or to separate two species with size differences. Lastly, freshwater alewives in our study lakes exhibited greater TS than similar sizes of Atlantic herring, but the reasons for this difference remain to be determined.

REFERENCES

Argyle, R. L. 1992. Acoustics as a tool for the assessment of Great Lakes forage
fishes. Fisheries Research 14:179–196.

Barange, M., I. Hampton, S. C. Pillar, and M. A. Soule. 1994. Determination of
composition and vertical structure of fish communities using in situ
measurements of acoustic target strength. Canadian Journal of Fisheries and
Aquatic Sciences 51:99–109.

Belsley, D. A., E. Kuh, and R. E. Welsch. 1980. Regression diagnostics. Wiley, New
York.

Bjerkeng, B., R. Borgstrrm, X. Brabrand, and B. Faafeng. 1991. Fish size distribution
and total fish biomass estimated by hydroacoustical methods: a statistical
approach. Fisheries Research 11:41–73.

Blaxter, J. H. S., E. J. Denton, and J. A. B. Gray. 1979. The herring swimbladder as a
gas reservoir for the acoustico-lateralis system. Journal of the Marine
Biological Association of the United Kingdom 59:1–10.

Brandt, S. B. 1996. Acoustic assessment of fish abundance and distribution. Pages
385–432 in B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd
edition. American Fisheries Society, Bethesda, Maryland.

Brandt, S. B., D. M. Mason, E. V. Patrick, R. L. Argyle, L. Wells, P. A. Unger, and D.
J. Stewart. 1991. Acoustic measures of the abundance and size of pelagic
planktivores in Lake Michigan. Canadian Journal of Fisheries and Aquatic
Sciences 48:894–908.

Burczynski, J. J., P. H. Michaletz, and G. M. Marrone. 1987. Hydroacoustic
assessment of the abundance and distribution of rainbow smelt in Lake Oahe.
North American Journal of Fisheries Management 7:106–116.

Craig, R. E., and S. T. Forbes. 1969. A sonar for fish counting. Report on Norwegian

Fishery and Marine Investigations 15:210–219.

Ehrenberg, J. E. 1972. A method for extracting the fish target strength distribution from acoustic echoes. Pages 61–64 *in* Proceedings of the 1972 Institute of Electrical and Electronic Engineering conference of engineering in the ocean environment. Institute of Electrical and Electronic Engineering, Newport, Rhode Island.

Flath, L. E., and J. S. Diana. 1985. Seasonal energy dynamics of the alewife in southeastern Lake Michigan. Transactions of the American Fisheries Society 114:328–337.

Fleischer, G. W., R. L. Argyle, and G. L. Curtis. 1997. *In situ* relations of target strength to fish size for Great Lakes pelagic planktivores. Transactions of the American Fisheries Society 126:786–794.

Fleischer, G. W., and L. M. TeWinkel. 1998. Buoyancy characteristics of the bloater (*Coregonus hoyi*) in relation to patterns of vertical migration and acoustic backscattering. Archiv fuer Hydrobiologie Special Issues Advanced Limnology 50:219–225.

Foote, K. G. 1979. On representing the length dependence of acoustic target strengths of fish. Journal of the Fisheries Research Board of Canada 36:1490–1496.

Foote, K. G. 1980. Effects of fish behavior on echo energy: the need for measurement of orientation distributions. Journal du Conseil, Conseil International pour l'Exploration de la Mer 39:193–201.

Foote, K. G. 1987. Fish target strengths for use in echo integrator surveys. Journal of the Acoustical Society of America 82:981–987.

Gal, G., L. G. Rudstam, and C. H. Greene. 1999. Acoustic characterization of *Mysis relicta*. Limnology and Oceanography 44:371–381.

Goyke, A. P., and S. B. Brandt. 1993. Spatial models of salmonine growth rates in

Lake Ontario. Transactions of the American Fisheries Society 122:870–883.

Hansson, S., and L. G. Rudstam. 1995. Gillnet catches as an estimate of fish abundance: a comparison between vertical gillnet catches and hydroacoustic abundances of Baltic Sea herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). Canadian Journal of Fisheries and Aquatic Sciences 52:75–83.

Horne, J. K., and C. S. Clay. 1998. Sonar systems and aquatic organisms: matching equipment and model parameters. Canadian Journal of Fisheries and Aquatic Sciences 55:1296–1306.

Horne, J. K., and J. M. Jech. 1999. Multi-frequency estimates of fish abundance: constraints of rather high frequencies. ICES Journal of Marine Science 56:184–199.

Jensen, A. L. 1986. Functional regression and correlation analysis. Canadian Journal of Fisheries and Aquatic Sciences 43:1742–1745.

Lassen, H., and K. J. Stæhr. 1985. Target strength of Baltic herring and sprat measured in situ. International Council for the Exploration of the Sea C. M./1985/B:41, Copenhagen.

Lindem, T., and O. Sandlund. 1984. New method in assessment of pelagic freshwater fish stocks—coordinated use of echosounder, pelagic trawl, and pelagic nets. Fauna 37:105–111. (In Norwegian, English summary.)

Love, R. H. 1971. Dorsal-aspect target strength of an individual fish. Journal of the Acoustical Society of America 49(3):816–823.

Love, R. H. 1977. Target strength of a fish at any aspect. Journal of the Acoustical Society of America 62:1397–1403.

Luo, J., and S. B. Brandt. 1993. Bay anchovy (*Anchoa mitchilli*) production and consumption in mid-Chesapeake Bay based on a bioenergetics model and acoustic measures of fish abundance. Marine Ecology Progress Series 98:223–

236.

Machias, A., and N. Tsimenides. 1996. Anatomical and physiological factors affecting the swimbladder cross-section of the sardine *Sardina pilchardus*. Canadian Journal of Fisheries and Aquatic Sciences 53:280–287.

MacLennan, D. N., and E. J. Simmonds. 1992. Fisheries Acoustics. Chapman and Hall, New York.

Mason, D. M., A. P. Goyke, S. B. Brandt, and J. M. Jech. 2000. Acoustic fish stock assessment in the Laurentian Great Lakes. *In* M. Munawar, editor, Great Lakes of the World Ecovision World Monograph Series, Backhuys, Leiden, The Netherlands.

Mathsoft. 1999. S-PLUS 2000 guide to statistics, volume 1. Mathsoft, Inc., Seattle.

McClatchie, S., J. Alsop, and R. F. Coombs. 1996. A re-evaluation of relationships between fish size, acoustic frequency, and target strength. ICES Journal of Marine Science 53:780–791.

Mukai, T., and K. Iida. 1996. Depth dependence of target strength of live kokanee salmon in accordance with Boyle's law. ICES Journal of Marine Science 53:245–248.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models. McGraw-Hill, New York.

O'Gorman, R., O. E. Johannsson, and C. P. Schneider. 1997. Age and growth of alewives in the changing pelagia of Lake Ontario, 1978–1992. Transactions of the American Fisheries Society 126:112–126.

Ona, E. 1990. Physiological factors causing natural variation in acoustic target strengths of fish. Journal of the Marine Biological Association of the United Kingdom 70:107–127.

Orlowski, A. 1998. Acoustic methods applied to fish environmental studies in the

Baltic Sea. Fisheries Research 34:227–237.

Parkinson, E. A., B. E. Rieman, and L. G. Rudstam. 1994. Comparison of acoustic and trawl methods for estimating density and age composition of kokanee. Transactions of the American Fisheries Society 123:841–854.

Rudstam, L. G., C. S. Clay, and J. J. Magnuson. 1987. Density and size estimation of cisco (*Coregonus artedii*) using analysis of echo peak PDF from a single-transducer sonar. Canadian Journal of Fisheries and Aquatic Sciences 44:811–821.

Rudstam, L. G., T. Lindem, and S. Hansson. 1988. Density and in situ target strength of herring and sprat: a comparison between two methods of analyzing single-beam sonar data. Fisheries Research 6:305–315.

Rudstam, L. G., S. Hansson, T. Lindem, and D. W. Einhouse. 1999a. Comparison of target strength distributions and fish densities obtained with split and single beam echosounders. Fisheries Research 898:1–8.

Rudstam, L. G., T. Lindem, and G. Labar. 1999b. The single beam analysis. Pages 6–12 *in* E. Ona, editor. Methodology for target strength measurements with special references to *in situ* techniques for fish and mikro-nekton. International Council for the Exploration of the Sea Cooperative Research Report 235.

Rudstam, L. G., A. J. Vandevalk, and M. D. Scheuerell. 2002. Comparison of acoustic and Miller high speed estimates of larval fish abundance in Oneida Lake. Fisheries Research 57:145-154.

Sawada, K., M. Furusawa, and N. J. Williamson. 1993. Conditions for the precise measurement of fish target strength *in situ.* Journal of the Marine Acoustical Society of Japan 20:73–79.

Simrad. 1996. Simrad EY500 portable scientific echosounder, version 5.2. Instruction manual. Simrad, Horten, Norway.

Smith, C. L. 1985. Inland fishes of New York. New York State Department of
Environmental Conservation, Albany.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry, 2nd edition. Freeman, New York.

Soule, M., M. Barange, H. Solli, and I. Hampton. 1997. Performance of a new phase
algorithm for discriminating between single and overlapping echoes in a split-
beam echosounder. ICES Journal of Marine Science 54:934–938.

Traynor, J. J., and N. J. Williamson. 1983. Target strength measurements of walleye
pollock *Theragra chalcogramma* and a simulation study of the dual beam
method. FAO (Food and Agriculture Organization of the United Nations)
Fisheries Reports 300:112–124.

Williamson, N. J., and J. J. Traynor. 1984. *In situ* target strength estimation of Pacific
whiting (*Merluccius productus*) using dual-beam transducer. Journal du
Conseil, Conseil International pour l'Exploration de la Mer 41:285–292.

Wulff, A. 1986. Mathematical model for selectivity of gill nets. Archiv fuer
Fischereiwissenschaft 37:101–106.

CHAPTER TWO

Cercopagis pengoi as a new prey item for alewife (*Alosa pseudoharengus*) and

rainbow smelt (*Osmerus mordax*) in Lake Ontario

ABSTRACT

Diets of alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*)

were examined before (1997) and after (1998 and 1999) the establishment of the

predatory cladoceran *Cercopagis pengoi* in Lake Ontario. *Cercopagis pengoi* was

absent in both fish stomachs and zooplankton samples in 1997, but by August 1998,

its distribution was lake-wide and spines of this organism were present in stomachs of

both fish species. Incidence of *C. pengoi* spines was highest in adult alewives. Spines

occurred in 72, 100, and 90% of stomachs in August 1998, August 1991, and October

1999, respectively. Spines were found in 15 and 53% of YOY alewife stomachs in

August 1998 and October 1999, respectively. *Cercopagis pengoi* spines were least

common in rainbow smelt stomachs (12% in August 1998 and 6% in October 1999).

Low frequency of occurrence in rainbow smelt likely resulted from limited spatial

overlap with *C. pengoi*. No *C. pengoi* spines were found in alewives < 66 mm total

length (TL) which suggests that consumption of *C. pengoi* by YOY alewife is limited

by the long caudal spine. Low consumption of *C. pengoi* by YOY alewife may

explain the remarkably rapid population increase of *C. pengoi* in Lake Ontario in 1998

in the presence of a strong alewife year class. These results indicate that *C. pengoi* is a

competitor of YOY alewives for zooplankton during the summer but also a potential

prey item for larger fish throughout the year and for YOY alewife in the fall.

33

INTRODUCTION

Cercopagis pengoi is a predatory cladoceran endemic to the Ponto-Caspian basin (MacIsaac *et al.* 1999). It is among the most widely distributed species of the genus *Cercopagis* and has recently been introduced to the Baltic Sea and the Laurentian Great Lakes of North America (Ojaveer and Lumberg 1995, MacIsaac *et al.* 1999, Gorokhova *et al.* 2000). Genetic similarity between the Baltic Sea and Great Lakes populations suggests that colonization of North America was the result of transoceanic shipping from the Baltic Sea (Cristescu *et al.* 2001). *Cercopagis pengoi* is euryhaline (Mordukhai-Boltovskoi and Rivier 1971) and consequently individuals or diapausing eggs of this organism may survive in ballast tanks even if they are flushed with salt water. *Cercopagis pengoi* was first observed in Lake Ontario in July 1998 (MacIsaac *et. al.* 1999). By 1999, *C. pengoi* was also documented in Lake Michigan, Cross Lake (New York), and five of New York State's Finger Lakes (Charlebois *et al.* 2001, Makarewicz *et al.* 2001). *Cercopagis pengoi* became a major component of the Lake Ontario zooplankton community the same year that is was first observed (Ojaveer *et al.* 2001, Makarewicz *et al.* 2001).

The extent to which planktivorous fish species, such as alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) use *C. pengoi* as prey has important ecological implication and may vary between size classes and species. Because of its consistent presence and, at times, high abundance, *C. pengoi* may decrease food availability for planktivorous fish if it substantially decreases the density of other zooplankton through predation and does not serve as a suitable alternate prey. Smaller fish may be deterred from consuming *C. pengoi* by its up to 10-mm-long caudal appendage that is more than five times longer than its body length. Barnhisel and Harvey (1995) found that lake herring (*Coregonus artedi*) < 70 mm

total length (TL) did not consume *Bythotrephes longimanus* (previously *cederstroemi*), a similar cladoceran that also has a long caudal spine.

While the potential for negative impacts exists, *C. pengoi* may provide an additional food source for larger planktivorous fish in Lake Ontario. After its establishment in Lakes Erie and Ontario, *Bythotrephes longimanus* became a common prey item of adult planktivorous fish (Mills *et al.* 1992, Parker *et al.* 2001). In the Gulf of Riga, Baltic Sea, *C. pengoi* accounted for the majority (up to 100%) of stomach contents of juvenile and adult Baltic herring (*Clupea harengus membras*) in 1994 (Ojaveer and Lumberg 1995). These authors suggested that an increase in *C. pengoi* could contribute to improved feeding conditions and growth of Baltic herring since the Cladoceran is suitable, energetically beneficial, and readily consumed prey.

Whether the presence of *C. pengoi* increases or decreases availability of prey to planktivorous fish in Lake Ontario will depend both on the impact of *C. pengoi* on other zooplankton the extent planktivorous fish utilize *C. pengoi*. In the paper, the frequency of occurrence of the readily identifiable caudal spine of *C. pengoi* was investigated in the stomach contents of alewives and rainbow smelt sampled with mid-water trawls at various location and depths across Lake Ontario. Differences in the proportion of the two species that had consumed *C. pengoi*, differences in *C. pengoi* consumption between young-of –the-year (YOY) and older alewife, and differences in *C. pengoi* consumption by YOY in August and October were tested for. Lastly, because fish may be more effective samplers of rare large zooplankton than plankton nets, the diet of fish captured in 1997 was also investigated to determine if *C. pengoi* was present but not detected in plankton samples in 1997.

METHODS

Fish were collected at night aboard the R/V *Seth Green* during joint trawl/hydroacoustic surveys of Lake Ontario by the Ontario Ministry of Natural Resources and New York State Department of Environmental Conservation. Trawling was conducted with a 9 m x 7 m mid-water trawl at depths ranging from the surface to 44 m. A depth and temperature sensor was located on the head rope. Each tow lasted 15 minutes and tow speed was approximately 6.5 km/h (Schaner and Lantry 2000). For each fish, fork length (mm), location, trawl depth, and water temperature at depth of capture were recorded. Fork length measurements were converted to TL using a linear regression equation developed from Lake Ontario alewives and rainbow smelt (D.M. Warner, unpublished data). The digestive tracts of all alewives and rainbow smelt were removed and preserved in formaldehyde in the field.

Zooplankton were collected concurrent with fish samples in August 1997 to 1999 and October 1999 with a conical 50-cm-diameter, 153-μm-mesh nylon net equipped with a flow meter at offshore sites (top 40 m of the water column). Also included were *C. pengoi* samples collected aboard the USEPA *Lake Guardian* in August 1999 and previously reported by Makarewicz *et al.* (2002). They were included because when combined with the August 1999 samples collected aboard the R/V *Seth Green*, lake-wide density could be estimated from a larger spatial area. Specimens were preserved in the field in 70% ethyl alcohol after they were anesthetized with antacid tablets. *Cercopagis pengoi* specimens have a tendency to clump, and as a result, they were separated (with other large zooplankton) from smaller zooplankton with a 1.02-mm-mesh sieve. Once separated, *C. pengoi specimens* were spread homogenously in a gridded Petri dish, and at least 100 organisms from a random sub-sample were counted and measured with a microprojector at 20x magnification and a digitizer interfaced with a computer.

Fish stomachs were examined from fish caught with the same trawl, trawling techniques, and using the same preservation techniques in 1997, 1998, and 1999. Stomachs were examined from fish caught at five sites in western and central Lake Ontario in August 1997, 11 sites throughout the western, central, and eastern portions of the lake in August of 1998, one site in the southeastern portion of the lake in August 1999, and nine sites within the eastern half of the lake in October 1999 (Figure 2.1). Stomach contents from each fish were emptied into a Petri dish and examined individually with a stereo dissecting microscope. Because fish were collected throughout the night, and alewives feed primarily during the day, the stomach contents were often highly digested. However, the characteristic chitinous caudal spine of *C. pengoi* was still recognizable because it is more resistant to digestion than other structures. Therefore, only the presence/absence of *C. pengoi* spines as frequency of occurrence (including empty stomachs) is presented. Alewives were sorted into YOY and adult (age 1 and older) age classes while all rainbow smelt were adults. Statistical comparisons of the proportion of stomachs that contained *C. pengoi* spines were made using a t-test of arcsine-transformed data, as recommended by Sokal and Rohlf (1969) for testing equality of two proportions. Trawls were considered the sampling unit to decrease the potential for pseudoreplication. Among-year differences in frequency of occurrence of *C. pengoi* spines in fish stomachs were analyzed using the same methods. Two-tailed tests were used in all cases except when the hypothesis that *C. pengoi* spines occurred in a smaller proportion of small YOY stomachs (August 1998) than in large YOY (October 1999) was tested. Comparison of frequency of occurrence of spines in stomachs and *C. pengoi* density among sites was tested with Spearman's correlation coefficient (Sokal and Rohlf 1995). A Kruskall-Wallis test was used to make comparisons of median *C. pengoi* density among years. A probability level of < 0.05 was considered significant in all statistical tests.
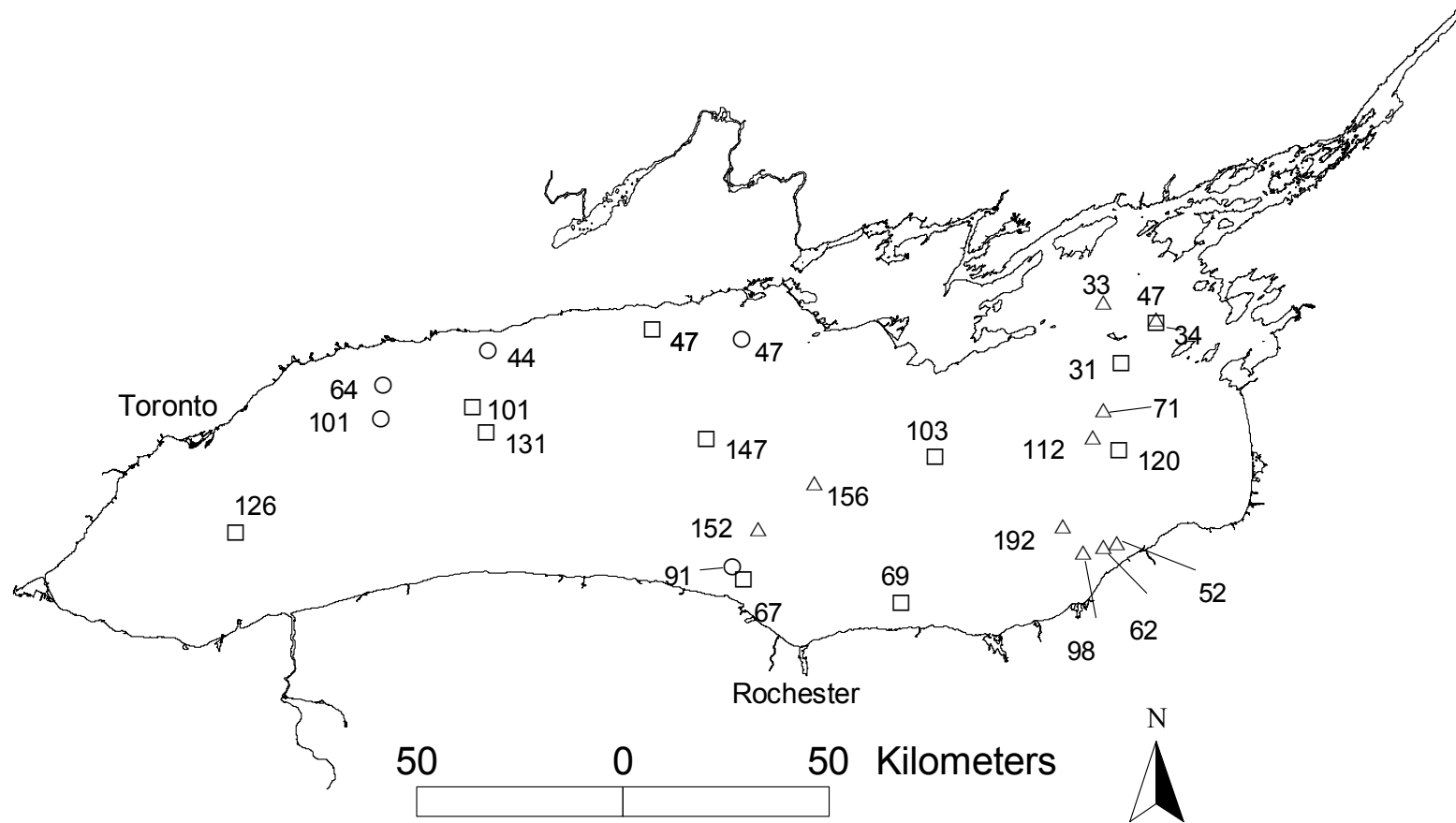
Figure 2.1. Lake Ontario locations sampled for *Cercopagis pengoi*, alewives, and rainbow smelt in 1997 to 1999. Numbers adjacent to the symbols correspond to the bottom depth (m) at that location. Open circles represent locations sampled in 1997, while open squares and open triangles represent locations sampled in 1998 and 1999, respectively.

RESULTS

Cercopagis pengoi was absent in zooplankton samples collected in 1997, but it occurred at relatively high densities across Lake Ontario by August 1998, 1 month after it was first observed in eastern Lake Ontario (MacIsaac et al. 1999). Average epilimnetic density at night in August 1998 was 450 per m^3 (range 30 to 1,190 per m^3, 21 sites). Similar densities were also found in August 1999 (mean = 448 per m^3, range 35 to 1,370 per m^3, 23 sites). There was no difference between median *C. pengoi* densities in August 1998 and 1999 (Kruskall-Wallis test: P = 0.68). Densities in October 1999 were lower (mean = 136 per m^3, range 0 to 535 per m^3, 11 sites), but these samples represented a more limited area of the lake.

Alewife samples from 1998 and 1999 (years when *C. pengoi* was present) included fish ranging from 35 to 180 mm TL (Table 2.1, Fig. 2.2). Because age-1 and older alewives generally exceed 100 mm TL during their second summer (O'Gorman *et al.* 1997), alewife were separated into adults (>104 mm) and YOY (<104 mm) in both years (Table 2.1). No *C. pengoi* spines were found in stomachs of alewives caught in 1997, but they occurred in a high percentage of adult alewife stomachs from 1998-99 (Table 2.1). The proportion of adult alewife stomachs that contained *C. pengoi* spines in 1998 and 1999 were not significantly different (test for equality of proportions, t = 1.52, p = 0.14, N = 16 for 1998, 10 for 1999). A higher proportion of adult than YOY alewives had consumed *C. pengoi* in both years (Table 2.1, Figure 2.2; 1998: t = 3.84, p < 0.001, N =10 for YOY and 16 for adults; 1999: t = 2.54, p = 0.02, N = 7 for YOY and 10 for adults). The occurrence of *C. pengoi* in stomachs of small YOY (August 1998, mean length = 56 mm) was significantly lower than in larger YOY (October 1999, mean length = 70 mm, t = 1.92, p = 0.04, N =10 in 1998 and 7 in 1999). There was no significant correlation between the frequency of

occurrence of *C. pengoi* in adult alewives and *C. pengoi* density in either year (1998, r = -0.26, N = 17, P = 0.28; 1999, r = 0.36, N = 10, P = 0.28).

When the percentages of alewives in each of 16 10-mm size classes that consumed *C. pengoi* in 1998 to 1999 were plotted against alewife length, it appeared that alewife size was a good predictor of *C. pengoi* consumption (Figure 2.3). The non-linear regression function was used in SigmaPlot 2000 to develop a model for predicting the percentage of alewives consuming *C. pengoi*. The resulting 3-parameter sigmoidal model was:

$$y = \frac{81.4}{1 + e^{-(\frac{length_{(mm)} - 66.3}{4.57})}}$$

(1)

where y = the percentage of alewives at a given length consuming *C. pengoi*. The model was highly significant (F = 50.6, p < 0.0001, r^2 = 0.89).

Rainbow smelt captured in 1998 and 1999 ranged in length from 56 to 190 mm TL (Figure 2.4). Only seven of the 111 fish examined contained *C. pengoi*, precluding any meaningful analysis of differences between fish sizes. The smallest rainbow smelt that was found to consume *C. pengoi* was 96 mm TL. No difference in rainbow smelt consumption of *C. pengoi* was detected between years (Table 1.1; t = 0.67, p = 0.51, N = 11 for both years). *Cercopagis pengoi* spines occurred in rainbow smelt stomachs at lower frequencies than in adult alewife stomachs in both years (Table 1; 1998: t = 4.33, p < 0.001, N = 16 for alewives, N = 11 for rainbow smelt; 1999: t = 10.29, p < 0.001, N = 10 for alewives and 11 for rainbow smelt). Frequency of occurrence of *C. pengoi* spines in YOY alewife and rainbow smelt stomachs did not differ in 1998 (t = 0.25, p = 0.80, N = 10 for alewives and 11 for rainbow smelt), but

Table 2.1. Average length, percentage of stomachs with *C. pengoi* spines, and sample size for alewives and rainbow smelt collected from Lake Ontario in 1997, 1998, and 1999. Numbers of empty stomachs are shown in parentheses next to the total number of stomachs examined. Alewives are separated into YOY and adult based on total length because consumption of *C. pengoi* differs between these groups. Adult alewife refers to age 1 and older fish (larger than 105 mm).

| | | Alewives | | | |
| | | Length (mm) | | | |
Month/year	Age	Range	Mean	% with spines	Number of stomachs
August 1997	Adult	101-166	139	0.0	21
August 1998	YOY	35-78	56	15.8	29 (1)
	Adult	118-178	152	71.9	54 (2)
August 1999	Adult	124-182	154	100.0	5
October 1999	YOY	43-104	72	52.4	31
	Adult	112-184	141	90.0	48
		Rainbow smelt			
August 1998	All	56-190	117	11.9	59
October	All	78-164	115	5.7	56 (4)
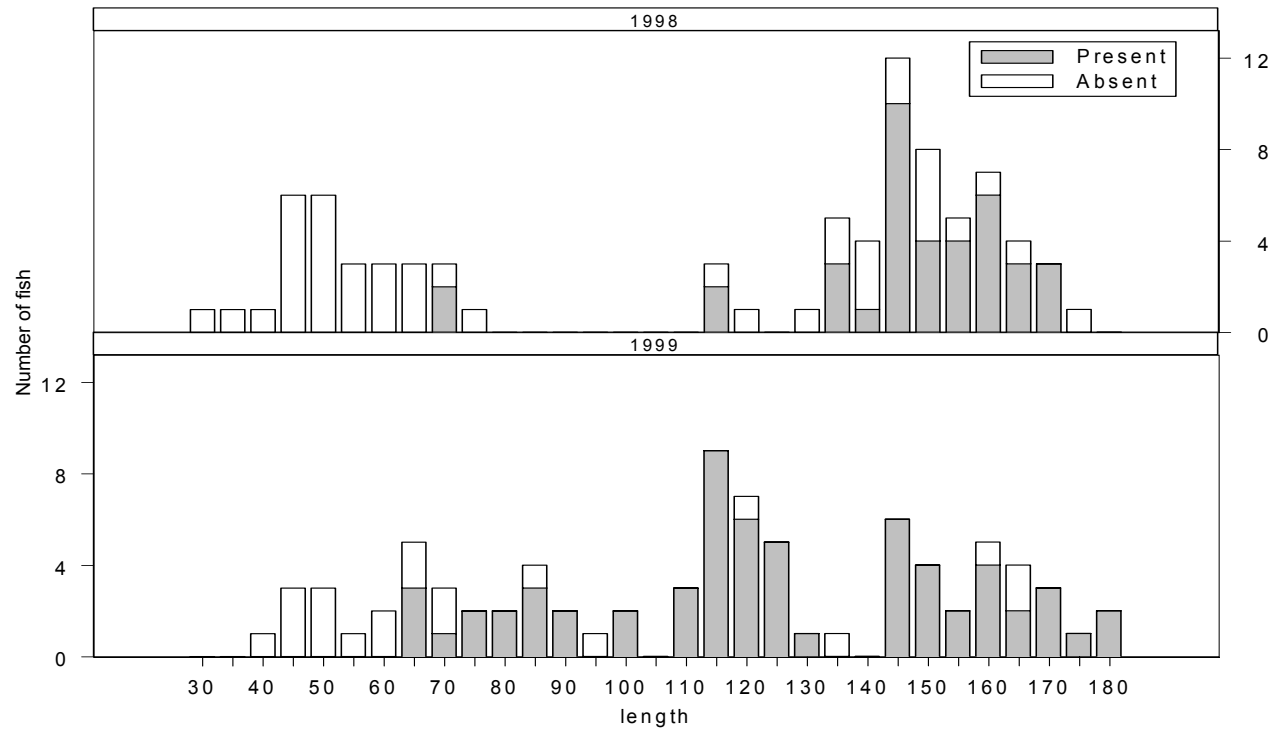
Figure 2.2. Length frequency distributions of alewife collected in Lake Ontario in August 1998 and 1999 and October 1999 whose stomachs were examined for the presence of *Cercopagis pengoi* spines. Bar height corresponds to the number of fish in each 5-mm size class. The shaded portion of the bars represents the number of fish whose stomachs contained *C. pengoi* spines and the unshaded portion the number that did not contain *C. pengoi* spines. The total number of alewife stomachs examined = 167 (empty stomachs =4).

in 1999 *C. pengoi* spines were significantly more common in YOY alewife diets than in rainbow smelt stomachs (t = 3.30, p < 0.01, N = 7 for alewives and 11 for rainbow smelt). The dominant prey item in rainbow smelt stomachs was *Mysis relicta*.

DISCUSSION

Although the analysis of alewife and rainbow smelt diets presented here was limited to quantifying the frequency of occurrence of *C. pengoi* spines, several important conclusions can be drawn from these data. First, alewives smaller than 66 mm TL did not consume *C. pengoi*, probably because these small fish have difficulty handling the long caudal spine. Second, although the relative importance of *C. pengoi* in alewife and rainbow smelt diets remains unknown, it is apparent that consumption of *C. pengoi* by larger alewives is widespread (spines were found in at least 70% of fish larger than 70 mm TL). Consumption of *C. pengoi* by rainbow smelt was less common, probably because of limited spatial over lap between these two species. Third, *Cercopagis pengoi* spines were found in the stomachs of both alewife and rainbow smelt in 1998 and 1999, but not in August 1997. This is consistent with the absence of *C. pengoi* in 1997 zooplankton samples. Thus, *C. pengoi* was either rare or absent in Lake Ontario in 1997 and expanded rapidly through the whole lake in 1998.

Observed densities of *C. pengoi* in August 1998 and August and October 1999 were similar to those previously reported for those years in Lake Ontario (MacIsaac *et al*. 1999, Makarewicz *et al*. 2001, Ojaveer *et al*. 2001, Benoit *et al*. 2002). August has been identified as the peak month for *C. pengoi* abundance in Lake Ontario (Makarewicz *et al*. 2001, Benoit *et al*. 2002). Therefore, much of the data presented here are for the period when *C. pengoi* is likely most important as predator and prey.
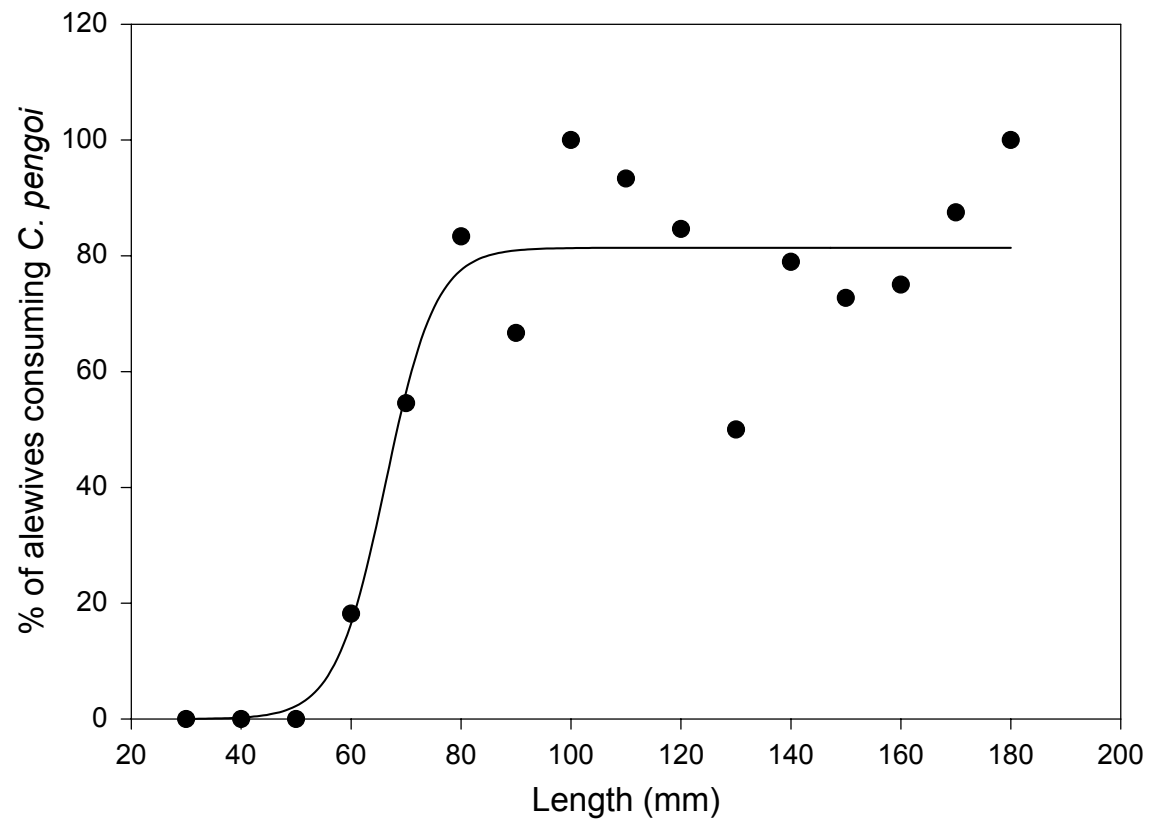
Figure 2.3. Relationship between the percentages of alewives in each size class that consumed *C. pengoi* and alewife length. The line represents a 3-parameter sigmoidal model fitted to the observed data.
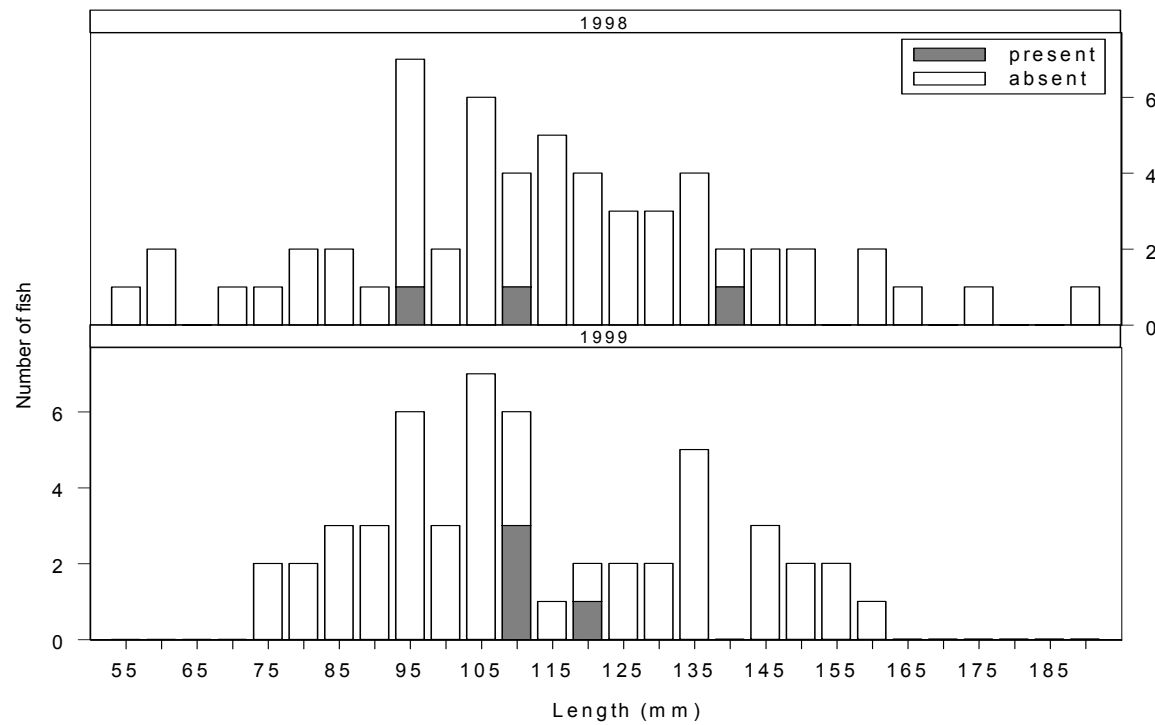
Figure 2.4. Length frequency distributions of rainbow smelt collected in Lake Ontario in August 1998 and 1999 and October 1999 whose stomachs were examined for the presence of *Cercopagis pengoi* spines. Total bar height corresponds to the number of fish in each 5-mm size class. The shaded portion of the bars represents the number of fish whose stomachs contained *C. pengoi* spines and the unshaded portion the number that did not contain *C. pengoi* spines. The total number of rainbow smelt stomachs examined = 115 (empty stomachs =4).

Young –of –the-year alewives may have difficulty feeding on *C. pengoi*, as the smallest alewife found to consume *C. pengoi* in 1998 and 1999 had total lengths of 72 mm and 66 mm, respectively. None of the stomachs examined from 30 alewives smaller than 66 TL mm contained *C. pengoi* spines (Fig. 2.3). Other YOY fish species have difficulty feeding on the related cercopagid *B. longimanus*, which also has a long chitinous spine (yellow perch, *Perca flavescens*, Barnhisel 1991, Jarnagin 1998; cisco, *Coregonus artedi*, lake whitefish *C. clupeaformis*, Barnhisel and Harvey 1995). In Lake Ontario, Mills *et al.* (1992) found lower numbers of YOY alewives containing *B. longimanus* spines relative to adult alewives and Urban and Brandt (1993) did not find any *B. longimanus* in YOY alewives stomachs. In the Baltic Sea, *C. pengoi* has been found to be common in adult but not YOY Baltic herring (*Clupea harengus*) (Ojaveer and Lumberg 1995). Small fish may have problems handling *C. pengoi* because of gape size limitations. The gape height and width of a 65 mm TL alewife are 7.6 and 4.5 mm, respectively (Brooking *et al*. 1998). Therefore, it is conceivable that the ability of a small alewife to consume a *C. pengoi* with a 7 to 11-mm-long spine is limited by gape size.

Cercopagis pengoi spines were found in a larger proportion of both YOY alewives and adult alewives than in rainbow smelt. It is possible that this is due to differences in overlap between *C. pengoi* and these two fish species. Alewives are generally concentrated in the epi and metalimnion at 14 to 24° C (O'Gorman *et al*. 1997); whereas, rainbow smelt are found at or below the thermocline at 8 to 14° C (Lantry and Stewart 1993). My observations of capture depth and temperature of alewives and rainbow smelt were similar. In August 1998, the average capture depth and temperature for alewife was 16 m (range 3 to 41 m) and 17° C (range 4 to 23° C); whereas, similar values for rainbow smelt were 25 m (range 8 to 41 m) and 12° C (range 4 to 22° C). *Cercopagis pengoi* is primarily found in the epilimnion (Uitto *et*

al. 1999, Ojaveer *et al*. 2001), often with an abundance peak in the lower epilimnion
(Benoit *et al*. 2002). Of the seven rainbow smelt that did consume *C. pengoi* six were
captured in water 17° C or greater which is generally considered outside the normal
temperature range of rainbow smelt (Lantry and Stewart 1993). It is possible that the
lower frequency of *C. pengoi* in rainbow smelt stomachs is not because rainbow smelt
avoid *C. pengoi* but because these fish do not regularly encounter *C. pengoi*.

The rapid expansion of the *C. pengoi* population in 1998 in the alewife-
dominated environment of Lake Ontario was surprising. Mills *et al*. (1992) suggested
that predation by alewives prevented high abundance of *B. longimanus* in Lake
Ontario. A similar control on *C. pengoi* abundance by alewives would be expected,
but densities observed in this study exceeded 1,000 per m^3 in 1998. Makarewicz et al.
(2001) attributed the rapid expansion in 1998 to low numbers of adult alewife in
combination with high fecundity, asexual reproduction, and defensive spines of *C.
pengoi*. Young –of –the-year alewives were abundant in 1998 (R. O'Gorman, Oswego
Biological Station, Oswego, N.Y., personal communication) but the data in this study
suggest that these fish do not consume *C. pengoi* until they reach length of over 66
mm TL and would therefore have little effect on *C. pengoi* abundance until the fall. It
is likely that low adult alewife abundance in 1998 contributed to both the strong YOY
alewife cohort and the rapid expansion of *C. pengoi* that year.

However, *C. pengoi* densities remained high in 1999, even though the
abundance of yearling alewife large enough to consume *C. pengoi* was high that year
(R. O'Gorman, personal communication). It is possible, but not likely, that adult
alewives only consume a small number of *C. pengoi*. The data presented in this study
did not provide a quantitative assessment of the importance of *C. pengoi* in the diet of
alewives, but many of the stomachs examined contained very large number of *C.
pengoi* spines. It is conceivable that spines are retained for some times in alewife

stomachs (as observed for rainbow smelt feeding on *B longimanus*, Parker *et al.* 2001) and spines may therefore be poor indicators of feeding rates on *C. pengoi*. However, examination of a small number of stomachs from adults alewives collected in August 2001 indicated that ~80% of the organisms found in the stomachs (based on counts of bodies, not spines), were *C. pengoi*. Elsewhere, adult Baltic herring heavily utilized *C. pengoi* (Ojaveer and Lumberg 1995). If predation on *C. pengoi* is high, *C. pengoi* must be able to maintain high rates of population growth. Straille and Hälbich (2000) found that *B. longimanus* exhibited multiple antipredator defenses including high fecundity, diel vertical migration, and spines. *Cercopagis pengoi* is smaller and may have shorter generation time then *B. longimanus*, resulting in faster population growth rates. In addition, the number of *C. pengoi* present in the lake in the beginning of 1999 must have been substantially larger than in the beginning of 1998, potentially allowing the species to increase despite higher predation rates.

The ecological relationship between *C. pengoi* and planktivorous fish in Lake Ontario is dependent on the age and species of fish and the abundance of *C. pengoi*. Benoit *et al.* (2002) have shown that *C. pengoi* probably decreased abundance of small nauplii and copepodites and possibly small cladocerans, as well as caused some of these vulnerable prey to avoid surface waters. Thus, *C. pengoi* may depress the zooplankton prey of small alewife (< 66 mm) without providing an additional food source for these fish. This may result in decreased growth of YOY alewives, possibly leading to lower overwinter survival (O'Gorman *et al.* 1997). The interactions between *C. pengoi* and YOY alewife will depend on the timing of alewife reproduction and the timing and magnitude of the effect of *C. pengoi* on other zooplankton. Effects on adult alewife growth remain unclear but could be positive. *Cercopagis pengoi* is larger and may be a more profitable prey than the smaller

zooplankton that may decline due to *C. pengoi* predation. The effect of *C. pengoi* on rainbow smelt is likely minimal.

REFERENCES

Barnhisel, D.R. 1991. The caudal appendage of the cladoceran *Bythotrephes cederstroemi* as defense against young fish. J. Plankton Res. 13:529-537.

_____, and Harvey, H.A. 1995. Size-specific fish avoidance of the spined crustacean *Bythotrephes*: field support for laboratory predictions. Can. J. Fish. Aquat. Sci. 52:768-775.

Benoit, H. P., Johannsson, O.E., Warner, D.M., Sprules, W.G., and Rudstam, L.G. 2002. Assessing the impact of a recent predatory invader: the population dynamics, vertical distribution, and potential prey of *Cercopagis pengoi* in Lake Ontario. Limnol. Oceanogr. 47:626-635.

Brooking, T.E., Rudstam, L.G., Olsen, M.H., and VanDeValk, A.J. 1998. Size-dependent alewife predation on larval walleyes in laboratory experiments. N. Am. J. Fish. Manage. 18:960-965.

Charlebois, P.M., Raffenberg, M.J., and Dettmers, J.M. 2001. First occurrence of *Cercopagis pengoi* in Lake Michigan. J. Great Lakes Res. 27:258-261.

Cristescu, M.E., Hebert, P.D.N., Witt, J.D.S., MacIsaac, H.J., and Grigorovich, I.A. 2001. An invasion history for *Cercopagis pengoi* based on mitochondrial gene sequences. Limnol. Oceanogr. 46:224-229.

Gorokhova, E., Aladin, N., and Dumont, H.J. 2000. Further expansion of the genus *Cercopagis* (Crustacea, Branchiopoda, Onychopoda) in the Baltic Sea, with notes on the taxa present and their ecology. Hydrobiologia 429:207-218.

Jarnagin, S.T. 1998. Direct and indirect estimates of death rates and predator-mediated dispersal of *Bythotrephes cederstroemi*. Ph.D. thesis. Michigan Technological University, Houghton, Michigan.

Lantry, B.F., and Stewart, D.J. 1993. Ecological energetics of rainbow smelt in the

Laurentian Great Lakes: An interlake comparison. Trans. Am. Fish. Soc. 122:951-976.

MacIsaac, H.J., Grigorovich, I.A., Hoyle, J.A., Yan, N.D., and Panov, V.E. 1999. Invasion of Lake Ontario by the Ponto-Caspian predatory cladoceran *Cercopagis pengoi*. Can. J. Fish. Aquat. Sci. 56:1-5.

Makarewicz, J.C., Grigorovich, I.A., Mills, E.L., Damaske, E., Cristescu, M.E., Pearsall, W., LaVoie, M.J., Keats, R., Rudstam, L., Herbert, P., Halbritter, H., Kelly, T., Matkovich, C., and MacIsaac, H.J. 2001. Distribution, fecundity, and genetics of *Cercopagis pengoi* (Ostroumov) (Crustacea, Cladocera) in lake Ontario. J. Great Lakes Res. 27:19-32.

Mills, E.L., O'Gorman, R., DeGisi, J., Hegerger, R.F., and House, R.A. 1992. Food of the alewife (*Alsoa pseudoharengus*) in Lake Ontario before and after the establishment of *Bythotrephes cederstroemi*. Can. J. Fish. Aquat. Sci. 49:2009-2019.

Mordukhai-Boltovskoi, Ph.D. and Rivier, I.K. 1971. A brief survey of the ecology and biology of the Caspian Polyphemoidea. Mar. Biol. 8:160-169.

O'Gorman, R., Johannsson, O.E., and Schneider, C.P. 1997. Age and growth of alewives in the changing pelagia of Lake Ontario, 1978-1992. Trans. Am. Fish. Soc. 126:112-126.

Ojaveer, H., and Lumberg, A. 1995. On the role of *Cercopagis pengoi* (Ostroumov) in Pärnu Bay and the NE part of the Gulf of Riga ecosystem. Proc. Estonian Acad. Sci. Ecol. 5:20-25.

_____, Kuhns, L.A., Barbiero, R.P., and Tuchman, M.L. 2001. Distribution and population characteristics of *Cercopagis pengoi* in Lake Ontario. J. Great Lakes Res. 27:10-18.

Parker, S.L., Rudstam, L.G., Mills, E.L., and Einhouse, D.W. 2001. Retention of

Bythotrephes spines in the stomachs of eastern Lake Erie rainbow smelt. Trans. Am. Fish. Soc. 130:988-994.

Schaner, T., and Lantry, B.F. 2000. Pelagic planktivores. Lake Ontario Management Unit 1999 Annual Report. New York State Department of Environmental Conservation, Albany, N.Y. Section 20.

Sokal, R.R., and Rohlf, F.J. 1969. Biometry. San Francisco, California. W.H. Freeman and Company.

_____, and Rohlf, F.J. 1995. Biometry, 3rd Edition. New York. W.H. Freeman and Company.

Straille, D., and A. Hälbich. 2000. Life history and multiple antipredator defenses of an invertebrate pelagic predator, *Bythothrephes longimanus*. Ecology 81:150-163.

Uitto, A., Gorokhova, E., and Välipakka, P. 1999. Distribution of the non-indigenous *Cercopagis pengoi* in the coastal waters of the eastern Gulf of Finland. ICES J. Mar. Sci. 56 Suppl.: 49-57.

Urban, T.P., and Brant, S.B. 1993. Food and habitat partitioning between young-of-year alewives and rainbow smelt in southeastern Lake Ontario. Env. Biol. Fishes 36:359-372.

CHAPTER 3

Changes in Seasonal Nearshore Zooplankton Abundance Patterns in Lake Ontario following Establishment of the Exotic Predator *Cercopagis pengoi*

ABSTRACT

Cercopagis pengoi, a zooplanktivore first discovered in Lake Ontario in 1998, may reduce availability of prey for planktivorous fish. To determine if the establishment of *C. pengoi* was followed by changes in the zooplankton community, I examined seasonal patterns in nearshore zooplankton collected from May to October 1995-2000. Because *C. pengoi* is most abundant in late summer and fall, I hypothesized that abundance of small zooplankton (bosminids and cyclopoids) species would decrease at that time. Early summer density of small zooplankton was similar or higher in all years while late summer and fall densities were significantly lower in 1998-2000 than in 1995-1997. The declines of zooplankton coincided seasonally with the peak in *C. pengoi* density. The presence of high levels of fish predation should have resulted in smaller zooplankton in 1998-2000 than in 1995-1997 and larger declines in *Daphnia* than other groups. Given that late summer density of *D. retrocurva* and mean zooplankton length was similar before and after *C. pengoi* establishment, it was not likely that fish predation caused late summer declines in small zooplankton. Mean length may have been moderated by selection of smaller prey by *C. pengoi* and selection of larger prey by alewives. Patterns in potentially important environmental variables were inconsistent with changes in zooplankton. Therefore, declines in zooplankton density were most likely the result of *C. pengoi* predation. The effect of added competition for alewives is unclear because *C. pengoi* has likely replaced a significant portion zooplankton biomass and adult alewife diet formerly made up of *Diacyclops thomasi* and *Bosmina longirostris.*

INTRODUCTION

Over the past 30 years, the zooplankton community of Lake Ontario has been subjected to important ecological changes including oligotrophication, major fluctuations in alewife abundance, and the introduction of exotic species (including predators). Total phosphorus (TP) concentrations declined approximately 50% from the 1960s to the mid 1980s (Mills et al. 2003; Millard et al. 2003), which led to a similar decline of approximately 50% in zooplankton abundance and biomass (Johannsson 2003). From the mid 1980s to the mid 1990s, TP concentrations were relatively constant with no apparent trend. During this period of relative nutrient stability, dreissenid mussels (1989), *Bythotrephes longimanus* (1982), and *Cercopagis pengoi* (1998) invaded the lake, which added competitive and predatory pressure on the zooplankton community and likely increased competition among zooplanktivores.

Like other size-dependent invertebrate planktivores (*sensu* Zaret 1980), *C. pengoi* is expected to prey selectively on small zooplankton (Dodson 1974). The effect of predation by *C. pengoi* has been documented in the Baltic Sea, where Ojaveer (2000) correlated the arrival of *C. pengoi* with a decline in *Bosmina coregonus maritimus*. Benoît et al. (2002) associated *C. pengoi* densities >200-300 ind. m^{-3} in the Kingston basin of Lake Ontario with significant late summer declines in juvenile cyclopoid and calanoid copepods as well as *Bosmina*. Similar declines were not observed at their study site prior to establishment of *C. pengoi* or at other sites where it was rare or absent. Laxson et al. (2003) found that consumption by *C. pengoi* exceeded zooplankton production in western Lake Ontario during most of the summer and attributed late summer declines in bosminids, *Diacyclops thomasi*, and *Daphnia retrocurva* to predation by *C. pengoi*. However, both these studies were spatially limited to either the Bay of Quinte/Kingston Basin (Benoit et al. 2002) or near

Brockport, N.Y. (Laxson et al. 2003). In addition, they provide different conclusions about the effect of *C. pengoi* on *Daphnia*, an important species selected by fish in Lake Ontario. Results from the invasion of *C. pengoi* elsewhere do not support either of the two previous studies in Lake Ontario. Ojaveer et al. (2000) did not observe changes in Baltic Sea copepods associated with *C. pengoi* invasion. Given the potential importance of *C. pengoi* predation in Lake Ontario, it is imperative that predictions by previous authors be reconciled and tested at a larger spatial and temporal scale.

Cercopagis pengoi has consistently been present at relatively high density every year since it was first observed in Lake Ontario in 1998 (Makarewicz et al. 2001; Ojaveer et al. 2001; Bushnoe et al. 2003). *Cercopagis pengoi* is rare or absent from May to early July, but it is abundant from mid-July to October (Makarewicz et al. 2001; Benoît et al. 2002; Laxson et al. 2003). I hypothesized that effects of *C. pengoi* predation should be most prominent during the July to October period when *C. pengoi* is most abundant (Benoît et al. 2002). Therefore, I compared zooplankton abundance and length in two seasonal periods (14 May to 9 July and 10 July to 2 October) in the years 1995-1997 with abundance and length during the same periods in the years 1998-2000. In this study, I tested for the effects of *C. pengoi* on zooplankton species predicted by Benoît et al. (2002) and Laxson et al. (2003) using a data set from seven nearshore sites in Lake Ontario sampled from 1995 to 2000. The ability to compare pre- and post-perturbation conditions is extremely helpful in assessing the effects of perturbations (e.g. introductions) on food webs (Carpenter 1990), and I consider the invasion of *C. pengoi* as a perturbation to the Lake Ontario ecosystem from 1998 to 2000 (and into the future). Although Benoît et al. (2002) conducted such an analysis, it was limited to the Bay of Quinte/Kingston basin, which may not be representative of the remainder of Lake Ontario. I also examined other

variables as alternative explanations for the observed patterns in zooplankton abundance.

METHODS

Zooplankton samples were collected during the day at seven locations in eastern and southern Lake Ontario every second week between the middle of May and the middle of October 2000. The sampling locations were located along the 10-m depth contour and included Chaumont Bay, Galloo Island, Sandy Pond, Sodus Bay, Oak Orchard Creek delta, and the Niagara River delta (Figure 3.1). At each location, 1-3 10-m vertical tows were made from just above bottom to the surface with a 0.5-m conical plankton net (153-μm mesh). Filtering efficiency was assumed to be 100%. Specimens were preserved in the field in either 4% sugar-formalin or 70% ethyl alcohol. Specimens preserved in alcohol were first anesthetized with antacid tablets. Crustacean zooplankton were counted and measured (at least 100 organisms) using 1-ml random sub-samples N=1-3). Density (ind. L^{-1}) and lengths (mm) from the replicate tows were averaged. In 1995-97, an electronic touch screen was used for measuring the zooplankton (Hambright and Friedman 1994). In later years, a microprojector (20x) was used to project images of zooplankton onto a digitizing tablet coupled with a computer. Starting in 1998 with the appearance of *C. pengoi*, the enumeration technique was altered. Because *C. pengoi* specimens form clumps, separate analyses were conducted on large (> 1mm) and small (<1mm) zooplankton, which were separated using a 1.02 mm sieve. In addition, once untangled, *C. pengoi* specimens were enumerated separately. They were spread homogenously in a gridded Petri dish and at least 100 organisms from a random sub-sample were counted and measured with the same microprojector system. Mean individual biomass was predicted from a equation 1 in Makarewicz et al. (2001). The mean of individual weights was used to predict the number of *C. pengoi* remaining in the

uncountedportion of the sample. Cladoceran lengths were measured from the distal point on the head to the base of the tail spine. Copepod lengths (copepodids were included with

adults) were measured from the distal point on the head to the base of the caudal rami. No effort was made to correct for preservative effects on length because Black and Dodson (2003) found no siginificant differences in mean length of *Daphnia* specimens preserved with formalin and ethanol.

Water temperature, TP and chlorophyll *a* were sampled concurrently with zooplankton sampling. Water samples were collected using an integrated tube sampler lowered to approximately 1 m above the bottom. Water temperature data were not available from Galloo Island in 1997; therefore this site was excluded from analyses of water temperature. At other sites, temperature data were collected at 1-m intervals with electronic samplers. Temperatures reported here are the means for each profile. A 50-ml aliquot of unfiltered water was frozen for TP analyses using persulfate digestion (Menzel and Corwin 1965). Chlorophyll *a* was sampled by filtering raw lake water through Whatman 934-AH filters, which were frozen in the field and kept dark until analyzed in the laboratory. Filters were assayed for chlorophyll *a* using the acetone extraction method (Strickland and Parsons 1972).

In order to test for evidence of *C. pengoi* predation on zooplankton, biweekly patterns of zooplankton abundance and size in 1995-1997 were compared to those in 1998-2000. Similar comparisons were made of mean epilimnetic water temperatures and two indices of trophic state (TP and chlorophyll *a* concentration). Data from each site were divided in two three-year periods (epochs) corresponding to the group of years in which *C. pengoi* was not present (1995-1997) and a second group (1998-2000) when *C. pengoi* was present. Additionally, data within each year were divided in 11 biweekly periods (biweek) with all data collected 14-28 May assigned to
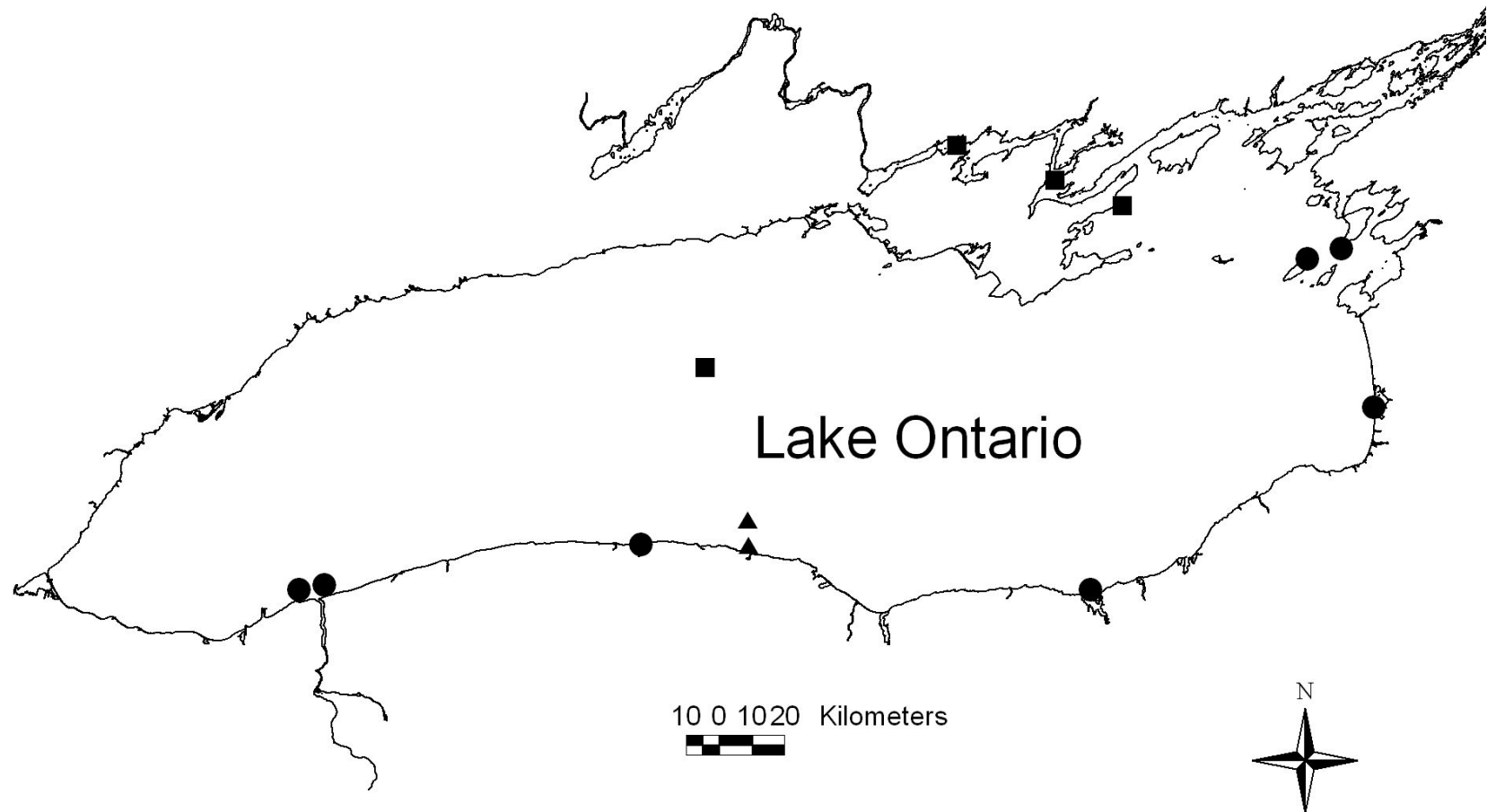
Figure 3.1. Map of Lake Ontario and the locations (closed circles) at which biweekly measurements of zooplankton, water temperature, total phosphorus, and chlorophyll *a* measurements were made May-October 1995-2000. Also shown are locations sampled by Benoît et al. (2002, closed squares) and Laxson et al. (2003, closed triangles).

biweek one, data collected 29 May – 11 June assigned to biweek two, and the remaining data assigned accordingly up to biweek 11.

Zooplankton abundance and size (as well as water quality variables) in Lake Ontario vary spatially and at both short-term (seasonal) and long-term (annual) temporal scales (Hall et al. 2003). In order to account for this variation while testing for significant differences in zooplankton density, I employed a generalized linear mixed model with repeated measures using SAS (GLIMMIX macro and PROC MIXED, Littel et al. 1996). Site was treated as a random variable for all analyses because sites were chosen to encompass the gradient of TP, chlorophyll a, and shoreline exposure that occurs in Lake Ontario. Because biweekly zooplankton densities were auto-correlated, a first-order autoregressive covariance structure was assumed. Epoch and biweek were treated as fixed factors. Zooplankton densities were not normally distributed; like other count data, the densities were approximately Poisson-distributed (variance similar to the mean, large number of low values). Therefore, density was assumed to have a Poisson error structure and it was further assumed that a log link function was appropriate. The link function relates the linear predictor of the general linear model to the mean response (Neter et al. 1996). Normal error structure and identity link functions were assumed to be appropriate for all other variables. The GLIMMIX macro corrected for effects of over-dispersion and under-dispersion by scaling the deviance and adjusting the F-statistics. Scaled deviance was used to assess model fit. In cases where the epoch x biweek interaction was significant, a test for simple effect of epoch on the biweekly mean of each variable was used to compare least-squares means of zooplankton density, zooplankton size, water temperature, TP, and chlorophyll a to determine which biweeks were different among epochs. In attempt to reduce the occurrence of Type I errors, an experiment-wise significance level of 0.05 was employed by correcting for the number of tests

using the formula α/n where α is the experiment-wise error rate (0.05) and n is the number of statistical tests.

RESULTS

Differences in water temperature among epochs were not significant. There were significant differences among biweeks because of the seasonal pattern in water temperature (Table 3.1). The epoch x biweek interaction term was not significant, indicating that seasonal patterns in water temperature were similar in both epochs (Figure 3.2).

Both TP and chlorophyll *a* exhibited significant variability. Differences in TP concentrations among epochs and biweeks were significant (Table 3.1), but the interaction term was not significant. Total phosphorus values were higher in the 1998-2000 than in 1995-1997. The significant biweek effect was the result of the seasonal pattern in TP, with low early and late summer concentrations and higher midsummer concentrations. The epoch x biweek interaction was not significant. Chlorophyll *a* concentrations did not differ significantly among epochs, but there were significant biweekly differences that reflected the general pattern of higher midsummer concentrations and lower early and late summer concentrations (Table 3.1). The epoch x biweek interaction was not significant, indicating that the seasonal pattern did not differ among epochs (Figure 3.2).

Cercopagis pengoi was not present until 1998. Therefore, it was not possible to include an epoch term in the model for *C. pengoi* abundance. There were not significant differences among years, but there were significant differences among biweeks (Table 3.2, Figure 3.3). *Cercopagis pengoi* density was highest in late summer.

Bosminid density and length exhibited significant variability. The epoch x biweek effect for density was significant (Table 3.2), indicating that the seasonal

Table 3.1. Summary of repeated measures generalized linear mixed models comparing (Type 3 tests) epoch, and biweekly mean water temperature, total phosphorus ($\mu g \cdot L^{-1}$), and chlorophyll a concentrations ($\mu g \cdot L^{-1}$) between May and October 1995-2000 at seven nearshore sites in Lake Ontario. Values in parentheses are F-test degrees of freedom (numerator, denominator). Values in boldface type were significant ($P<0.0167$) after adjustment for the number of statistical tests were made to achieve an experiment-wise $\alpha = 0.05$.

Response variable		Epoch	Biweek	Epoch x biweek
Water temperature	F	0.03 (1, 122)	**58.15 (10, 297)**	1.58 (10, 298)
	P	0.85	**<0.0001**	0.11
Total phosphorus	F	**9.46 (1, 90)**	**2.37 (10, 332)**	1.41 (10, 333)
	P	**0.003**	**0.012**	0.17
Chlorophyll a	F	0.25 (1, 108)	**3.46 (10, 333)**	1.60 (10, 334)
	P	0.62	**0.0002**	0.10
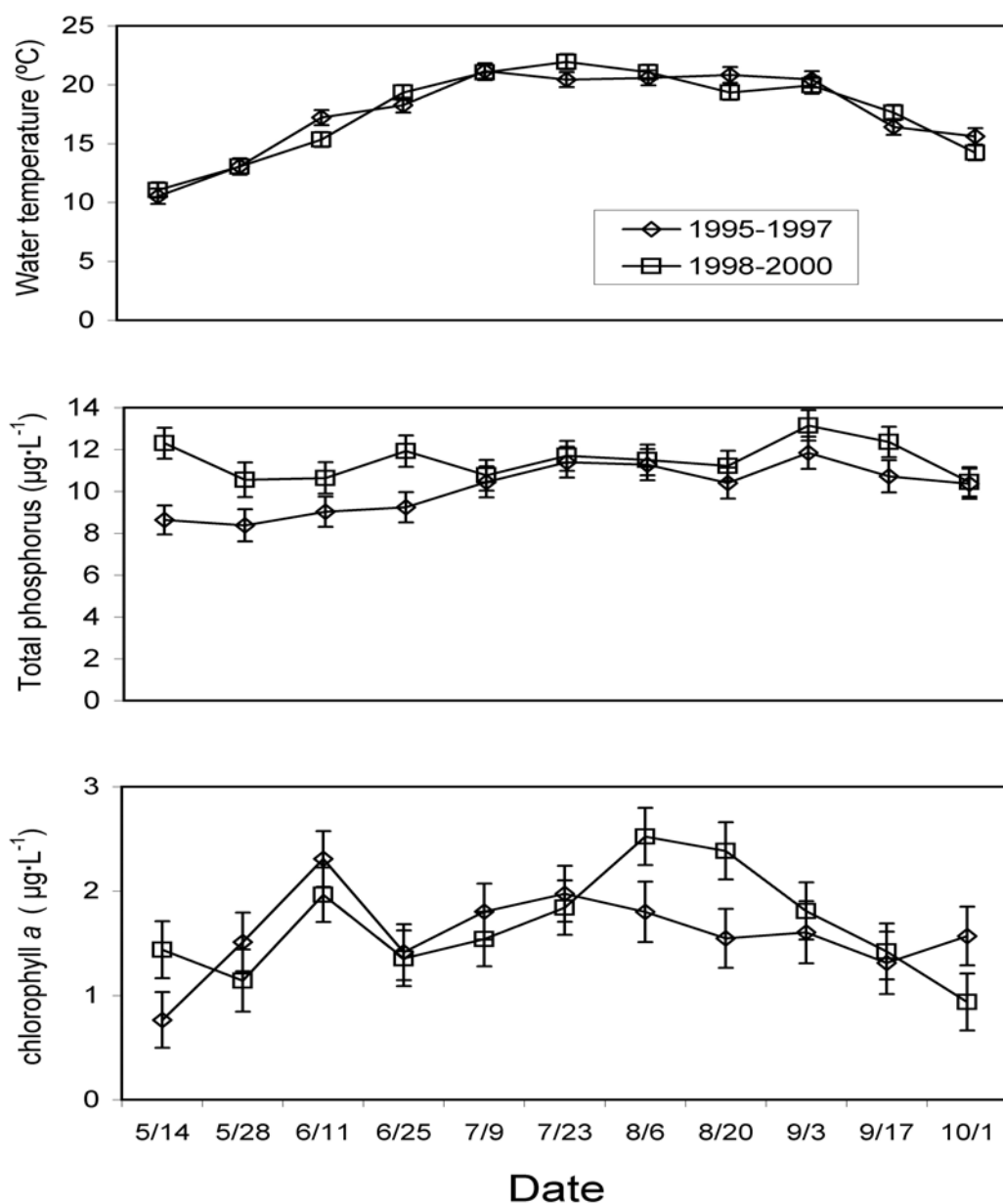
Figure 3.2. Seasonal patterns in least squares mean (± SE) water temperature, total phosphorus, and chlorophyll *a* at seven nearshore locations in southern and eastern Lake Ontario during May-October in 1995-1997 and 1998-2000. The date at the beginning of each biweekly period is shown on the x-axis.

pattern in density differed among epochs. Late summer density was significantly

higher in 1995-1997 than in 1998-2000. Early summer density was similar in both

epochs with the exception of late June/early July, when density was significantly

higher in 1998-2000 than in 1995-1997 (Figure 3.4). Bosminid length also exhibited

significant biweekly differences among epochs (the epoch x biweek interaction term

was significant, Table 3.3). Mean length was significantly higher in biweeks during

early summer 1995-1997 than in 1998-2000. However, during late summer biweekly

mean length was similar in both groups of years.

Density and mean length of *Daphnia retrocurva* exhibited variability within

seasons (density) and seasonal variability among epochs (mean length). Density was

significantly higher in late summer than in early summer in both groups of years.

Seasonal patterns in mean length exhibited significant differences among epochs;

mean length was significantly higher in May-June of 1995-1997 than in 1998-2000,

while during the remainder of the season lengths were similar.

Density of *Diacyclops thomasi* exhibited significant variability, while mean

length did not. The seasonal pattern of *D. thomasi* density differed significantly

among epochs (the epoch x biweek interaction was significant), with late summer

densities in 1995-1997 significantly higher than in 1998-2000 (Figure 3.4, Table 3.2).

Mean length was similar throughout the year in both epochs, and neither the epoch,

biweek, nor interaction terms were significant.

The main effect of biweek and the epoch x biweek interaction were significant

in comparisons of naupliar density (Table 3.2), while mean length exhibited only

seasonal differences. The epoch x biweek interaction for density was significant

because the seasonal pattern in 1995-1997 was relatively flat, whereas in 1998-2000

Table 3.2. Summary of repeated measures generalized linear mixed models comparing (Type 3 tests) epoch and biweekly mean zooplankton density (ind·L^{-1}) between May and October 1995-2000 at seven nearshore sites Lake Ontario. Values in parentheses are F-test degrees of freedom (numerator, denominator). Values in boldface type were significant ($P<0.01$) after adjustment for the number of statistical tests were made to achieve an experiment-wise $\alpha = 0.05$.

Response		Epoch	Biweek	Epoch x biweek
Bosminids	F	12.3 (1, 203)	**7.0 (10, 338)**	**4.9 (10, 338)**
	P	0.23	**<0.0001**	**<0.0001**
D. retrocurva	F	0.11 (1, 258)	**3.4 (10, 338)**	2.3 (10, 342)
	P	0.74	**0.0003**	0.019
D. thomasi	F	**22.9 (1, 119)**	1.77 (10, 332)	**4.6 (10, 332)**
	P	**<0.0001**	0.065	**<0.0001**
Nauplii	F	5.8 (1, 91)	**3.73 (10, 345)**	**2.7 (10, 344)**
	P	0.018	**<0.0001**	**0.004**
C. pengoi[1]	F	4.3 (2, 80)	**2.62 (10, 175)**	NA
	P	0.017	**0.006**	

[1]Results in the epoch column for *C. pengoi* correspond to comparison of densities among years (1998, 1999, and 2000), not epochs.
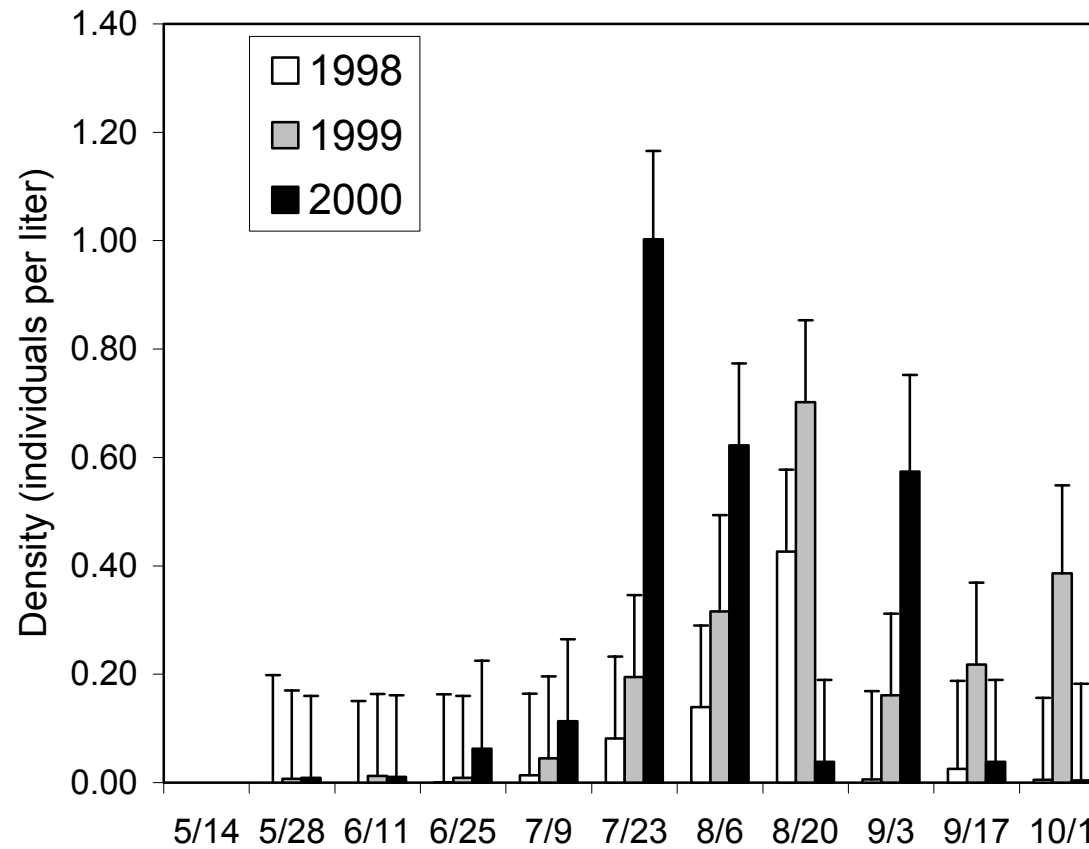
Figure 3.3. Seasonal patterns in least squares mean (± SE) of biweekly *C. pengoi* density at seven nearshore locations in Lake Ontario during May-October of 1998-2000. The date at the beginning of each biweekly period is shown on the x-axis.
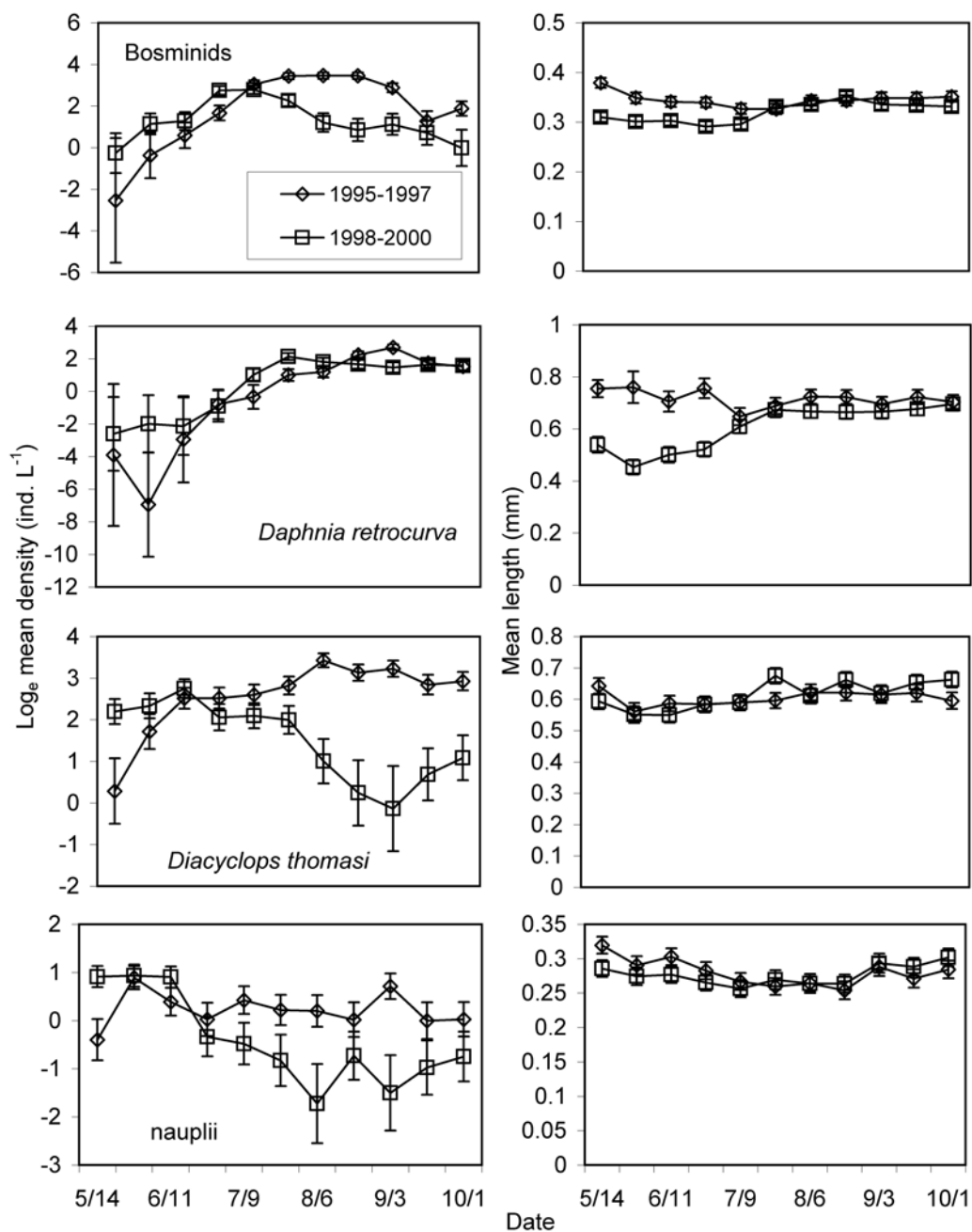
Figure 3.4. Seasonal patterns in least squares mean (± SE) density and length of bosminids, *D. retrocurva*, *D. thomasi*, and copepod nauplii at seven nearshore locations in southern and eastern Lake Ontario during May-October in 1995-1997 and 1998-2000. The date at the beginning of each biweekly period is shown on the x-axis.

Table 3.3. Summary of repeated measures generalized linear mixed models comparing (Type 3 tests) epoch and biweekly mean zooplankton length (mm) between 1995-2000 at seven sites Lake Ontario. Bosminids include *Bosmina* and *Eubosmina* spp. Values in parentheses are F-test degrees of freedom (numerator, denominator). Values in boldface type were significant ($P<0.0046$) after adjustment for the number of statistical tests were made to achieve an experiment-wise $\alpha = 0.05$.

Response		Epoch	Biweek	Epoch x Biweek
Bosminids	*F*	**12.3 (1, 63)**	2.2 (10, 324)	**2.43 (10, 324)**
	P	**0.0008**	0.020	**0.008**
D. retrocurva	*F*	**37.6 (1, 79)**	2.2 (10, 252)	**4.19 (10, 252)**
	P	**<0.0001**	0.022	**<0.0001**
D. thomasi	*F*	0.5 (1, 91)	2.2 (10, 331)	1.6 (10, 332)
	P	0.47	0.016	0.11
Nauplii	*F*	0.3 (1, 92)	2.4 (10, 312)	0.87 (10, 313)
	P	0.58	0.010	0.56

there was a distinct decreasing trend from early summer to late summer (Figure 3.4). Comparisons of simple effects (biweeks among epochs) revealed that of the 11 biweeks, three were significantly different among epochs. Density during the biweek including the last half of May 1998-2000 was significantly higher than in May 1995-1997, while density during the first half of August and the first half of September was significantly higher in 1995-1997 than in 1998-2000. Naupliar length did not vary significantly among epochs, but there were significant differences among biweeks (Table 3.3) across epochs, with lower mean lengths in mid summer. The epoch x biweek interaction was not significant for naupliar length.

DISCUSSION

My primary hypothesis was that late summer abundance of small copepods and cladocerans would decline as a result of predation by *C. pengoi* because *C. pengoi* is most abundant from mid-July to October. Results support this hypothesis. I observed significant declines in abundance of bosminids, *D. thomasi*, and copepod nauplii during peak *C. pengoi* abundance in 1998-2000 relative to the same seasonal period (mid-July to October) in 1995-1997. Additionally, the decrease in density I observed between the 1995-1997 and 1998-2000 periods occurred only during the months when *C. pengoi* was abundant (July-September). Early summer densities (May to early July) of bosminids and *D. retrocurva* in 1998-2000 were similar to those observed in 1995-1997, while the abundance of *D. thomasi* and nauplii in late May was significantly higher in 1998-2000 than in 1995-1997.

Mean zooplankton lengths observed in this study indicated a mixture of vertebrate and invertebrate predation was responsible for structuring the zooplankton community. Considering that both alewives and invertebrates prey on the taxa examined in this study, this is not surprising. Mean lengths of bosminids and *D. retrocurva* were significantly lower in early summer 1998-2000 than in 1995-1997,

suggesting higher levels of vertebrate planktivory in spring during the latter three years of this study. Decreases in zooplankton abundance and mean length have been correlated with alewife spawning migrations in the past (O'Gorman et al. 1991), and relatively strong year classes of alewife in 1995 and 1998 (Owens et al. 2003) could have resulted in higher yearling and adult alewife abundance in 1999-2000 than in 1995-97. Even so, alewife density was relatively low in the nearshore area of Hamlin, NY during early summer 2000 (~0.01 fish·m^{-2}, Warner 2004) and both mean density and length of *D. retrocurva* in late summer were similar in both epochs. Other factors like food quality may have contributed as well.

I observed significantly lower density of several zooplankton groups during peak *C. pengoi* abundance but not in its absence. While this is indicative of predation by *C. pengoi*, other factors could have produced similar results. For example, zooplankton abundance, community composition, and size structure are influenced by such factors as water temperature, availability of food, and predation. Temporal patterns in these factors, however, did not indicate that they were connected with observed changes in the zooplankton community. For instance, seasonal water temperature patterns during the post-*C. pengoi* years of our study period were similar to those during pre-*C. pengoi* years (1995-1997). Therefore, I concluded that the declines observed in late-season bosminid, *D. thomasi*, and nauplii densities were not the result of an altered thermal regime. Total phosphorus and chlorophyll *a* concentrations did not show late summer declines; TP and chlorophyll *a* concentrations were slightly higher in 1998-2000 than in 1995-1997. These findings suggest that zooplankton were not deprived of algal food resources.

Lake Ontario has several invertebrate predators in addition to *Cercopagis pengoi* including *Mysis relicta* (Johannsson et al. 2001), the predatory cladocerans *Bythotrephes longimanus* and *Leptodora kindtii*, and the cyclopoid copepods (e.g.

Diacyclops thomasi, Leblanc et al. 1997). Because the nearshore sites studied have no *Mysis relicta* during summer, and biomass of predatory copepods (with the exception of *D. thomasi*) and predatory cladocerans other than *C. pengoi* was extremely low, *C. pengoi* was the invertebrate predator most likely to affect the nearshore zooplankton community. *Cercopagis pengoi* biomass was between 5-200 times greater than that of *L. kindtii* and 9-138 times greater than the biomass of *B. longimanus*. Although *D. thomasi* was numerically a large component of the zooplankton community and has been identified as predaceous (McQueen 1968; LeBlanc et al. 1997), the consumptive demand of this species was lower in 1998-2000 (i.e. due to significantly lower densities) than in 1995-1997.

Relationships between vertebrate predators and the Lake Ontario zooplankton community have been studied extensively, with the majority of previous work focused on the most abundant planktivorous fish, the alewife (Rand et al. 1995; Urban and Brandt 1993; O'Gorman et al. 1991; Johannsson et al. 1991). Alewives selectively feed on large zooplankters and cause a shift in community size structure towards smaller organisms (Brooks and Dodson 1965, Harman et al. 2003). Although *D. retrocurva* length was lower in early summer 1998-2000 than in 1995-1997, late summer (when density of other taxa declined) *D. retrocurva* abundance and lengths were similar in the two time periods, suggesting the decreased late summer abundance of other taxa was not the result of predation by alewives.

Young-of-the-year alewife biomass and therefore plankton consumption increases over the summer, suggesting this planktivore could cause a late summer decline of zooplankton. Diets of alewives are believed to be similar at all life stages (Strus and Hurley 1992) and consist primarily of bosminids, cyclopoid copepods, and daphnids, while nauplii are a much smaller proportion of the diet (Norden 1968; Urban and Brandt 1993; Mills et al. 1995). By mid-August, high predation by young-

of-the-year alewives should cause shifts in zooplankton community structure similar to predation by adults (decreased zooplankton size, decreased abundance of *Daphnia*). This was not observed. Others argue that larval alewife may select the smaller specimens or species of zooplankton (Zaret 1980; Nigro and Ney 1982), and nauplii have been identified as important alewife prey in at least one study (Leslie and Moore 1985). If larval alewife feed in this manner, this dichotomy in prey selection between larval and adult alewife could result in a zooplankton community size structure similar to that resulting from invertebrate predation (reduced abundance of smaller individuals, Dodson 1974). Larval alewife abundance may have been high in 1998, because catch of the 1998 cohort as yearlings was high. (Robert O'Gorman, U.S.G.S. Oswego Biological Station, Oswego, N.Y., personal communication). However, Klumb et al. (2003) found that June-August densities of larval alewives in the nearshore and embayments (Chaumont, Sodus, and Irondequoit Bays) were similar in both 1997 and 1998, and that larval densities in both years were similar to those observed in the late 1970s. Yearling abundance in 2000 and 2001 did not suggest unusually high abundance of alewife larvae in 1999 and 2000, and the observed changes in zooplankton abundance was consistent for all three post-*C. pengoi* years. Therefore, I concluded that vertebrate predation cannot account for the observed changes in late summer zooplankton abundance.

There were several limitations of the dataset that could influence the interpretation of our findings. First, I encountered missing values in the dataset (52 out of 462 possible). Missing values can lead to biased variance estimates using standard ANOVA techniques, but generalized linear mixed models are generally more robust to missing values (Littell et al. 1996). Second, zooplankton collections were made without use of flow meters, and as a result, density was likely underestimated because filtering efficiency was <100% (McQueen and Yan 1993). Filtering

efficiency of plankton nets can vary seasonally and annually (McQueen and Yan 1993), but it is unlikely that the observed decline in bosminids, *D. thomasi*, or nauplii resulted from seasonal variation in net efficiency because other species did not decline at the same time. Third, the plankton nets used in this study (153 μm mesh) are not as effective as nets with smaller mesh at sampling copepod nauplii (Johannsson et al. 1999). However, all sampling throughout the study was done with the same mesh size and therefore comparisons among years are valid even if nauplii density was biased low.

Our study supports the hypothesis presented by Benoît et al. (2002) and Laxson et al. (2003) that predation by *Cercopagis pengoi* has caused large late-summer decreases in several smaller zooplankton groups in Lake Ontario including bosminids, *D. thomasi* copepodites, and nauplii. However, our results do not support the conclusion by Laxson et al. (2003) that predation by *C. pengoi* has resulted in seasonal declines in *D. retrocurva* density. Laxson et al. (2003) based this conclusion on data from a small area of the lake. Our comparison of pre- and post-*C. pengoi* seasonal patterns in *D. retrocurva* abundance occurred over a larger spatial scale and is less sensitive to local variation in zooplankton dynamics.

Additional predation pressure on the nearshore zooplankton community in Lake Ontario may have a negative impact on the growth and overwinter survival of alewives.   Survival of YOY alewives through the winter of 1998-1999 was high, but may have been aided by mild winter water temperatures. Ability of *C. pengoi* to depress zooplankton abundance could ultimately impact alewife recruitment during winters with average or high severity. Cohorts of *C. pengoi* that are numerically abundant in August and September are likely to suppress available zooplankton resources for the smallest YOY alewife. Although young alewife can subsist on small zooplankton and *C. pengoi*, growth is likely suppressed when zooplankton densities

decline because YOY alewives do not eat *C. pengoi* until they are >6 cm (Bushnoe et al. 2003). As more years with *C. pengoi*, alewife, and piscivorous salmonines in Lake Ontario unfold, the extent to which competition and predation on zooplankton indirectly impacts energy transfer to top piscivores will become more evident.

REFERENCES

Benoît, H. P., O. E. Johannsson, D. M. Warner, W. G. Sprules, and L. G. Rudstam. 2002. Assessing the impact of a recent predatory invader: The population dynamics, vertical distribution and potential prey of *Cercopagis pengoi* in Lake Ontario. Limnology and Oceanography 47:626-635.

Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. Science 150:28-35.

Black, A. R., and S. I. Dodson. 2003. Ethanol: a better preservation technique for *Daphnia*. Limnology and Oceanography: Methods 1:45-50.

Bushnoe, T. M., D. M. Warner, L. G. Rudstam, and E. L. Mills. 2003. *Cercopagis pengoi* as a new prey item for alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) in Lake Ontario. Journal of Great Lakes Research 29:205-212.

Carpenter, S. R. 1990. Large-scale perturbations: opportunities for innovation. Ecology **7**1:2038-2043.

Dodson, S. I., 1974. Zooplankton competition and predation: an experimental test of the size-efficiency hypothesis. Ecology 55:605-613

Hall, S.R., N. K. Pauliukonis, E. L. Mills, L. G. Rudstam, C. P. Schneider, S. J. Lary, and F. Arrhenius. 2003. A comparison of total phosphorus, chlorophyll *a*, and zooplankton in embayment, nearshore, and offshore habitats of Lake Ontario. Journal of Great Lakes Research. 29:54-69.

Hambright, K.D. and S. Friedman. 1994. CAPAS: A computer-assisted plankton analysis system for the MacIntosh. Fisheries 19:6-8.

Harman, W. N., M. F. Albright, and D. M. Warner. 2003. Trophic changes in Otsego Lake, NY following the introduction of the alewife (*Alosa pseudoharengus*). Lake and Reservoir Management 18:215-226.

Johannsson, O. E.. 2003. A history of changes in zooplankton community structure and function in Lake Ontario: responses to whole-lake remediation and exotic invasions. State of Lake Ontario (SOLO): Past Present and Future. Ed. M. Munawar. Leiden, The Netherlands, Backhuys Publishers.

Johannsson, O. E., M. F. Leggett, L. G. Rudstam, M. R. Servos, M. A Mohammadian, G. Gal, R. M. Dermott, and R. H. Hesslein. 2001. Diet of *Mysis relicta* in Lake Ontario as revealed by stable isotope and gut content analysis. Canadian Journal of Fisheries and Aquatic Science 58: 1975-1986.

Johannsson, O.E .**,** C. Dumitru, and D. M. Graham. 1999. Estimation of zooplankton mean length for use in an index of fish community structure and its application to Lake Erie. Journal of Great Lakes Research 25:179-186.

Johannsson, O. E., E. L. Mills, and R. O'Gorman. 1991. Changes in the nearshore and offshore zooplankton communities in Lake Ontario 1981-1988. Canadian Journal of Fisheries and Aquatic Science 48:1546-1557.

Klumb, R. A., L. G. Rudstam, E. L. Mills, C. P. Schneider, and P. M. Sawyko. 2003. Importance of Lake Ontario embayments and nearshore habitats as nurseries larval fishes with emphasis on alewife (*Alosa pseudoharengus*). Journal of Great Lakes Research 29:181-198

LeBlanc, J., Taylor, W.D., Johannsson, O.E., 1997. The feeding ecology of the cyclopoid copepod *Diacyclops thomasi* in Lake Ontario. Journal of Great Lakes Research 23: 369-38.

Laxson, C. L., K. N. McPhedran, J. C. Makarewicz, and I. V. Telesh. 2003. Effects of Cercopagis pengoi on the lower food web of Lake Ontario. Freshwater Biology 48:2094-2106.

Leslie, J. K. and J. E. Moore. 1985. Ecology of young-of-year fish in Muscote Bay (Bay of Quinte), Ontario. Canadian Technical Report Fisheries Science 1337.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS System for Mixed Models. SAS Institute, Cary, North Carolina USA.

Makarewicz, J. C., I. A. Grigorovich, E. Mills, E. Damaske, M. E. Cristescu, W. Pearsall, M. J. LaVoie, R. Keats, L. Rudstam, P. Hebert, H. Halbritter, T. Kelly, C. Matkovich, and H. J. MacIsaac. 2001. Distribution, fecundity, and genetics of *Cercopagis pengoi* (Ostroumov) (Crustacea, Cladocera) in Lake Ontario. Journal of Great Lakes Research 27: 19-32.

McQueen, D. J., and N. D. Yan. 1993. Metering filtration efficiency of freshwater zooplankton hauls: reminders from the past. Journal of Plankton Research 15:57-65.

McQueen, D. J. 1968. Reduction of zooplankton standing stocks by predaceous *Cyclops bicuspidatus thomasi* in Marion Lake, British Columbia. Journal of the Fisheries Research Board of Canada 26:1605-1618.

Menzel, D., and N. Corwin. 1965. The measurement of total phosphorus on the liberation of the organically bound fraction of persulfate oxidation. Limnology and Oceanograhy 10:280-282.

Millard, E. E., O. E. Johannsson, M. A. Neilson, and A. H. El-Shaarawi. 2003. Long -term, seasonal and spatial trends in nutrients, chlorophyll *a*, and light attenuation in Lake Ontario. In: *The State of Lake Ontario Ecosystem (SOLO) – past, present, and future*. Ed. M. Munawar. Backhuys Publishers, Leiden, The Netherlands (in press).

Mills, E. L., and 17 co-authors. 2003. Lake Ontario: Food web dynamics in a changing ecosystem (1970-2000). Canadian Journal of Fisheries and Aquatic Science 60:471-490.

Mills, E. L., R. O'Gorman, E. F. Roseman, C. Adams, and R. W. Owens. 1995. Planktivory by alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus*

mordax) on microcrustacean zooplankton and dreissenid (Bivalvia: Dreissinidae) veligers in southern Lake Ontario. Canadian Journal of Fisheries and Aquatic Science 52:925-935.

Neter, J., M. H. Kutner, C. J. Nachtshiem, and W. Wasserman. 1996. Applied Linear Statistical Models, 4th edition. McGraw-Hill, Boston.

Norden, C. R. 1968. Morphology and food habits of the larval alewife, *Alosa pseudoharengus* (Wilson) in Lake Michigan. Proceedings of the Conference Great Lakes Research 11:103-110.

O'Gorman, R., E. L. Mills, and J. DeGisi. 1991. Use of zooplankton to assess the movement and distribution of alewife *Alosa pseudoharengus* in south-central Lake Ontario in spring Canadian Journal of Fisheries and Aquatic Science 48: 2250-2257.

Ojaveer, H., L. A. Kuhns, R. P. Barbiero, and M. L. Tuchman. 2001. Distribution and population characteristics of *Cercopagis pengoi* in Lake Ontario. Journal of Great Lakes Research 27: 10-18.

Ojaveer, H., M. Simm, A. Lankov, and A. Lumberg. 2000. Consequences of invasion of a predatory cladoceran. ICES C. M. 2000/U:16.

Owens, R. W., R. O'Gorman, T. H. Eckert, and B. F. Lantry. 2003. The offshore fish community in southern Lake Ontario 1972-1998. *in* M. Munawar, editor. State of Lake Ontario. Backhuys Publishers, Leiden, the Netherlands.

Rand, P.S., D.J. Stewart, B. F. Lantry, L. G. Rudstam, O. E. Johannsson, A. P. Goyke, S. B. Brandt, R. O'Gorman, and G. W. Eck, 1995. Effect of lake-wide planktivory by the pelagic fish community in Lakes Michigan and Ontario. Canadian Journal of Fisheries and Aquatic Sciences 52:1546-1563.

Strickland, J.D.H., and T. R. Parsons. 1972. *A practical handbook of seawater analysis.* Bulletin of the Fisheries Research Board of Canada 167.

Strus, R. H., and D. A. Hurley. 1992. Interactions between alewife (*Alosa pseudoharengus*), their food, and phytoplankton biomass in the Bay of Quinte, Lake Ontario. Journal of Great Lakes Research 18:709-723.

Urban, T. P., and S. B. Brandt. 1993. Food and habitat partitioning between young-of-year alewives and rainbow smelt in southeastern Lake Ontario. Environmental Biology of Fishes 36:359-372.

Warner, D. M. 2004. The role of *Cercopagis pengoi* in nearshore areas of Lake Ontario. Ph.D. thesis. Cornell University. Ithaca, NY.

Zaret, T. M. 1980. Predation and freshwater communities. Yale University Press. New Haven, Connecticut.

CHAPTER FOUR

Zooplankton Production and Consumption in Nearshore Waters of Lake Ontario

ABSTRACT

Recent evidence suggests predation by *Cercopagis pengoi* in Lake Ontario leads to depressed abundance of bosminids, *Diacyclops thomasi*, and nauplii during late summer. The added competition and predation resulting from the establishment of the *C. pengoi* population occurred at a time when zooplankton abundance and production had decreased from historic levels due to a reduction in nutrient loading to the lake. These factors may result in lower food availability for alewives. The objectives of this study were to estimate nearshore crustacean zooplankton production, to compare seasonal patterns in production among years, and to contrast crustacean zooplankton production with predatory demands of *C. pengoi* and adult alewives. Production estimated biweekly (May-October) at six nearshore sites showed significant seasonal and annual variability. Late summer production in 1998-2000 was significantly lower than in 1996-1997, but not 1995. Mean growing season production was between 3.3 g dry wt m^{-2} in 1999-2000 and 24.8 g dry wt· m^{-2} in 1997. Mean biweekly *Cercopagis pengoi* abundance (all sites) ranged from 0-10 ind · m^{-2}, with densities at some sites reaching >25 ind · m^{-2}. Growing season consumption estimates for *C. pengoi* ranged from 0.53 g dry wt m^{-2} in 1998 to 1.74 g dry wt· m^{-2} in 1999 (9.6-56% of growing season production). Alewife density ranged from 0.01 – 0.12 fish· m^{-2}. Between May and July, consumption by yearling and older (YAO) alewives in 2000 was 1.8 g dry wt m^{-2} (52% of production). Alewife consumption peaked in mid-June, while consumption by *C. pengoi* peaked in mid-July and late August. Although *C. pengoi* and YAO alewives had similar daily consumption rates, *C. pengoi* was abundant in the nearshore for a longer portion of the growing season.

79

INTRODUCTION

Zooplankton occupy a pivotal role in aquatic food webs, reflecting patterns in both bottom-up (nutrients) and top-down (predation) forces (McQueen et al. 1986; McQueen et al. 1992). In Lake Ontario, they form the largest part of the alewife diet (Mills et al. 1992), and this important species is believed to exert high levels of predation pressure on the zooplankton community (Rand et al. 1995). Anthropogenic influences on the Great Lakes including overfishing, cultural eutrophication, and introduction of exotic species all had significant effects including near extinction of major native fish stocks by the early 1970s, (Christie 1972), degradation in water quality (Schelske 1991), and modification of the food web (Mills et al. 2003). Management efforts in the Great Lakes led to a reduction in phosphorus loading and total phosphorus (TP) concentrations of approximately 50% by 1981 (Johengen et al. 1994). The decrease in TP was accompanied by a reduction in zooplankton biomass and production (Johannsson 2003) as well as a 42% reduction in alewife abundance between the early 1980s and early 1990s (Mills et al. 2003).

The establishment of *Cercopagis pengoi* coincided with the occurrence of large-scale, late summer declines in the density of bosminids, *Diacyclops thomasi*, and nauplii as well as later stages of oligotrophication of Lake Ontario. These declines have been attributed to predation by *C. pengoi* (Benoît et al. 2002; Laxson et al. 2003; Warner et al submitted). Laxson et al. (2003) found that consumption rates of *C. pengoi* were high enough to account for the late summer decrease in abundance of bosminids, *Diacyclops thomasi*, and nauplii at two sites in western Lake Ontario, which supported the conclusions drawn by Benoît et al. (2002) from an earlier study in a limited area of Lake Ontario. Neither of these studies compared consumption by *C. pengoi* with that of other major planktivores. The organisms whose abundance declined during peak *C. pengoi* abundance are important prey for alewives (Norden

1968; Strus and Hurley 1992; Mills 1995), and because alewives <66 mm in total length do not consume *C. pengoi* (Bushnoe et al. 2003) estimates of the relative magnitude of planktivory by *C. pengoi* in nearshore nursery areas (Klumb et al. 2003) may provide some insight as to the importance of this new competitor relative to young-of-year alewives.

The relative importance of *Mysis relicta, B. longimanus,* and *C. pengoi* as alewife competitors is dependent on several factors including diet composition and degree of spatial overlap. Because of low abundance of *M. relicta* (Johannsson 1995) and *B. longimanus* (Warner, Chapter 3) in the areas sampled for this study, only *C. pengoi* consumption is considered here. However, it should be noted that *B. longimanus* might become more important if alewife abundance drops to levels low enough to allow this species to become more abundant. The primary objectives of this study were to (1) estimate daily production by the nearshore zooplankton community, (2) estimate and compare nearshore zooplankton consumption by *C. pengoi* with zooplankton production estimates, and (3) estimate nearshore zooplankton consumption by adult alewives, and 4) estimate surplus production available for YOY alewife. Production estimates and comparisons were based on data from widely separated sites representative of the range of nearshore environmental conditions present in Lake Ontario (Hall et al. 2003). The focus on nearshore areas was based on the conclusion by Klumb et al. (2003) that nearshore areas of Lake Ontario are important as a nursery area for alewives. Although we did not measure consumption rates by *C. pengoi*, we assumed a conservative consumption rate in comparisons with production at the same sites and with alewife consumption at one site. Consumption by *C. pengoi* has been examined in only one study; Laxson et al. (2003) studied *C. pengoi*-zooplankton interactions in southern Lake Ontario but their data were collected

from only two sites quite near each other. There are no existing comparisons of consumption by *C. pengoi* with consumption by alewives.

METHODS

Zooplankton samples included in the nearshore analyses were collected during the day every second week between 14 May and 15 October 1995-2000 at six locations in eastern and southern Lake Ontario (Figure 4.1). At each location, 10-m vertical tows from just above bottom to the surface were made with a 0.5-m conical plankton net (153 μm mesh). Specimens were preserved in the field in 70% ethyl alcohol after they were anesthetized with antacid tablets.

Crustacean zooplankton were counted and measured (at least 100 organisms) from 1-ml random sub-samples (N=1-3). Density (individuals/m^{-3}) and lengths (mm) from the replicate tows were averaged. Because *C. pengoi* specimens form clumps, separate analyses were conducted on large (> 1mm) and small (<1mm) zooplankton, which were separated using a 1.02 mm sieve. Once untangled, *C. pengoi* specimens were spread homogenously in a gridded Petri dish and at least 100 organisms from a random sub-sample were counted and measured with a microprojector at 20X magnification and a digitizer interfaced with a computer. Mean individual weight was estimated using the weight-length equation in Makarewicz et al. (2001). Cladoceran lengths were measured from the top of the head to the base of the tail spine. Copepod lengths were measured from the distal point on the head to the base of the caudal rami. Individual biomass (μg) was estimated from linearized allometric functions relating total length to dry weight (E. L. Mills, Cornell Biological Field Station, Appendix 4.1). Biomass of a given species was calculated as the product of individual biomass and density. Volumetric biomass was converted to areal biomass (g·m^{-2}) abundance by multiplying the number of individuals·m^{-3} by the depth of each tow.

Daily production (g dry wt. $\cdot m^{-2} \cdot d^{-1}$) was estimated for three taxonomic groups (cladocerans, cyclopoid copepods, and calanoid copepods) with the taxa-specific P/B –water temperature models of Shuter and Ing (1997). All organisms captured except *C. pengoi* were included in the production estimates. Mean water column water temperature for each site was calculated as the mean of measurements made at 1m intervals from the surface to just above bottom. Biweekly estimates of daily production by zooplankton were made from biomass and temperatures grouped in one of 11 biweekly periods according to collection date with the first period ranging from 14-28 May. A repeated measures generalized linear mixed model (SAS PROC MIXED and the GLIMMIX macro) was used to compare seasonal and multi-annual patterns in production and consumption. Year (1995-2000), biweek, and year x biweek interaction terms were the fixed effects. Site was included as a random effect because the sites sampled were chosen as representative of the range of conditions in nearshore areas of Lake Ontario (Hall et al. 2003). The model assumed that measurements within a site and year were serially correlated and an autoregressive covariance structure was used to account for this serial correlation. The nature of count data (in this study production and consumption were derived from density) and examination of production histograms by site, week, and year suggested that the data should be modeled with a Poisson error structure and a log link function (Little et al. 1996). Least-squares biweekly means of zooplankton production and consumption were calculated for each year with the model described above. The mean biweekly values for all sites combined were used to estimate production and consumption for the growing season (14 May – 14 October) by integrating the area under the production vs. day of sampling period curve. If the year x biweek interaction was significant, a test of simple effects was used to determine the biweekly periods for
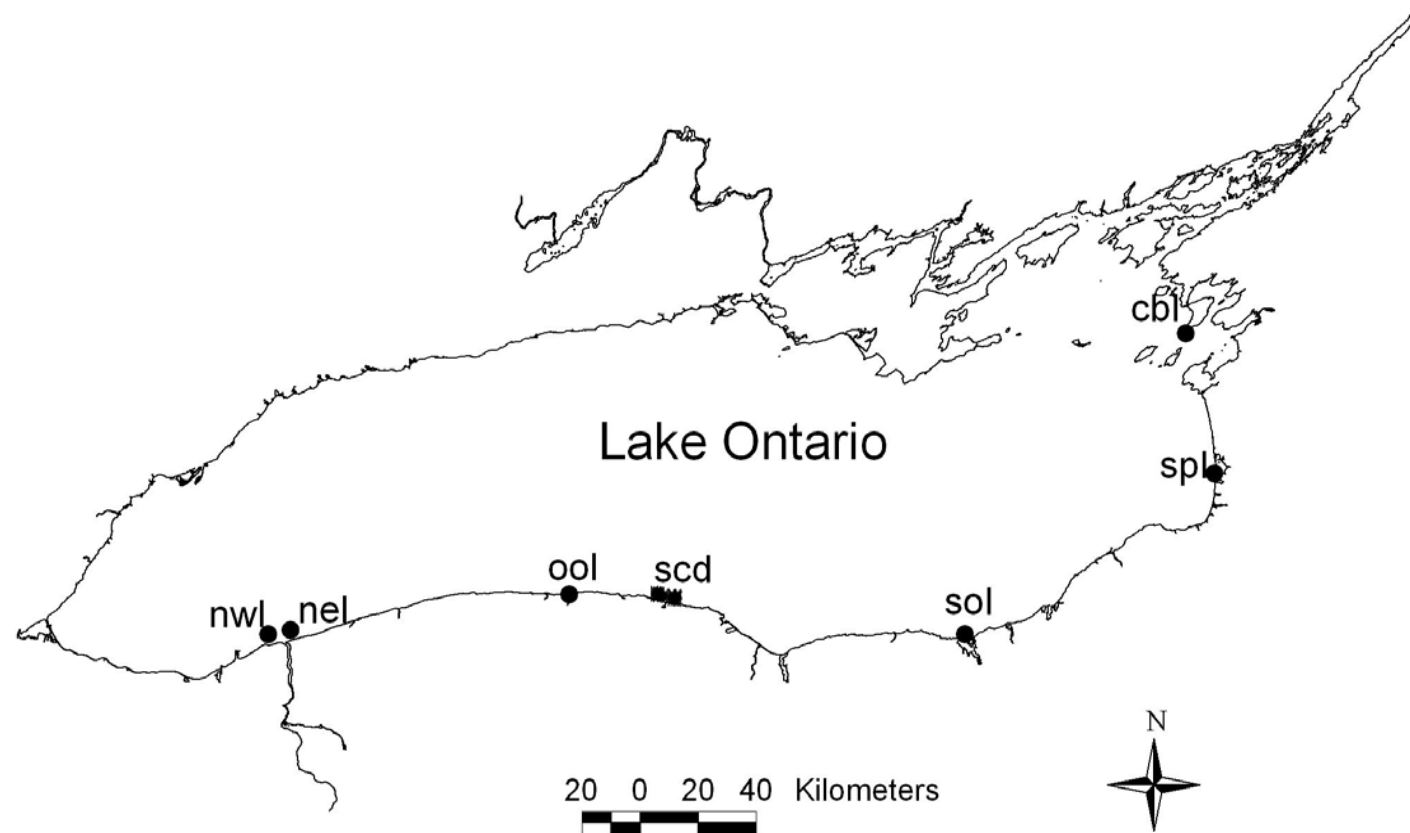
Figure 4.1. Nearshore locations in Lake Ontario at which zooplankton, water temperature (1995-2000, closed circles), and acoustic data (2000, scd = Sandy Creek Delta) were collected during this study.

which production varied among years. Because four response variables were tested (total, cladoceran, cyclopoid, and calanoid production), an experiment-wise α =0.05 was approximated by employing α =0.0125 (0.05/number of statistical tests) to reduce the probability of a Type I error.

Zooplankton consumption by *C. pengoi* was estimated from biomass on each date by assuming a constant mass-specific consumption rate. Although field consumption rates of *C. pengoi* are unavailable, Laxson et al. (2003) found that *C. pengoi* consumed 2.8 *Daphnia* or *Bosmina* per day. Given a mean mass of 5.6 µg for *C. pengoi* and a mean mass of 0.8 and 1.5 µg for Bosmina longirostris and Daphnia retrocurva respectively, this number of prey is equivalent to 40-70 of body mass per day. Estimates for similar predators like *B. longimanus*, *Leptodora kindtii* range from 6-200% of individual body mass per day (Pichlová and Brandl 2003; Wojtal et al. 1999; Yurista and Schulz 1995; Lehman and Branstrator 1995; Luecke et al. 1992; Branstrator and Lehman 1991). Given this wide range, I assumed *C. pengoi* consumed 100% of it's own mass daily. Use of a constant assumed consumption rate provided no information about the actual consumption rates, but it was effective as a tool to 1) compare assumed consumption rate with estimated zooplankton production and 2) compare assumed consumption rates of *C. pengoi* with energetic model estimates of alewife consumption. Total consumption for the growing season (May-October) in each year at each site was calculated by integrating the area under the mean biweekly consumption (all sites) vs. day of sampling period.

Alewife abundance was estimated acoustically on five dates from 22 May to 19 July in the nearshore area at Sandy Creek delta. The location was sampled approximately every second week. Acoustic data were collected using a Simrad EY500 70 kHz split beam echosounder (11.1° half-power beam width and 0.2 ms pulse length). This acoustic system was calibrated three times between late May and

late July 2000 using 32-mm copper calibration sphere (theoretical TS -39.1 dB) and the Simrad Lobe program. On each of these occasions, the measured value of the calibration sphere on a given date was typically within 0.6 dB of the theoretical value, and Warner et al. (2003) found that this unit was relatively consistent between 1996-2000. Echo integration and single target data were recorded with a laptop computer running Simrad EY500 collection software. Echo integration and single target thresholds (–80 and –67 dB respectively) were employed during data collection. Acoustic surveys typically consisted of two or three transects perpendicular to the shoreline and separated by approximately 2-4 km and 2-4 km in length. Bottom depths in the areas surveyed ranged from 2-35 m. Each transect was treated as an independent sample of fish density in the surveyed area, and the mean water column density of all transects was treated as the mean density in the survey area.

Acoustic data were analyzed using Echoview 3.0. Areal density of all scatterers (individuals/m^{-2}) for the whole water column was estimated for two or three transects on each date by dividing the area backscattering coefficient ($m^2 \cdot m^2$) for each transect by the mean backscattering cross-section (linearized mean target strength, in m^2) of all targets between –67 and –15 dB.

Young-of-year alewives were not likely to be present on most of the dates, but other similarly-sized species were present, including spottail shiners (*Notropis hudsonius*), emerald shiners (*Notropis atherinoides*), rainbow smelt (*Osmerus mordax*) were present. Therefore; allocation of total density to the larger alewives present would have resulted in densities that were biased high. To avoid overestimation of adult alewife density, the total density was reduced to reflect the expected TS distribution of adult alewives by multiplying absolute density and the proportion of total individual targets that fell within the expected TS range for adult alewives. Determination of this TS range was based on the length-TS equation of

Warner et al. (2002), acoustic observations of caged alewives, a theoretical scattering model of caged adult alewives 12-14 cm in length (J. Horne, University of Washington School of Fisheries, personal communication), and the tilt angle distributions of tracked fish on each date. Tracks were accepted if they had at least four individual target measurements, four pings, and a maximum ping gap =1. The TS range was determined from the scattering model as the minimum and maximum TS of a fish over a range of tilt angles equal to the mean tilt angle ± 2 SD for fish tracked on that date. The range of fish sizes in the scattering model was almost identical to the mean lengths from netting, and TS predicted from the scattering model at a given tilt angle was within 0-4 dB of TS predicted from length with the Warner et al. (2002) equation. The lower TS threshold used was either −54 or −53 dB (depending on the date) and the upper threshold was −37 dB.

Three additional techniques were employed to aid in the interpretation of *in situ* target strength data. First, the Nv index of Sawada et al. (1993) was calculated to provide an indication whether fish densities were high enough to bias *in situ* TS estimates. High fish densities can lead to poor resolution of individual targets and *in situ* TS values that are biased high (Sawada et al. 1993). This type of TS bias would have resulted in density estimates that were biased low. Second, fish tracking was used to estimate tilt angle distributions. This step was taken to provide a measure of the likelihood that fish TS values were measured at or near dorsal aspect. Third, water column alewife densities were corrected for the proportion of fish above the depth of the vertically-oriented transducer using vertical distribution data from the gill nets. The proportion of total alewives caught in the upper 2m was multiplied by the acoustic density. This product was then added to the acoustic density to provide a corrected water column density.

Fish community composition and size distribution were sampled using variable mesh monofilament vertical gill nets. Gill nets were deployed prior to the start of each acoustic survey and retrieved at the end of the survey. The nets measured 6-m high and 60-m wide and were comprised of equal areas of seven different mesh sizes (6.25, 8, 10, 12.5, 15, 18.75, and 25 mm bar mesh). One or two of these nets was deployed at each of the 6, 12, and 25-m depth contours. At the 6-m contour, one net fished from the surface to a depth of 6 m on all dates. At the 12 m contour, one net fished from 0-6 m while a second was fished from 6-12 m on all dates but 7 June, when only the 6-12 m panel was used. At the 25 m contour, one net fished from 0-6 m while a second fished from 19-25 m on 22 May and 29 June. On 7 June only one net was used to fish the 19-25 m stratum at the 25 m contour. On 19 June, only one net was used to fish the 0-6 m stratum at the 25 m contour. Fish were also collected from shore with a 30 m seine.

Daily zooplankton consumption (g dry wt $\cdot$ d^{-1}) by adult alewives was estimated using an individual-based bioenergetics model (Hanson et al. 1997), using the parameters developed by Stewart and Binkowski (1986) and applied to Lake Ontario by Rand et al. (1995). The model output provides consumption in units of prey wet weight, which was converted to dry weight assuming that dry weight was 11% of wet weight (Hewett and Kraft 1993; Kraft 1993). Daily consumption by the survey area population was estimated as the product of areal density and daily individual consumption. Daily individual consumption was modeled assuming a maintenance diet (minimal growth). This is likely an underestimate of the period during which growth occurs, but an increase in this time period results in the implementation of a maintenance diet in the model. Diet composition was assumed to be constant and to consist of crustacean zooplankton with an average energy density of 1,987-joules$\cdot$ g^{-1} wet wt., which was the mean of the energy densities of cladocerans

and copepods used by Hewett and Stewart (1989). Energy density of alewives was measured with a bomb calorimeter during May, June, and July (Cunningham 2000).

RESULTS

Total zooplankton production exhibited significant biweekly, annual variation, and the interaction of biweek and year was significant (Table 4.2). Total daily production in early August was significantly higher in 1997 than in 1998. Additionally, total daily production in early September was significantly higher in 1996 and 1997 than in 1998, 1999, and 2000. Peak daily total production occurred during September in four of the six years (1995, 1996, 1997, and 2000). In 1998-1999, peak daily production occurred in mid-July. There were taxonomic differences in the seasonal pattern of production as well (Figure 4.3). Cyclopoids generally dominated early summer production and cladocerans dominated production from mid-June through October. Calanoids were generally a minor part of the community. Cladoceran production varied significantly among years, with production in 1996 significantly higher than in 2000 (Table 4.2). Cyclopoid production also exhibited significant differences among years, with production significantly higher in 1995-1997 than in 1998. Cyclopoid production was also significantly higher in 1996 than in 1999-2000 (Table 4.2). Calanoid production differed significantly among years, with production in 1996 significantly higher than in 1998-1999.

Abundance and consumption by *C. pengoi* (daily) was temporally variable. Daily consumption estimates ranged from 0-0.07 g dry wt·m^{-2}. The biweekly means of daily consumption (all six sites) ranged from 0-0.04 g dry wt·m^{-2}, with a peak in late July and again in early September. Consumption by *C. pengoi* exceeded zooplankton production on at least one occasion during 1999 and 2000 and peaks in consumption by *C. pengoi* were generally accompanied by local minima in zooplankton production. Total consumption by *C. pengoi* during the growing season

Table 4.1. Energy density (joules · g wet weight) and percent dry weight (± 95% CI) of alewives captured near the Salmon River and Sandy Creek deltas during May, June, and July 2000. The number of fish whose energy density was measured in each month is shown under N_{ed}. The number of fish whose percent dry weight was measured is shown under N_{drywt}

Date	Energy density	N_{ed}	N_{drywt}	% dry weight
22 May 2000	7,677	5	59	20±3
30 May 2000	5,927		11	25±1
13 June 2000	4,998	6	35	22±2
26 June 2000	5,291		20	23±1
11 July 2000	4,630	4	22	22±1
25 July 2000	4,759		12	22±1

Table 4.2. Summary of repeated measures generalized linear mixed models comparing (Type 3 tests) annual and biweekly mean zooplankton production (g dry wt· m^{-2}) between May and October 1995-2000 at six nearshore sites in Lake Ontario. Values in parentheses are estimated F-test degrees of freedom (numerator, denominator) determined with the Kenward-Rogers method. Values in boldface type were significant ($P<0.0125$) after adjustment for the number of statistical tests were made to achieve an experiment-wise $\alpha = 0.05$.

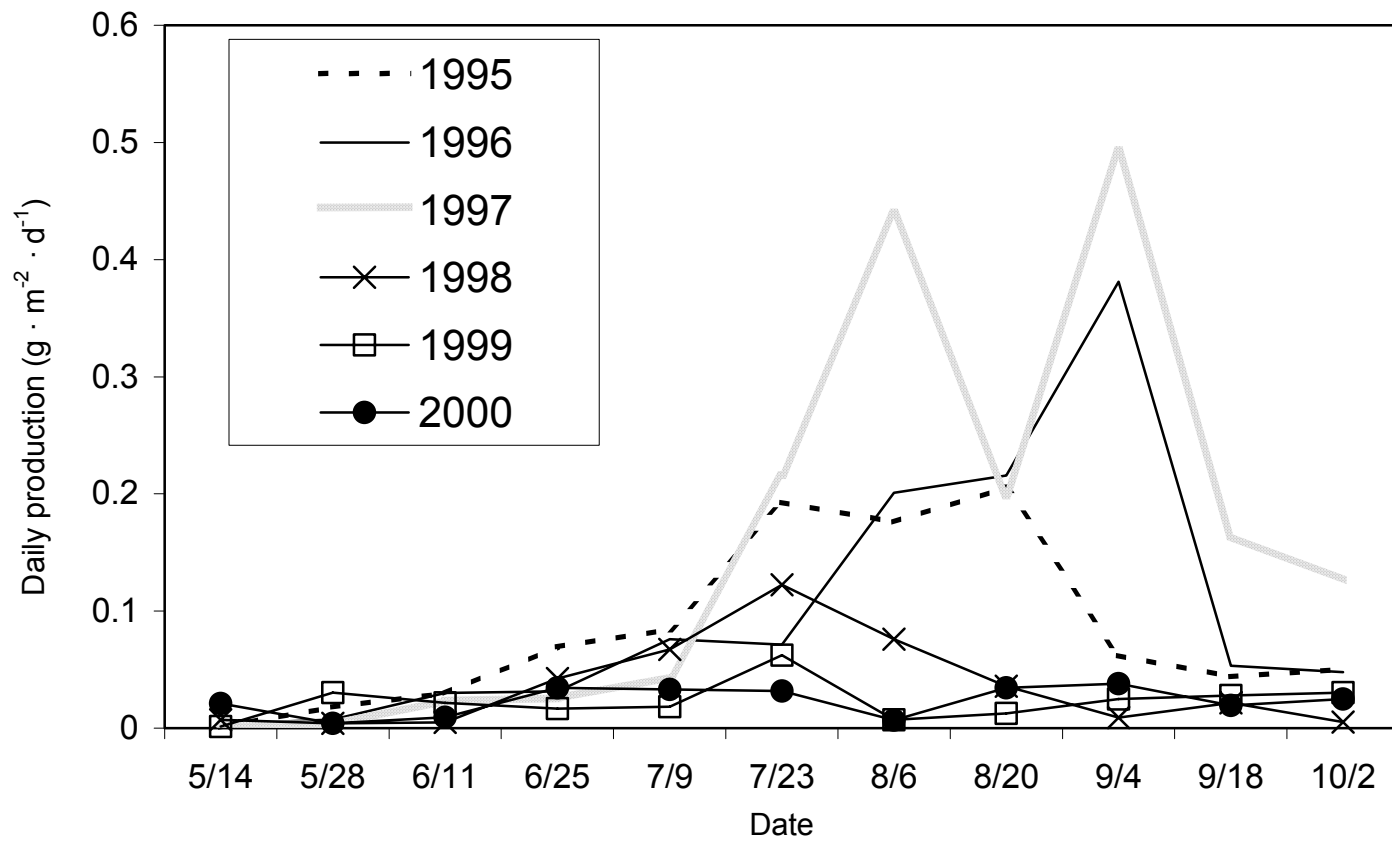| Response		Year	Biweek	Year x biweek
Total production	*F*	2.1 (5, 91)	**3.8 (10, 271)**	**1.62 (50, 258)**
	P	0.08	**<0.001**	**0.01**
Cladocera	*F*	0.46 (5, 93)	**4.28 (10, 273)**	1.51 (50, 258)
	P	0.80	**<0.001**	0.022
Cyclopoida	*F*	**5.4 (5, 114)**	0.72 (10, 261)	2.3 (50, 257)
	P	**0.002**	0.70	0.065
Calanoida	*F*	**3.7 (5, 84)**	1.1 (10, 272)	1.3 (50, 258)
	P	**0.0041**	0.34	0.092

Figure 4.2. Seasonal patterns in total crustacean zooplankton production (excluding *C. pengoi*) at six nearshore sites in Lake Ontario between May and October 1995-2000.

ranged from 0.53 g dry wt·m^{-2} in 1998 to 1.74 g dry wt·m^{-2} in 1999. These consumption values corresponded to 9.6% and 56% of growing season production.

Gill net data indicated that alewives were the dominant species observed in the catch between the shoreline and 25 m contours. The percentage of the gill net catch that was available to acoustic sampling (deeper than 2 m) ranged from 30-100% and was on average about 77%. A total of 1,882 alewives were captured in gill nets 2,311 were captured by seine. Several species were captured, including alewives, spottail shiners (*Notropis hudsonius*), emerald shiners (*Notropis atherinoides*), rainbow smelt (*Osmerus mordax*), slimy sculpin (*Cottus cognatus*), and three spined stickleback (*Gasterosteus aculeatus*), smallmouth bass (*Micropterus dolomieui*), rock bass (*Ambloplites rupestris*), brown trout (*Salmo trutta*), lake trout (*Salvelinus namaycush*), and Chinook salmon (*Oncorhynchus tshawytscha*). However, alewives made up between 90-98% of the gill net catch. Rainbow smelt were only captured at the 12 m contour, while alewives were caught at all contours.

Alewives ranged in size from 8-18 cm and 4-46 g. The peak in numbers of fish caught with the gill nets occurred on 29 June 2000, while the peak with the seine occurred on 7 June 2000. The seasonal pattern Numbers of fish caught (sum of catch from both gears as a relative index) agreed well with acoustic densities on the dates on which both gill nets and seines were used. On average, 79% of the alewife catch was at the six and 12-m contours, but in May more than half the catch was further offshore at the 25-m contour.

Acoustic data indicated conditions were good for estimation of alewife density and consumption. Individual transect Nv values ranged from 0.002-0.020, well below the Nv threshold recommended by Gauthier and Rose (2001). Tilt angle distributions for tracked fish were approximately normal with mean tilt angle near zero on each occasion (Figure 4.4). Adult alewife density ranged from 100-1,200 fish ·ha.
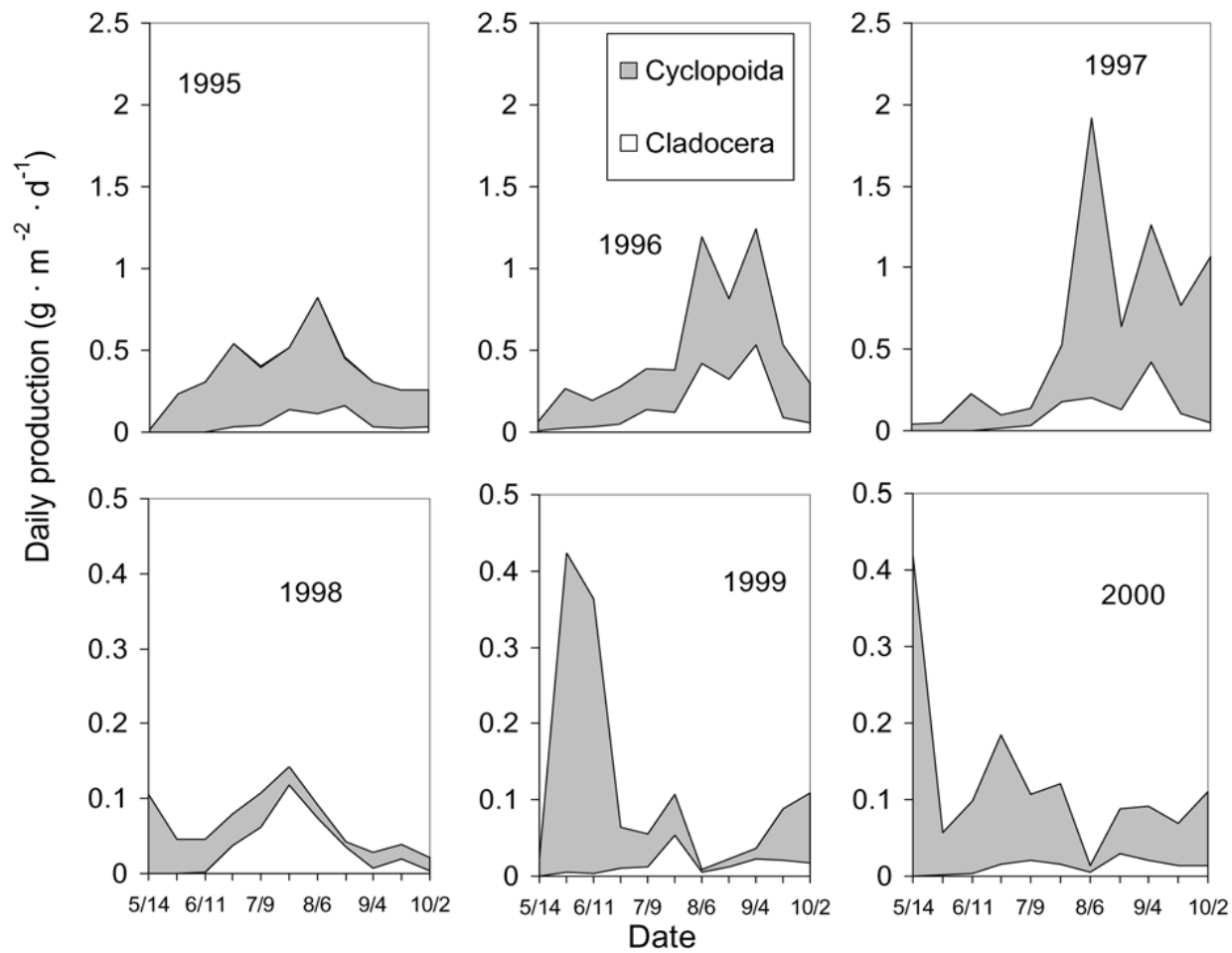
Figure 4.3. Seasonal patterns in daily production of cladocerans and cyclopoids at six sites in Lake Ontario in the years 1995-2000.

Consumption by adult alewives ranged from 0.006 and 0.039 g dry wt$\cdot$ m$^{-2}\cdot$d^{-1}, with the lowest value observed on 22 May and the highest value on 19 June (Table 4.3). These consumption rates corresponded to between 24 and 38% of maximum consumption. Consumption exceeded production in late May and early June, but declined to a level much lower than production after 19 June (Figure 4.6). The mean daily consumption for the dates surveyed ($\pm$SE) was 0.027$\pm$0.018 g dry wt m$^{-2}\cdot$d^{-1}, which was similar to that observed for *C. pengoi* on the dates it was present. Total YAO alewife consumption between May and July was 1.76 g dry wt m$^{-2}\cdot$d^{-1}, which corresponded to 56% of growing season production.

<div align="center">DISCUSSION</div>

The results of this study support several conclusions. First, zooplankton production was significantly lower after establishment of *C. pengoi* than prior to its establishment. Nearshore total zooplankton production was generally lower in 1998-2000 than in 1995-1997. The decrease in production was driven primarily by a decline in the production of cyclopoid copepods. Second, consumption estimates for *C. pengoi* (42-56% of growing season production) indicate that predation by *C. pengoi* was a plausible explanation for the decline in production during 1999-2000, but not in 1998 (9.6% of growing season production). Third, nearshore planktivory rates of YAO alewives and *C. pengoi* are likely of similar magnitude and in concert are sufficient to greatly reduce the availability of crustacean zooplankton prey to YOY alewives.

Two localized studies have suggested that predation by *C. pengoi* has resulted in seasonal alteration of the Lake Ontario zooplankton community (Benoît et al. 2002; Laxson et al. 2003). Results of this study generally concur with those of Laxson et al. (2003), who found that predation by *C. pengoi* was sufficient to reduce the abundance

Table 4.3. Mean density (fish· m^{-2} ±SE, N), Nv, mean weight (g), daily consumption (g dry wt· m^{-2}·d^{-1}), and mean tilt angle (degrees, ±SD, N) of fish tracks between 2-35 m depth contours near the Sandy Creek delta (Hamlin, NY) between 22 May and 19 July 2000.

Date	Density	Nv	Mean Weight[1]	Consumption	Tilt angle
22 May	0.014±0.002 (3)	0.003	22.4	0.003	0.3±5.3 (71)
7 June	0.071±0.006 (2)	0.007	19.8	0.019	-4.6±7.0 (124)
19 June	0.126±0.099 (2)	0.004	25.8	0.040	-0.8±4.2 (166)
29 June	0.061±0.001 (2)	0.006	21.1	0.020	-1.5±4.8 (297)
19 July	0.020±0.007 (2)	0.013	19.8[2]	0.007	-1.1±3.9 (239)

[1]Mean weight was predicted from mean length using the equation ln (weight, g) = -11.37+2.9 ln (length, mm)

[2] Fish length was estimated from shore seine data because gill nets were not used on this date
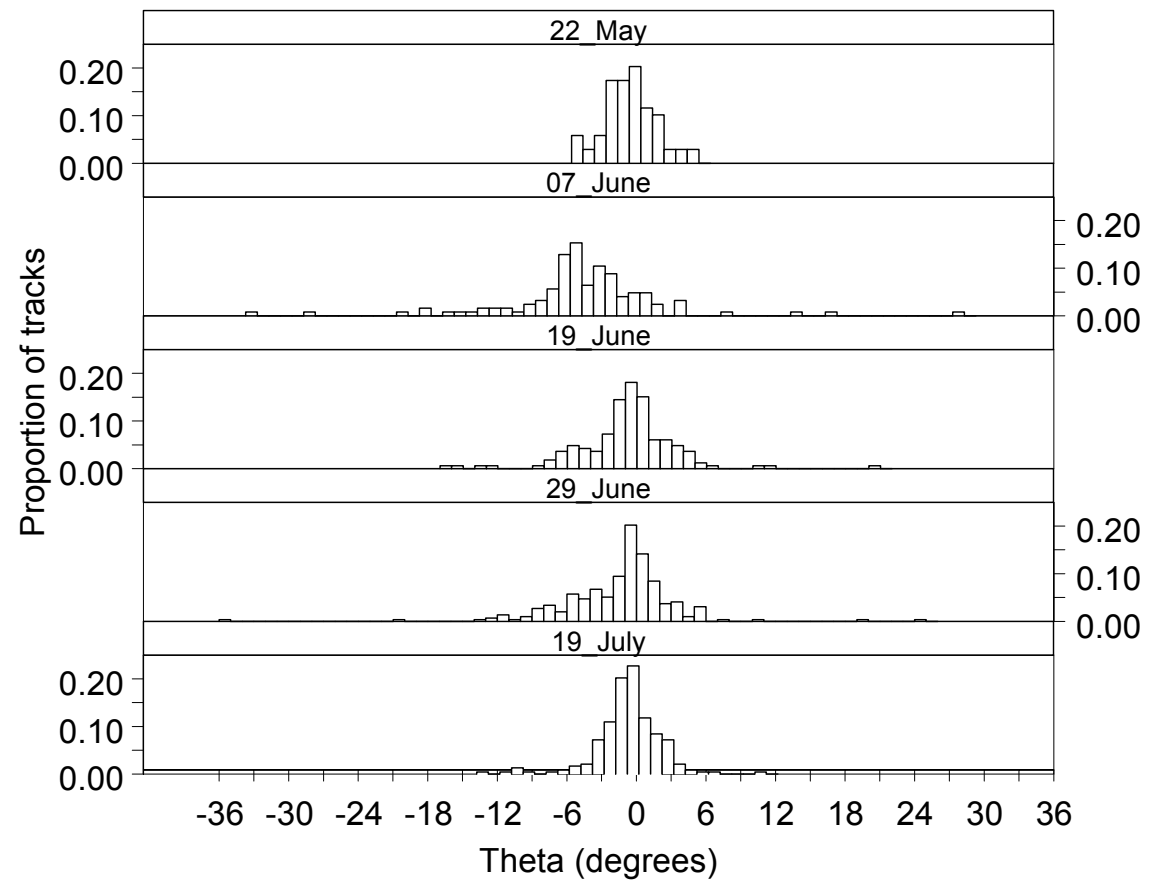
Figure 4.4. Estimated *in situ* tilt angle distributions for alewives tracked with split beam acoustic gear in nearshore areas of Lake Ontario during summer 2000.
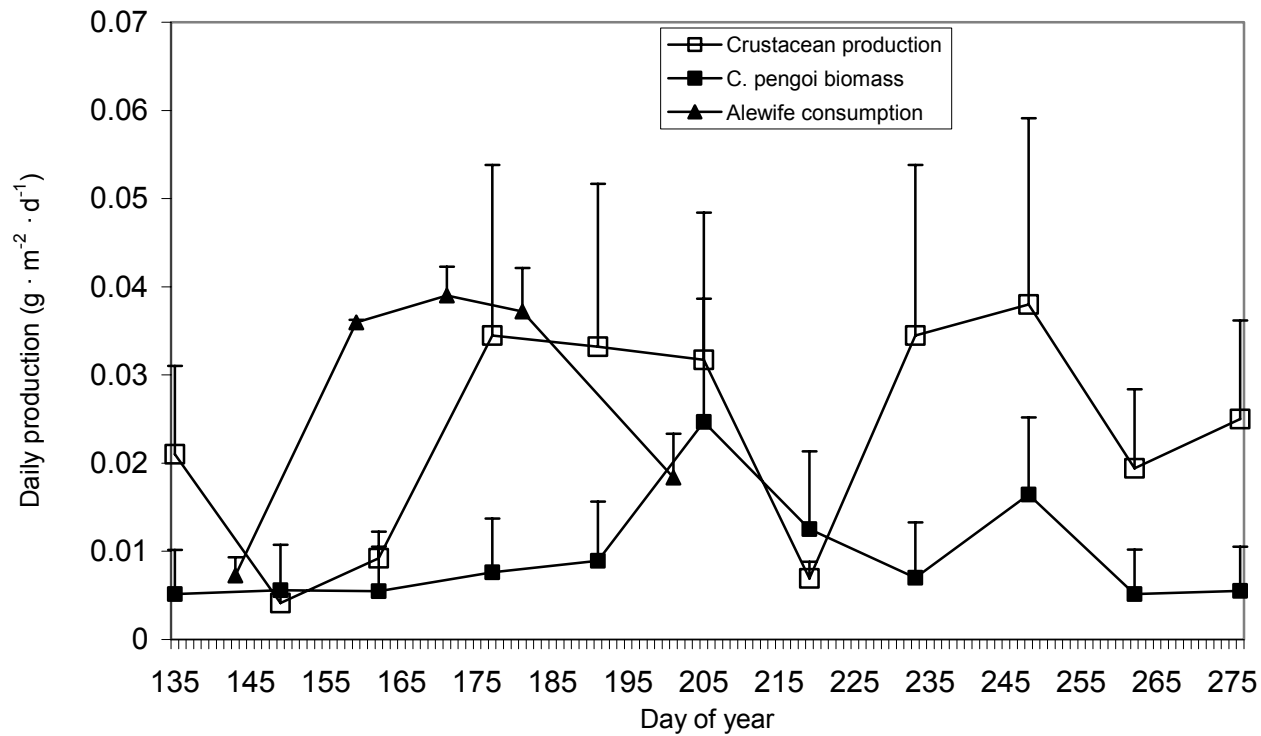
Figure 4.5. Daily production by crustacean zooplankton (open squares) available to the plankton nets used to sample zooplankton and *C. pengoi* biomass at six nearshore sites in Lake Ontario between May and October 2000. Also shown are estimates of daily consumption by adult alewives at one site near Hamlin, N.Y. between May and July 2000. Error bars are absent to preserve visual clarity.

of bosminids, cyclopoids, and *Daphnia retrocurva* at two locations in southern Lake Ontario. Warner (Chapter 3), who examined data from seven locations over a larger geographical area, observed changes similar to those observed by Benoît et al. (2002) and like Benoît et al. (2002) did not detect any change in the abundance of *D. retrocurva*. However, the abundance of *C. pengoi* at the locations studied by Laxson et al. (2003) was higher than the nearshore average in this study.

The majority of nearshore crustacean zooplankton biomass produced between May and October 2000 would have been required to meet the energetic needs of both YAO alewives and *C. pengoi*. Consumption by YAO alewives occurred primarily in early summer, while consumption by *C. pengoi* occurred in late summer. Assuming the density of YAO alewives at Hamlin Beach N.Y. was similar to that occurring elsewhere in the nearshore, total growing season consumption by alewives was similar to that estimated for *C. pengoi* in nearshore waters. However, based on the results of Laxson et al. (2003, Figure 6), it was likely that consumption by *C. pengoi* in 2000 at the location of the acoustic surveys presented in this study was higher than that of alewives. This suggests that *C. pengoi* and adult alewives may exert a similar top-down influence on the nearshore crustacean zooplankton community. The predatory demand of *C. pengoi* was variable in 1998-2000, with the highest growing season consumption occurring in 1999. However, consumption in both 1999 and 2000 were similar and corresponded to a large proportion of growing season production (40-52%).

Several assumptions and methodological limitations inherent to the acoustic methods of this study warrant discussion here. Rose and Gauthier (2000) found that factors such as species, distribution of fish, variation in target strength, detectability, and species identification contributed to uncertainty in density estimates. The primary effect of fish distribution is likely to be on the variance estimate for the area surveyed,

not the mean density (Rivoiard aet al. 2000). Although the level of uncertainty in

alewife biomass was somewhat lower than for *C. pengoi* biomass, the former variable

was measured at one location, while the latter variables were measured at six

locations. Variation in target strength can result in biased density estimates if the

mean tilt angle is less than or greater than that at maximum scattering aspect.

Simultaneous *in situ* measurements of tilt angle for tracked alewives 2-15 cm long in

Otsego Lake, NY with two frequencies (70 and 120 kHz) suggests that summer

nighttime tilt angle is normally distributed with mean near zero (D. M. Warner,

unpublished data). A similar pattern with little seasonal variation was observed for

tracked fish in this study. Detectability was probably high and had little influence

because at night alewives are typically not associated with bottom in the Great Lakes

(Jansen and Brandt 1980). However, gill net data indicated that acoustic density was

underestimated because only 77% of the catch was at a depth below the detection

depth of the echosounder. This resulted in consumption estimates that were biased

low. Species identification was probably not a major problem because alewives

accounted for 89-98% of the catch (in numbers).

All methods used for prediction of zooplankton production have limitations

and inherent error (Huntley and Lopez 1992). Egg ratio methods suffer from being

prohibitively labor intensive for the purpose of estimating community production at

large spatial scales and from uncertainty in egg development times (Huntley and

Lopez 1992). Regressions to predict production from individual growth rates require

both mass-specific growth rates and biomass (Huntley and Lopez 1992; Shuter and

Ing 1997). Kleppel et al. (1996) and Stockwell and Johannsson (1997) suggested that

these models could be inaccurate because they may not take into account the effects of

food limitation on individual growth rates and reproductive capacity. However,

Huntley and Lopez (1992) showed that variability in individual growth was low

relative to temporal and spatial variability in biomass and suggested that individual growth of zooplankton is rarely limited by food in nature. Although not explicitl in the Shuter and Ing (1997) model, variation in reproductive capacity due to limitations in food quantity or quality should have been integrated by the zooplankton community and detected by measuring biomass frequently (every two weeks) for a period of months (approximately the scale of life cycles). Furthermore, meta-analyses by Huntley and Lopez (1992) and Shuter and Ing (1997) found that most (80-90%) of the variation in weight-specific production was explained by water temperature alone.

Estimates of consumption by *C. pengoi* presented here were not dependent on temperature (other than the unknown temperature effect on *C. pengoi* abundance). Poikilotherm metabolic rates are typically temperature dependent. Therefore, it seems likely that at higher temperatures the consumption estimates presented here are low, while at low temperatures they are probably high. Because *C. pengoi* is most abundant when water temperatures are above 12-14 ºC, it is likely that overall the consumption was under-estimated in this study.

Bioenergetic estimation of consumption by alewives was also dependent on important assumptions. This study and others (Hewett and Stewart 1989; Rand et al. 1995) were potentially hampered by the lack of a validated model. As a result, it is difficult to draw conclusions as to its accuracy. In addition to model parameters, results are sensitive to input data including diet composition, prey energy content, alewife energy content, growth rate, and water temperature. The diet composition assumed in this study was an oversimplification, but was probably representative of alewife diet (solely zooplankton). Energy density of prey items was assumed constant. This is somewhat unrealistic, but without seasonal prey energy density measurements there was no alternative. Alewife energy density was measured several times during the sampling period so any influence of this variable was present *in situ*

and in the model. Alewife growth was assumed negligible, a reasonable assumption during the reproductive period, which can last from May to August. Consumption estimates may have been somewhat low because energetic costs of reproduction were not included in the model. Water temperatures used in the model were measured in the environment encountered by alewives in the nearshore zone.

Mean seasonal zooplankton production at the nearshore sites studied in 1995-2000 ranged 3.3 g dry wt m^{-2} in 1999-2000 to 23.8 g dry wt m^{-2} in 1997. Mid-lake production levels from 1986-1995(8-19 g dry wt m^{-2}, 1986-1995) and those in the Kingston basin from 1993-1995 (7-13 g dry wt m^{-2}, 1993-1995) reported by Johannsson (2003) were similar to those observed in 1995-1997 in this study but were somewhat higher than in 1998-2000. The results of this study are not directly comparable to the Johannsson (2003) study because in this study 153-μm plankton nets were utilized, whereas Johannsson (2003) used a 64 μm net. However, because of the potential errors associated with these production estimates and the assumption that a 153 μm net underestimates abundance of smaller taxa, nearshore production estimates from this study should most likely be viewed as similar to those from the Kingston Basin in the early 1990s. Historical estimates of nearshore zooplankton production in Lake Ontario do not exist, but the production estimates presented in this study were similar to or slightly higher than Johannsson et al. (2000) observed in the nearshore of Lake Erie in 1993 and 1994 in spite of differences in plankton nets used (153 vs. 64-μm).

The magnitude of seasonal consumption by YAO alewives was comparable to estimates for alewives and Baltic herring in previous studies. At the individual level, consumption by alewives (14-22% of body weight d^{-1}) was somewhat higher than the 1-5% of body weight d^{-1} observed for Baltic herring (*Clupea harengus*, Möllman and Köster 1999) but was more similar to the 10-20% per day observed by Rudstam et al.

(1992) for age-1 Baltic herring between 8.5 and 13.1 cm in length. This difference can be explained in part by the smaller body size of alewives in Lake Ontario and potentially warmer water temperatures they occupy. At the population level, YAO alewives consumed a proportion of zooplankton production (57%) within the range observed for Baltic herring by Möllman and Köster (41-57%, 1999) and the range of 30-60% observed by Rudstam et al. (1994). The estimate from this study was also similar to the range for alewives in Lake Michigan (60-80%, Rand et al. 1995). However, Rand et al. (1995) found that alewife consumption exceeded zooplankton production in Lake Ontario in 1990. If both YOY and YAO alewives occupied the nearshore areas concurrently, it is likely that total consumption by alewives and *C. pengoi* would have exceeded nearshore zooplankton production (excluding *C. pengoi*) in 2000. However, it is also likely that in 1998-2000 *C. pengoi* replaced other organisms in the diet of YAO alewives (Bushnoe et al. 2003).

Although there were limitations to the approach used to compare zooplankton consumption and production, several conservative conclusions can be made from the results presented here. First, it appears that there is a seasonal progression in the magnitude of planktivory. Second, the dominant planktivore varies seasonally. Yearling and older alewife are the dominant nearshore planktivores in early summer, while *C. pengoi* and YOY alewives are the primary consumers of zooplankton in late summer. Although it was not possible to estimate consumption by YOY in this study, much of it likely occurs during peak consumption by *C. pengoi* and it is likely that planktivory rates in the nearshore of Lake Ontario are highest in late summer when both of these organisms are abundant. Second, based on consumption estimates for *C. pengoi,* it is likely that YOY alewives face energetic limitation until they begin to feed

on *C. pengoi*. The consequences of such a limitation are not clear, but reduced growth early in life may reduce overwinter survival (O'Gorman et al. 1997). Third, it appears possible for predation by *C. pengoi* to have caused late summer declines in abundance of bosminids, *D. thomasi*, and nauplii observed by Benoît et al. (2002) and Warner (Chapter 3). Fourth, it appears that on a daily basis, consumption by YAO alewives and *C. pengoi* is of similar magnitude. There is mounting evidence that *C. pengoi* is important as a predator {(this study; Benoît et al. 2002; Warner (Chapter 3)} and as alewife prey (Bushnoe et al. 2003). Additional research will be necessary to develop a better understanding of how *C. pengoi* has influenced energy flow in the nearshore of Lake Ontario and whether growth and survival of YOY alewives has been affected. Key to this understanding will be examination of temporal and spatial patterns in the abundance of alewives and habitat overlap between alewives and *C. pengoi*.

Appendix 4.1. Coefficients used to estimate the dry weight (W) of zooplankton from body length (L) in the model: $\ln W = \alpha + \beta * \ln(L)$, where α is the natural logarithm of the intercept from the weight-length regression (E. L. Mills, unpublished data).

Species	Parameter	
	α	β
Bosminids		
Bosmina longirostris	2.3700	2.1200
Eubosmina coregoni	3.2810	3.1300
Daphnids		
Daphnia galeata mendotae	1.6090	2.840
D. longiremis	1.6090	2.840
D. pulicaria	1.6090	2.840
D. retrocurva	1.6090	2.840
D. schødleri	1.6090	2.840
Copepods		
Acanthocyclops vernalis	1.6557	2.1463
Diacyclops thomasi	1.7050	2.4600
Diaptomus ashlandii	1.7050	2.4600
D. minututs	1.7050	2.4600
D. oregonensis	1.7050	2.4600
D. sicilis	1.7050	2.4600
D. siciloides	1.7050	2.4600

Appendix 4.1 continued. Coefficients used to estimate the dry weight (W) of zooplankton from body length (L) in the model: $\ln W = \alpha + \beta * \ln(L)$, where α is the natural logarithm of the intercept from the weight-length regression (E. L. Mills, unpublished data).

Species	Parameter	
	α	β
Epischura lacustris	2.1095	2.7319
Eucyclops spp.	1.7050	2.4600
Eurytemora affinis	1.7050	2.4600
Harpacticoida	1.7050	2.4600
Mesocyclops edax	1.7050	2.4600
Limnocalanus macrurus	1.8960	2.8900
Tropocyclops prasinus mexicanus	1.7050	2.4600
Calanoid copepodites	1.7050	2.4600
Cyclopoid copepodites	1.7050	2.4600
Nauplii	1.4350	2.4800
Other Cladocera		
Alona spp.	1.3910	3.4800
Bythotrephes longimanus	2.4100	2.7700
Cercopagis pengoi	1.7164	2.3703
Ceriodaphnia quadrangular	2.2370	2.2590

Appendix 4.1 continued. Coefficients used to estimate the dry weight (W) of zooplankton from body length (L) in the model: $\ln W = \alpha + \beta * \ln(L)$, where α is the natural logarithm of the intercept from the weight-length regression (E. L. Mills, unpublished data).

Species	Parameter	
	α	β
Chydorus sphaericus	1.3910	3.4800
Diaphanosoma spp.	1.6090	2.8400
Holopedium gibberum	2.4170	3.0400
Leptodora kindtii	-0.8210	2.6700
Polyphemus pediculus	1.9360	2.1500
Sida crystallina	1.6090	2.8400

REFERENCES

Benoît, H. P., O. E. Johannsson, D. M. Warner, W. G. Sprules, and L. G Rudstam
2002. Assessing the impact of a recent predatory invader: The population
dynamics, vertical distribution, and potential prey of *Cercopagis pengoi* in
Lake Ontario. Limnology and Oceanography 47: 626-635.

Bushnoe, T. M., D. M. Warner, L. G. Rudstam, E. L. Mills. 2003. *Cercopagis pengoi*
as a new prey item for alewife (*Alosa pseudoharengus*) and rainbow smelt
(*Osmerus mordax*) in Lake Ontario. Journal of Great Lakes Research 29: 205-
212.

Christie, W. J. 1972. Lake Ontario - Effects of exploitation, introductions, and
eutrophication on salmonid community. Journal of the Fisheries Research
Board of Canada 29(6): 913-929.

Cunningham, K. 2001. Energy density of alewife (Alosa pseudoharengus) in Lake
Ontario. Cornell Biological Field Station Intern Report.

Gauthier, S., and G. A. Rose 2001. Diagnostic tools for unbiased *in situ* target strength
estimation. Canadian Journal of Fisheries and Aquatic Sciences 58(11): 2149-
2155.

Hall, S. R., N. K. Pauliukonis, E. L. Mills, L. G. Rudstam, C. P. Schneider, S. J. Lary,
and F. Arrhenius. 2003. A comparison of total phosphorus, chlorophyll a, and
zooplankton in embayment, nearshore, and offshore habitats of Lake Ontario.
Journal of Great Lakes Research 29: 54-69.

Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish
bioenergetics 3.0 for Windows. University of Wisconsin Sea Grant Institute,
technical Report WISCU-T-970-001, Madison.

Hewett, S. W., and C. E. Kraft. 1993. The relationship between growth and consumption: comparisons across fish populations. Transactions of the American Fisheries Society 122:814-821.

Hewett, S. W., and D. J. Stewart. 1989. Zooplanktivory by alewives in Lake Michigan: ontogenetic, seasonal, and historical patterns. Transactions of the American Fisheries Society 118: 581-596.

Huntley, M. E. and M. D. G. Lopez (1992). Temperature-dependent production of marine copepods - a global synthesis. American Naturalist 140: 201-242.

Jansen, J., and S. B. Brandt. 1980. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 37:177-184.

Johannsson, O. E., L. G. Rudstam, G. Gal, and E. L. Mills. In press. *Mysis relicta* in Lake Ontario: population dynamics, trophic linkages, and further questions. *In* State of Lake Ontario: Past, Present, and Future. M. Munawar, editor. Ecovision World Monograph Series, Backhuys publishers, Leiden, the Netherlands.

Johannsson, O. E. In press. A history of changes in community structure and function in Lake Ontario: responses to whole-lake remediation and exotic invasions. *In* State of Lake Ontario: Past, Present, and Future. M. Munawar, editor. Ecovision World Monograph Series, Backhuys publishers, Leiden, the Netherlands.

Johannsson, O. E., R. Dermott, D. M. Graham, J. A. Dahl, E. S. Millard, D. D. Myles, and J. LeBlanc. 2000. Benthic and pelagic secondary production in Lake Erie after the invasion of *Dreissena* spp. with implications for fish production. Journal of Great Lakes Research 26: 31-54. Johengen, T. H., O. E. Johannsson, G. L. Pernie, and E.S. Millard. 1994. Temporal and seasonal

trends in nutrient dynamics and biomass measures in Lakes Michigan and Ontario in response to phosphorus control. Canadian Journal of Fisheries and Aquatic Sciences 51: 2570-2578.

Kleppel, G. S., C. S. Davis, et al. 1996. Temperature and copepod growth in the sea: A comment on the temperature-dependent model of Huntley and Lopez. American Naturalist 148: 397-406.

Klumb, R. A., L. G. Rudstam, et al. 2003. Importance of Lake Ontario embayments and nearshore habitats as nurseries for larval fishes with emphasis on alewife (*Alosa pseudoharengus*). Journal of Great Lakes Research 29: 181-198.

Kraft, C. E. 1993. Phosphorus regeneration by Lake Michigan alewives in the mid-1970s. Transactions of the American Fishery Society 122:749-755

Laxson, C. L., K. N. McPhedran, J. C. Makarewicz, and I. V. Telesh. 2003. Effects of Cercopagis pengoi on the lower food web of Lake Ontario. Freshwater Biology 48:2094-2106.

Lehman, J. T., and D. K. Branstrator. 1995. A model for growth, development, and diet selection by the invertebrate *Bythotrephes cederstroemi*. Journal of Great Lakes Research 21: 610-619.

Luecke, C., L. G. Rudstam, and Y. Allen. 1992. Interannual patterns of planktivory 1987-1989: an analysis of vertebrate and invertebrate planktivores. Pages 275-301 *In* Kithcel, J. F., editor, Food Web Management: A Case Study of Lake Mendota. Springer-Verlag New York.

Makarewicz, J. C., I. A. Grigorivich, E. L. Mills, E. Damaske, M. Cristescu, W. Pearsall, M. LaVoie, R. Keats, L. Rudstam, P. Hebert, H. Halbritter, T. Kelly, C. Malkovich, and H. J. MacIsaac. 2001. Distribution, fecundity, and genetics of *Cercopagis pengoi* (Ostroumov) (Crustacea, Cladocera) in Lake Ontario. Journal of Great Lakes Research 27: 19-32.

McQueen, D. J., E. L. Mills, J. L. Forney, M. R. S. Johannes, and J. R. Post. 1992. Trophic level relationships in pelagic food webs: comparisons derived from long-term data sets from Oneida Lake, New York and Lake St. George, Ontario (Canada). Canadian Journal of Fisheries and Aquatic Sciences 49: 1588-1596.

McQueen, D. J., J. R. Post, and E. L. Mills. 1986. Trophic relationships in freshwater pelagic ecosystems. Canadian Journal of Fisheries and Aquatic Sciences 43: 1571-1581.

Mills, E. L., J. M. Casselman, R. Dermott, J. D. Fitzsimons, G. Gal, K. T. Holeck, J. A. Hoyle, O. E. Johannsson, B. F. Lantry, J. C. Makarewicz, E. S. Millard, M. Munawar, I. F. Munawar, R. O'Gorman, R. W. Owens, L. G. Rudtsam, T. Schaner, and T. J. Stewart. 2003. Lake Ontario: food web dynamics in a changing ecosystem (1970-2000). Canadian Journal of Fisheries and Aquatic Sciences 60:471-490.

Mills, E. L., R. O. O'Gorman, E. F. Roseman, C. Adams, and R. Owens. 1995. Planktivory by alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) on microcrustacean zooplankton and dreissenid (Bivalvia:Dreissenidae) veligers in southern Lake Ontario. Canadian Journal of Fisheries and Aquatic Sciences 52:925-935.

Möllmann, C., and F. W. Köster. 1999. Food consumption in the central Baltic: evidence for top-down control? ICES Journal of Marine Science 56: 100-113.

Norden, C. R. 1968. Morphology and food habits of the larval alewife, *Alosa pseudoharengus* (Wilson) in Lake Michigan. Proceedings of the 11th Conference on Great Lakes Research 11: 103-110.

O'Gorman, R., O. E. Johannsson, and C. P. Schneider. 1997. Age and growth of alewives in the changing pelagia of Lake Ontario, 1978-1992. Transactions of the American Fisheries Society 126:112-126.

Pichlová, R., and Z. Brandl. 2003. Predatory impact of Leptodora kindtii on zooplankton in the Slapy Reservoir. Hydrobiologia 504:177-184.

Rand, P. S., D. J. Stewart, B. F. Lantry, L. G. Rudstam, O. E. Johannsson, A. P. Goyke, S. B. Brandt, R. O'Gorman, and G. W. Eck. 1995. Effect of lake-wide planktivory by the pelagic prey fish community in Lakes Michigan and Ontario. Canadian Journal of Fisheries and Aquatic Sciences 52: 1546-1563.

Rose, G., and S. Gauthier. 2000. Acoustic surveys in the full monte: simulating uncertainty. Aquatic Living Resources 13: 367-372.

Rudstam, L. G., G. Aneer, and M. Hildén. 1994. Top-down control in the pelagic Baltic ecosystem. Dana 10:105-129.

Rudstam, L. G., S. Hansson, S. Johansson, and Ulf Larsson. 1992. Marine Ecology Progress Series 80:159-173.

Sawada, K., M. Furusawa, Y. Takao, and N. J. Williamson. 1993. Conditions for the precise measurement of fish target strength *in situ*. J. Mar. Acoust. Soc. Japan 20: 73-79.

Schelske, C. L. 1991. Historical nutrient enrichment of Lake Ontario - paleolimnological evidence. Canadian Journal of Fisheries and Aquatic   110 Sciences 48: 1529-1538.

Shuter, B. J., and K. K. Ing. 1997. Factors affecting the production of zooplankton in lakes. Canadian Journal of Fisheries and Aquatic Sciences 54: 359-377.

Stewart, D. J., and F. P. Binkowski. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics-modeling synthesis. Transactions of the American Fisheries Society 115: 643-661.

Stockwell, J. D., and O. E. Johannsson. 1997. Temperature-dependent allometric models to estimate zooplankton production in temperate freshwater lakes. Canadian Journal of Fisheries and Aquatic Sciences 54: 2350-2360.

Strus, R. H. and D. A. Hurley. 1992. Interactions between alewife (*Alosa pseudoharengus*), their food, and phytoplankton biomass in the Bay of Quinte, Lake Ontario. Journal of Great Lakes Research 18: 709-723.

Warner, D. M. 2004. The Role of *Cercopagis pengoi* in Nearshore Areas of Lake Ontario. Ph. D. dissertation, Department of Natural Resources, Cornell University. Ithaca, NY.

Warner, D. M., L. G. Rudstam, and R. A. Klumb. 2002. *In situ* target strength of alewives in freshwater. Transactions of the American Fisheries Society 131: 212-223.

Wojtal, A., P. Frankiewicz, and M. Zalewski. 1999. The role of the invertebrate predator *Leptodora kindtii* in the trophic cascade of a lowwland reservoir. Hydrobiologia 416 215-233.

Yurista, P. M. and K. L. Schulz. 1995. Bioenergetic analysis of prey consumption by *Bythotrephes cederstroemi* in Lake-Michigan. Canadian Journal of Fisheries and Aquatic Sciences 52: 141-150.