

Top-Down Effects of Open-Water Salmonine Predators in the Great Lakes¹

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Abstract

Top-down influences by salmonine piscivores varied among the Great Lakes during 1970-2000, and both top-down and bottom-up influences appeared important across trophic levels. Chinook salmon grew fastest and alewives were densest in Lake Ontario, suggesting that top-down effects were least intense in Lake Ontario. Consumption of prey fish by salmonines was similar in Lake Superior to the other more productive lakes, indicating greater top-down effects there. High densities of alewife restricted to the epilimnion in Lake Ontario appear to have led to greater effects of planktivory in that lake. Large zooplankton were scarcer in Lake Ontario than in Lakes Michigan and Huron, even though total zooplankton density was as high. Contrasting with trophic cascade predictions, both total zooplankton density and *Ch a* were correlated with total phosphorus (TP), an indicator of system productivity, whereas TP did not explain variation in the density of large zooplankton. Compensation acted to limit the pervasiveness of top-down cascades. For example, although salmonine predators greatly reduced abundance of older alewife, high levels of alewife recruitment were sustained.

Introduction

The Laurentian Great Lakes (hereafter the Great Lakes) is a large, highly perturbed, and intensively managed freshwater system. All five of the Great Lakes rank among the 17 largest lakes in the world (by surface area), and the Great Lakes basin covers over 750 000 km² of North America, with a human population approaching 50-million people (Beeton et al. 1999). The Great Lakes support important commercial and recreational fisheries (Bence and Smith 1999; Brown et al. 1999), are widely used for other recreation, as a water source, and as an inland water transportation route. Once important fish and invertebrate species have gone extinct or have been greatly reduced, and exotic species have been introduced or invaded and now play a dominant role (Emery 1985; Mills et al. 1993; Eshenroder and Burnham-Curtis 1999). Populations of dominant top predators in the fish communities of Lakes Michigan, Huron, and Ontario are non-native salmonines, and the native salmonine lake trout (*Salvelinus namaycush*) is the dominant predator on Lake Superior. During the period covered by this report (1970-2000) the Pacific Chinook salmon (*Oncorhynchus tshawytscha*) was the most important non-native predator in Lakes Michigan, Huron and Ontario, and its most common prey in these lakes was the exotic alewife (*Alosa pseudoharengus*).

The top-down influence of hatchery maintained stocks of salmonines has been a dominant theme in both ecological studies of and management discussions on the Great Lakes for the past quarter century. A central and related issue has been balancing predatory demand of these hatchery-derived predators with the productivity of prey fish populations (Stewart et al. 1981; Jones et al. 1993; Lange et al. 1995). In part, this is a consequence of the development of valuable fisheries for Pacific salmon, and the fact that in Lakes Michigan, Huron and Ontario, Chinook salmon replaced lake trout as the top consumer of prey fish. Because predator recruitment was thought to be largely driven by hatchery releases, the natural feedback between recruitment and population abundance was viewed as largely decoupled (Jones et al. 1993). Some observers of Lake Michigan became concerned about potential overstocking of predators by the late 1970s (Stewart et al. 1981), and the concern reached crisis levels when dead Chinook salmon were found on beaches, Chinook salmon mortality spiked, and catch rates fell precipitously during the late-1980s (Holey et al. 1998; Madenjian et al. 2002; Benjamin and Bence 2003a, 2003b). Although Chinook salmon mortality declined in Lake Michigan by the late 1990s, following a modest reduction in stocking, concerns about potential overstocking remain (Madenjian et al. 2002). The Lake Michigan experience colored both perceptions and salmonine management across the Great Lakes, and led to caps and reductions in the number of predators stocked (Madenjian et al. 2002; Mills et al. 2003; Dobiesz et al. 2005). Even in Lake Superior, where self-sustaining populations of lake trout are the predominant predator, concerns about an imbalance between predator abundance and prey production have been expressed and evaluated (Ebener 1995; Mason et al. 1998; Kitchell et al. 2000).

Discussions of potential over-abundance of salmonines were occurring in the context of (a) evidence that these same systems were subjected to intense piscivory prior to the collapse of self-sustaining stocks of lake trout (e.g., Eshenroder and Amatangelo 2002), and (b) alewife is adversely affecting and serving as a prey for salmon and trout. Lake trout was an important part of the pre-European settlement open-water fish community of the Great Lakes, and is widely believed to have been the predominant piscivore in Lakes

Superior, Michigan, and Huron and in combination with Atlantic salmon (*Salmo salar*) in Lake Ontario (Brown 1972; Eshenroder and Burnham-Curtis 1999). Lake trout were at one time slower growing and had a more diverse diet (including substantial numbers of invertebrates) than contemporary populations (Smiley 1882; Dryer et al. 1965; Rahrer 1967; Sakagawa and Pycha 1971; Ferreri and Taylor 1996). Abundant populations of lake trout are thought to have delayed the expansion of populations of the exotic planktivores alewife and rainbow smelt (*Osmerus mordax*) in the Great Lakes (Eshenroder and Burnham-Curtis 1999; O’Gorman and Stewart 1999). By the late 1950s, Lakes Superior, Michigan, Huron and Ontario were lacking abundant top predators (due to the combined effects of fishing and sea lamprey, *Petromyzon marinus*), and by the 1960s, alewife was dominating fish biomass in Lakes Michigan, Huron and Ontario (Hansen 1999; O’Gorman and Stewart 1999), with rainbow smelt also being abundant in some areas. Where alewife (and to a lesser extent rainbow smelt) populations have become abundant, they are strongly suspected of adversely affecting native fish species both through competition for food and by predation on eggs and larvae (Crowder 1980; Eck and Wells 1987; Krueger et al. 1995; Mason and Brandt 1996; O’Gorman and Stewart 1999). Additional problems were associated with abundant alewife, including die-offs so substantial that dead alewife fouled beaches and shorelines making them unusable, and clogged water intake systems (Brown 1968). A diet consisting primarily of alewife is also linked to disease problems in salmonines, resulting from low thiamine levels stemming from thiaminase carried by alewife (Fitzsimons et al. 1999). Alewife never became an important part of the fish communities of Lakes Erie or Superior, apparently because of inappropriate thermal environment, and in these lakes rainbow smelt became important (Eshenroder and Burnham-Curtis 1999; O’Gorman and Stewart 1999).

The management response to Great Lakes fish communities dominated by low-valued planktivores was to invest in sea lamprey control and planting of hatchery-reared salmonines to re-establish top open-water predators (Kocik and Jones 1999; Hansen and Holey 2002). Following the development of successful control for sea lamprey by chemically treating streams infested with larvae (Smith and Tibbles 1980), planting of large numbers of salmonines commenced in the mid- to late 1960s. Given the long life span and relatively slow growth of lake trout, faster growing Pacific salmon were chosen to augment native predator populations, and provide for a valuable fishery. Chinook salmon became the predominant introduced predator, because they could be reared rapidly and relatively cheaply to the fingerling stage and proved widely successful in the lakes when released as fingerlings. Although naturalized Pacific salmon populations exist across the Great Lakes, hatchery-reared fish remain important. In spite of large numbers of hatchery-reared lake trout being released, self-sustaining populations of lake trout have yet to emerge except for Lake Superior and isolated areas of Georgian Bay, Lake Huron.

Trophic cascade theory argues that the top trophic level will reach abundance levels determined by system productivity and in freshwater systems spring total phosphorous levels (TP) are a reliable indicator of this productivity (Hairston et al. 1960; Fretwell 1977; Oksanen et al. 1981). Thus, for example, if we take a simplistic view of a freshwater ecosystem as consisting of piscivores, planktivores, planktonic herbivores, and phytoplankton a top-down trophic cascade would result in piscivore and planktonic

herbivores being limited by system productivity and planktivores and phytoplankton being limited by their predators. Consequently, piscivores and planktonic herbivore abundance would be correlated with TP whereas planktivores and phytoplankton would not be. Furthermore, we might expect evidence of food limitation for piscivores but not planktivores.

Top-down effects leading to trophic cascades and other forms of indirect interactions are of interest to ecologists studying the Great Lakes. First, such top-down influences have been emphasized in freshwater systems in general (Carpenter et al. 1985; Northcote 1988; Brett and Goldman 1996; Jeppesen et al. 2003). Second, in the Great Lakes, salmonines have been argued to influence lower trophic levels through their impact on alewife (Brooks et al. 1984; Scavia et al. 1986; Kitchell et al. 1987). Although stocking rather than just natural feedbacks contributes to among lake differences in piscivore abundance in the Great Lakes, as reviewed above, stocking decisions have been influenced by perceived productive capacity of the lakes. Furthermore, there is evidence that survival of stocked salmonines can be influenced by stocks of older salmonines (Elrod et al. 1995, Hansen et al. 1996, Bowlby and Daniels 2003).

Herein, we seek to identify, assess and contrast top-down effects of salmonine predators in the Great Lakes during 1970-2000. In this context, fish community and lower trophic level characteristics need to be considered in light of system productivity because top down effects are expected to act by modifying how system productivity is expressed, and both phosphorus inputs and piscivore populations have been subject to intensive management. Our emphasis is on Lakes Huron, Ontario, and Michigan during 1970-2000. By necessity, we concentrate on the more extensive observations from the 1980s and 1990s. We focus on the fish communities in Lakes Huron, Ontario, and Michigan because Chinook salmon and alewife are predominant species in these lakes. We also include Lake Superior in some fish comparisons because self-sustaining populations of the native lake trout are the top predator, and we include Lakes Erie and Superior when examining lower trophic levels to increase the range of system productivity. We compare biomass density and individual size-at-age of top predators and of their alewife prey to evaluate the extent to which these fishes are resource limited in different lakes. In addition, we compare estimates of prey fish consumption by top predators. We also consider temporal dynamics as indications of potential cause-effect relationships, and when making comparisons of the fish communities we consider differences among the lakes in the plankton communities, in TP, and in fish distribution. We specifically examine correlations of zooplankton and phytoplankton abundance with spring TP in light of trophic cascade expectations.

The analyses reported here are based on time-series developed during 2003-2005. To some extent new time-series data and information developed since then needs to be considered when interpreting the analyses reported here. Most importantly in this regard is a more complete time-series of zooplankton abundances across the Great Lakes that standardizes for changes in survey methodology, the availability of time series of algal biomass, and new results that speak to the limitations of the fish bottom trawl survey in Lake Superior (e.g., Yule et al. 2008).

Top predator abundance, prey consumption, and predator size-at-age

Based on quantitative stock assessments of predators, we considered top predator abundance from Lake Michigan, the main basin of Lake Huron, Lake Ontario, and

eastern US waters of Lake Superior. We restricted our attention to combined biomass of Chinook salmon and lake trout because these two species make up the bulk of prey consumption in each of the Great Lakes (70-80% in Lakes Michigan, Huron and Ontario (Jones et al. 1993; Dobiesz 2003; Szalai 2003) and nearly all consumption in Lake Superior (Kitchell et al. 2000)) except Lake Erie, and because estimates for these species are more readily available. We consider estimates of prey consumption and biomass because biomass turnover rate for lake trout exceeds that of Chinook salmon, sometimes by more than an order of magnitude, and thus estimates of predator consumption are better measures of use of the system's productivity than standing stock estimates.

Biomass density of lake trout and Chinook salmon reached higher levels in Lakes Michigan and Ontario than in Lake Huron (Figure 1), and lake trout densities were strikingly higher in eastern Lake Superior (note the different scale) than the combined lake trout and Chinook salmon density in the other lakes. In contrast, annual consumption of prey per hectare is much more similar among lakes (Figure 2). The highest rate of consumption was in Lake Ontario during the mid-1980s, and near the end of the 1990s, consumption per hectare was similar in Lakes Michigan, Ontario and Superior. Consumption per hectare, like biomass density, was lowest in Lake Huron, but the difference was not as pronounced as for biomass. Higher consumption per hectare in Lake Ontario than in the other lakes after the 1980s does not just reflect a difference in biomass, as higher consumption per unit biomass is needed to support the higher growth rate of Chinook salmon in Lake Ontario.

Comparisons of predator size-at-age and trends over time provide some clues to the extent to which these fish were limited by their food supplies. Chinook salmon reached sizes at age 3 in Lakes Michigan and Huron during the 1970s that are similar to large sizes seen in Lake Ontario during the 1980s and 1990s (Figure 3). When Chinook salmon reached their largest sizes, nearly all age-3 fish were mature, whereas a substantial number delayed maturity to age-4 or later when growth declined (Dobiesz 2003; Szalai 2003). Patterns of change in size suggest that Chinook salmon experienced increasing food limitation over time in Lakes Michigan and Huron, although detailed analysis suggests this might occur largely for young fish in Lake Huron (Dobiesz 2003) and at later ages in Lake Michigan (Szalai 2003).

We did not compare size-at-age between lake trout in Lake Superior and the other lakes because of large differences in available thermal habitat among lakes. Nonetheless, size-at-age of lake trout in Lake Superior declined substantially between the 1970s and 1990s (Sitar 2002; Bronte et al. 2003; Fig. 4), which suggests that food became increasingly limited for top predators in that lake as their abundance increased.

In Lakes Ontario, Michigan, and Huron, temporal trends in lake trout size-at-age were more modest or not evident. For example, in Lake Michigan, size-at-age of lake trout did not trend through time (Jonas et al. 2002a, 2002b, 2002c), and whole-lake variation did not appear to be related to prey density, so Szalai (2003) concluded that lake trout had a higher search rate for prey than Chinook salmon and fed near maximal rates. Likewise, Eby et al. (1995) concluded that growth rate of lake trout did not appear to be related to prey density across a wide range of densities in the Great Lakes. Contrasting with these observations, increments in size of young (ages 2 and 3) lake trout were correlated with prey fish abundance in Lake Ontario, whereas apparent growth of older ages of lake trout was not related to prey abundance (Elrod et al. 1996). Elrod et al. (1996) speculated that

a relationship between growth and prey abundance for older lake trout might be obscured by size-selective mortality, and also noted that size-at-ages 2-4 for lake trout were greater in Lake Ontario than the same ages (and strains) in Lake Michigan, whereas older fish were more similar in size. This suggests faster growth of young lake trout and slower growth of older lake trout in Lake Ontario, which might reflect the abundance of smaller prey fish in that lake, although differences in size-selective mortality could be contributory. Madenjian et al. (1998) found that smaller lake trout grew slower and large lake trout grew faster on an offshore reef in Lake Michigan, and that these differences corresponded to a scarcity of small prey fish and an abundance of large prey fish offshore.

Prey fish abundance and size-at-age

System productivity and predation have been influential determinants of prey fish densities. Estimates of prey fish biomass density for Lakes Michigan, Huron, western Lake Superior, and Lake Ontario, although based on different sampling methods, illustrate that prey fish biomass was substantially higher in Lake Ontario than in the other lakes in 1990, remained higher following declines during the 1990s, and was generally lowest in western Lake Superior (Figure 5). It is important to note that prey biomass estimates for Lake Superior are entirely based on daytime bottom trawls. Yule et al. (2007 & 2008) effectively argued that this survey underestimates fish biomass, with the most marked underestimation (on the order of 75 fold) for large cisco (>200 mm). Our interpretation of these results, however, suggests that Lake Superior most likely still has the lowest biomass density of prey fish, particularly of smaller sizes, among the Laurentian Great Lakes, this is an issue that warrants future analysis. The decline in prey fish biomass for Lake Ontario shown in Figure 5 may be exaggerated because the 1990 hydroacoustic survey was done in the fall and later surveys were done in late summer when fish distribution is markedly different. Moreover, biomass indices from bottom trawl surveys do not show as pronounced a decline. Higher prey biomass in Lake Ontario than in Lake Michigan was also reported by Mason et al. (2001), though they compared Lake Ontario in 1990 to Lake Michigan in 1987. Consistent with these patterns, O’Gorman and Schneider (1986) ranked adult alewife densities as southern Lake Ontario (1978-1982) > Lake Michigan (1967-1982) > western Lake Huron (1973-1982). They also reported higher alewife recruitment as yearlings in Lake Ontario than in Michigan or Huron (which were similar). Relative densities of prey fish reported here for the different lakes correspond in rank order to estimates of the magnitude of prey consumption by planktivores reported elsewhere for Lakes Superior, Michigan, and Ontario (Rand et al. 1995; Johnson et al. 1998). Temporal declines in prey fish biomass on Lakes Michigan and Huron, at least through the mid-1990s, are less severe than was suggested by some time-series indices of abundance (e.g. Szalai et al. 2003), primarily because our lake-wide biomass estimates include age-0 alewife and rainbow smelt, with an adjustment for different catchability of the two species.

Abundance of young, age-0 or age-1, alewife and rainbow smelt did not initially decline as stocks of older planktivores declined, which suggests that these species are productive at low stock sizes (Madenjian et al. 2002; Szalai 2003; O’Gorman et al. 2004; Madenjian et al. 2005). Trawl indices of age-0 alewife abundance in Lake Michigan declined in the late 1990s, which could partly reflect an earlier timing of the survey in those years as well as changes in predation intensity on age-0 fish prior to the fall survey.

Much of the decline in total prey-fish biomass density from the 1970s through the 1990s across Lakes Michigan, Huron and Ontario was due to a decline in survival resulting from increased densities of top predators (Madenjian et al. 2002; Mills et al. 2003; Dobiesz et al. 2005). Support for this view includes both that declines followed buildup of predator populations by stocking and that model-based calculations show that predators caused substantial mortality.

An important role for system productivity in determining prey biomass is suggested by the fact that prey fish densities in the different lakes have generally had the same rank order as offshore measures of spring total phosphorus concentrations (TP), which is a predictor of primary production. Notably, the same general patterns are evident for young alewife (age-0 or age-1; O’Gorman and Schneider 1986; Mason et al. 2001; unpublished data compiled for Figure 5), where differences in predation would be less influential. Top predators cannot explain the ordering among Lakes Huron, Michigan, and Ontario because they were generally most dense where prey fish were most dense. Temporal patterns in Lake Ontario also argue for a role of system productivity. O’Gorman et al. (2004) found that both predators and TP (as well as water temperature) explained interannual variation in alewife recruitment at age 2 (in the spring) in Lake Ontario. Furthermore, prey-fish biomass declined in Lake Ontario during the 1990s in conjunction with a decline in TP when predator density also declined, although other changes (proliferation of dreissenids, collapse of *Diporeia* populations, colonization of *Cercopagis pengoi*, and large-scale shifts in fish distributions (Mills et al. 2003)) were probably also involved. In contrast with O’Gorman et al.’s results for Lake Ontario, Madenjian et al. (2005) found that in Lake Michigan recruitment of adult alewife (in the fall) was negatively associated with salmonine predation and uncorrelated with TP. We suspect these differences reflect the fact that TP had declined substantially in Lake Ontario and had not in Lake Michigan.

In Lake Ontario and, more recently, Lake Michigan, declines in alewife growth have also contributed to lowering prey fish biomass (O’Gorman et al. 1997a, 1997b; Madenjian et al. 2003). Comparisons of alewife mass-at-age provide some clues to the extent to which these fish were limited by their food supplies. Mass at age 1 in fall was similar across the lakes and for an early (1983-1986 year classes) and later (1996-1999 year classes) time period, but increases in mass after age 1 were substantially less in Lake Ontario (Figure 6). In Lake Ontario, alewife size-at-age declined sharply during the mid-1980s (before the growth illustrated for the early period in Figure 6), largely due to decreased growth during the second year of life (O’Gorman et al. 1997a, 1997b), coincident with a decrease in zooplankton density (Johannsson et al. 1998). O’Gorman et al. (1997a) found that growth of age-1 alewife was affected by competition with age-0 alewife for zooplankton, and Owens et al. (2003) argued that decreased growth from age-1 to age-2 was due to a scarcity of zooplankton. Mass-at-age did not appear to have changed markedly in Lake Ontario after the 1980s (Figure 6). In Lake Michigan size-at-age remained relatively stable through 1994, but body condition and mass-at-age dropped abruptly in 1995 for all fish age-1 and older in the fall (Madenjian et al. 2003), and energy density also had declined by the late 1990s (Madenjian et al. 2006). Consequently, the difference in mass-at-age between Lakes Michigan and Ontario was not as extreme for the 1996-1999 year classes as it was for the 1983-1986 year classes (Figure 6). Madenjian et al. (2003) suggested that the decline in mass-at-age of alewife

in Lake Michigan could have been a response to the decline in the density of the large benthic invertebrate *Diporeia*. In Lake Huron, mass-at-age declined for ages 2 through 5, but to a lesser extent for ages 3 and older than on Lake Michigan, so size-at-age in these two lakes became more similar.

After the decline in size-at-age of alewife in Lakes Michigan and Huron, alewife remained larger at age 3 and grew substantially faster after that age than alewife in Lake Ontario. Although zooplankton densities were similar and sometimes higher in Lake Ontario than in Lake Michigan, large zooplankton were scarcer in lake Ontario (see below). In contrast with older ages, age-0 and age-1 alewife may have been able to better use abundant small zooplankton in Lake Ontario, which could explain why size of age 1 fish in the fall was always similar in Lakes Michigan and Ontario. Consistently poorer growth of alewife after age-2 in Lake Ontario can be explained by the lack of access to large invertebrate prey that results from their epilimnetic distribution (Mills et al. 1992; Madenjian et al. 2003).

Zooplankton and Phytoplankton

A very simple conceptual model of Great Lakes food webs is to view them as chain like, consisting of four main trophic levels: piscivores, planktivores, herbivorous zooplankton, and phytoplankton. In this context, and treating spring total phosphorous as a measure of potential primary production, a system strongly controlled by piscivores would exhibit a positive relationship between summer zooplankton biomass density and spring total phosphorus (TP) concentration, and no relationship between summer phytoplankton biomass and TP. These patterns would suggest a zooplankton community limited by system capacity, rather than planktivore predation, and a phytoplankton standing crop limited by zooplankton grazing. Of course the actual food web is more complex, including predatory invertebrates, a topic we return to below.

Contrasting with such expectations, there is a positive correlation between summer log algal biomass density (represented by log chlorophyll *a* (Ch *a*)) and spring log TP during 1983-2002 based on data collected by the Great Lakes National Program Office ($r^2 = 0.38$, $p < 0.001$, $n = 156$, Figure 7). We saw no evidence that deviations about the relationship were related to densities of either predators or pelagic prey fishes (e.g., by attempting to relate residuals from a Ch *a* versus TP regression to trends reported above for prey and predator fishes). Both for phytoplankton and below for zooplankton we use densities on a volumetric basis instead of the per unit area basis used for fish. These volumetric densities are proportional to areal densities for all the lakes excepting the much shallower Lake Erie.

In the early 1970s, the rank order of primary productivity among the Great Lakes was Erie > Ontario > Michigan > Huron > Superior (Vollenweider et al. 1974). This rank order was maintained through the 1990s as indicated by TP and chlorophyll *a* concentrations. However there had been notable declines in TP in Lakes Erie and Ontario, whereas TP has changed relatively little in the open waters of Lakes Superior, Michigan, and Huron. After the period covered by our analyses there is evidence of a decline in TP in Lake Huron (see review of this topic in Liskauskas et al. 2008). Of some note is a decline in TP in Lake Ontario during the 1990s (Mills et al. 2003), so that the difference in primary productivity between this lake and Lake Michigan noted by Johengen et al. (1994) in the early 1990s was not as large by the turn of the century.

We evaluate patterns in zooplankton abundance based on GLNPO data from 1998 and 1999, which was collected using consistent methods across the lakes (Barbiero et al. 2001), together with data collected on Lake Ontario in 1990-1991 using similar methods.¹ There was a significant positive correlation between log total summer crustacean zooplankton density (per unit volume) and log spring TP concentration, although the correlation was weaker than for Ch *a* ($r^2 = 0.24$, $p = 0.01$, $n = 23$, Figure 8). For just small (<1 mm) crustacean zooplankton, TP explains a similar amount of variation although the slope of the relationship is steeper ($r^2 = 0.23$, $p = 0.02$, Figure 8), whereas for larger (≥ 1 mm) crustacean zooplankton TP is not explanatory ($r^2 = 0.03$, $p = 0.40$, Figure 8). The strongest zooplankton relationship exists between spring TP and cladoceran zooplankton, excluding the large predators *Leptodora*, *Bythotrephes* and *Cercopagis* ($r^2 = 0.40$, $p = 0.001$, Figure 8). The relationships between zooplankton density and spring TP concentration suggest to us that zooplankton community size is being determined by both primary productivity and planktivory (along with other factors), with varying levels of planktivory in turn being partially a response by planktivores to top predators.

While the near-zero correlation with TP for larger zooplankton is consistent with a planktivore effect, in most cases a majority of the biomass in this category was contributed by larger, deep-living calanoid copepods (e.g., *Limnocalanus macrurus*, *Senecella calanoides*) and/or cyclopoid copepods, which by and large are not strictly herbivorous. However, a closer examination of crustacean community structure provides additional evidence of impacts of planktivory, particularly in Lake Ontario, where the highest densities of planktivores occurred (excluding Lake Erie where we did not evaluate this) and where alewife are constrained to feed in the epilimnion, increasing their impact on zooplankton (Mills et al. 1992). In August, 1998, average cladoceran length (excluding the large predators *Leptodora* and *Bythotrephes*) was substantially less in both Lake Ontario (0.50 mm) and the eastern basin of Lake Erie (0.36 mm), compared to Lakes Superior, Michigan and Huron (0.91, 1.19, 1.05 mm, respectively). Also, compared to the upper lakes a much higher percentage of crustacean biomass in Lake Ontario was contributed by cyclopoid copepods (Barbiero et al. 2001), which are not preferred fish food items. Furthermore, the especially low density of large zooplankton in Lake Ontario in 1990 corresponds to a time when planktivorous fish were abundant.

The roughly similar zooplankton biomass densities for Lakes Ontario and Michigan shown in Figure 8 are consistent with those reported by Barbiero et al. (2001); the much higher zooplankton densities they reported for Lake Ontario than for Lakes Huron or Michigan were on a numerical basis. When considering the plankton community structure in terms of functional groups, Fahnenstiel et al. (1998) argued that the Great Lakes were surprisingly similar and that much of the variation could be explained by physical factors. Our interpretations of the role of planktivores based on zooplankton size structure and relationships of zooplankton density to TP are not inconsistent with

¹ Data provided by G. Sprules, Univ. of Toronto, and are averages for three (1991) or four (1990) samples from offshore locations, collected during July or August with a 50 cm, 110 um metered tonet hauled from near bottom to surface, or from 100 m to surface if the station was deeper than 100 m. Samples were processed by microscope using a digital measuring caliper for body size, and these lengths were converted to fresh masses using a standard set of regressions, and subsequently converted to a dry mass basis based on 10:1 conversion factor.

their observations. For example, they report the smallest mean daphnid size for Lake Ontario, consistent with the patterns in zooplankton size-structure we report. In contrast with the positive correlation between zooplankton biomass density and TP we report, they found higher biomass densities of crustacean zooplankton in Lake Michigan than in Lake Ontario during August 1993-1995, with densities for Lake Huron being intermediate. Thus for those lakes and years, zooplankton biomass density may not have been related to system productivity.

Discussion

Due to high mortality caused by humans and sea lamprey, piscivore density fell to low levels across the Great Lakes, and in the early 1960s, densities of planktivores were high, especially in Lakes Michigan, Huron and Ontario (Madenjian et al. 2002; Mills et al. 2003; Dobiesz et al. 2005). High abundance of planktivores may have been made possible because piscivores were scarce (Eshenroder and Burnam-Curtis 1999; O’Gorman and Stewart 1999), which implies a trophic cascade, with humans and sea lamprey as the top trophic level. High densities of planktivores were thought to have had substantial effects on the zooplankton community, based on observations that larger species were replaced by smaller species in Lake Michigan when planktivores were abundant (Wells 1970), consequently cascades to the lower trophic levels seemed possible (Brooks et al. 1984; Scavia et al. 1986; Kitchell et al. 1987; Hewett and Stewart 1989).

Although the strength of Wells’ original evidence has been questioned (Evans 1992), the general link between abundance of planktivores and zooplankton size composition in Lake Michigan has been borne out (Madenjian et al. 2002). As Evans (1992) pointed out, changes in phytoplankton density that were tied to changes in open-water planktivory (Brooks et al. 1984) occurred inshore, rather than offshore, where most top predators lived. Barbiero et al. (2005) reported that offshore zooplankton biomass in Lake Huron was substantially higher during 1998-2002 than in the 1980s, and this change appeared to coincide with a decline of planktivore abundance. The temporal pattern reported by Barbiero et al. (2005) relied on comparisons across years as sampling methods changed, but subsequent analyses of sampling method effects and standardizations have confirmed this result. Notwithstanding this result from Lake Huron, it appears as though cascades have not dominated the dynamics of overall density of zooplankton and phytoplankton in offshore waters of Lakes Michigan, Huron, or Ontario. This claim is perhaps most obvious for Lake Michigan, where spring total phosphorus in offshore waters has not changed greatly over a three-decade period (Barbiero et al. 2002; Madenjian et al. 2002). In Lake Michigan, piscivore abundance increased substantially, thereby leading to a reduction in densities of planktivores, particularly at older ages. However, these changes in upper trophic levels did not appear to affect total zooplankton density (Makarewicz et al. 1995; Madenjian et al. 2002) or total algal density (Evans 1992; Madenjian et al. 2002). We found that planktivory has not completely disrupted the correlation between zooplankton biomass and total phosphorus in the Great Lakes, although it is possible it has acted to weaken the relationship. In contrast, there was no discernible relationship between large zooplankton abundance and TP. Furthermore, large zooplankton were less dense in Lake Ontario than in Lakes Michigan or Huron in 1998-1998, despite the long term trend in Lake Ontario since about 1983 toward larger zooplankton in response to a decline in planktivore abundance (Mills 2003; Johannsson 2003). Likewise, Dobiesz et

al. (2005) reviewed changes in the zooplankton community of Lake Huron and noted a shift toward daphnids and away from bosminids, during the 1980s and 1990s. Although this pattern is consistent with decreased planktivory, the emergence of exotic predatory cladocerans may have played a role. We believe that much more can be learned through additional analyses of updated and extended time series on zooplankton and algal biomass, disaggregated by species and size class, in the context of changes in higher trophic levels. These time-series estimates were not available when the analyses reported here were undertaken.

Nevertheless it is clear that strong trophic cascades do not dominate the patterns in the data we did analyze. We offer several potential explanations for why strong trophic cascades to the lowest trophic levels were not obvious across the open waters of the Great Lakes. First, our perceptions of trends in planktivore abundance are largely driven by older fish, which are vulnerable to capture in trawls. These older and larger fish tend to be most heavily affected by piscivores, while abundant age-0 fish consume a large portion of the zooplankton (Hewett and Stewart 1989). Compensatory recruitment appears to be the rule among Great Lakes prey fish (Jones et al. 1993; Madenjian et al. 2002; Mills et al. 2003; O’Gorman et al. 2004; Madenjian et al. 2005; Dobiesz et al. 2005), so young planktivores are not reduced in proportion to the spawning stock that produced them and even can be more abundant in the face of planktivory. In addition, compensation may occur at the community level among zooplankton, so species most vulnerable to planktivorous fish are reduced in abundance, whereas release from competition or invertebrate predators could allow less vulnerable species to become more abundant (Hall et al. 1976; Hart 2002; Blumenshine and Hambright 2003). Intraguild predation (feeding on more than one trophic level) may damp trophic cascades (Bowlby and Roff 1986, Polis and McCormick 1987). Such predatorion occurs among zooplankton species in the plankton food web which has become more complex with the addition of Dresseid veligers and exotic predatory cladocerans, and also likely occurs among members of the nominal trophic levels of fish. The predatory cladocerans have had substantial impacts on zooplankton community make-up (Barbiero and Tuchman 2004), although higher summer densities of predatory cladocerans in Lake Ontario than in Lakes Michigan or Huron (Barbiero et al. 2001) argues against high abundances of small zooplankton in Lake Ontario being an indirect effect through these predators. Barbiero and Rockwell (2008) discuss the influence of predatory cladocerans, particularly *Bythotrephes longimanus*, on zooplankton community structure.

A corollary of compensation within the plankton community is that top-down control could influence the zooplankton community, but not produce a dramatic cascade on density of the entire groups. Although variations in planktivory have not clearly altered zooplankton community filtration rates, additional compensation might also occur among algae species (e.g. via an increase in inedible types). In addition, the microbial food web will influence how changes in zooplankton abundance are translated to phytoplankton (Fahnensteil et al. 1998; Munawar et al. 2003). An improved understanding of the zooplankton and microbial food webs will help in predicting how top-down and bottom-up influences will operate in the Great Lakes in the future.

A final explanation is that the Great Lakes are not fully and equally saturated with top predators. For example, consumption by piscivores was similar in Lake Superior to that in the less productive Lakes Michigan, Huron or Ontario during the late 1990s. Thus,

self-sustaining stocks of lake trout in Lake Superior are clearly exerting greater top-down pressure than hatchery supplemented stocks of piscivores exert in the other lakes. In this regard the piscivore communities of Lakes Huron, Ontario, and Michigan may not providing the same function as the native lake trout does in Lake Superior.

Lake Ontario stands out as experiencing the most intense planktivory, and this remained so even following reductions in planktivore densities that started in the early 1980s. This might seem a puzzling result because among Lakes Michigan, Huron and Ontario, Lake Ontario has had the densest population of piscivores, which consumed the most prey per unit area. Part of this difference may reflect differences in primary productivity among lakes. An additional potential explanation rests in the size and topology of the lakes, with Lake Ontario having more shoreline per unit area. The contrast between Lake Michigan and Lake Ontario was noted by Rand and Stewart (1998a), who suggested that higher alewife densities in Lake Ontario are driven by higher inshore production of age-0 alewife. Competition for larger zooplankton and lack of access to large benthic invertebrates appears to limit alewife growth after the second year of life in Lake Ontario, which combined with high mortality rates of larger individuals due to piscivore predation, led to low densities of larger alewife. More intense planktivory may have been a characteristic of Lake Ontario, versus Lakes Michigan and Huron, prior to the reestablishment of large predator populations in any of these lakes. Watson and Carpenter (1974) remarked on the greater abundance of larger zooplankton in Lake Huron in 1971 than in Lake Ontario in 1970, and Chinook salmon apparently never quite realized as high a growth rate in the other lakes as they did in Lake Ontario.

Chinook salmon had grown substantially faster in Lake Ontario than in Lakes Michigan or Huron, and this appears to run counter to Mason et al.'s (1995) report that Lakes Michigan and Lake Ontario provide pelagic habitat with similar growth potential for Chinook salmon. Their results were, however, for early August, and may not extrapolate to season-long differences. In early August a larger proportion of alewife biomass is at temperatures near to and above 20°C in Lake Ontario than in Lake Michigan (Mason et al. 1995), and positive growth by Chinook salmon is not possible at these temperatures (Wurster et al. 2005). These results are consistent with occupation of warmer temperatures, poor body condition, and formation of "growth checks" on some Chinook salmon scales and otoliths during the summer in Lake Ontario (Wurster et al. 2005). In contrast with annual growth of Chinook salmon, larger lake trout grow more slowly in Lake Ontario than in Lake Michigan, although differences in size selective mortality may contribute (Elrod et al. 1996). If over the year Chinook salmon are better able to make use of small pelagic prey fish than lake trout of the same size, this would explain the difference between the species. Szalai (2003) emphasized the importance of knowledge of the search rate of piscivores for their prey to evaluate different policies for stocking piscivores in Lake Michigan. We believe an updated analysis to estimate piscivore search rates based on relating piscivore growth to prey fish abundance across lakes and years, following the general approach developed by Eby et al. (1995) (see also Rand 1994; Dobiesz 2003; Szalai 2003), would help meet this need, especially given more recent observations of declines in lake trout growth in locations other than Lake Superior (e.g., He et al. 2007).

Here we focused on top down effects and did not directly address the issue of whether predator populations are balanced with prey productivity. Our comparisons have some

relevance to this issue. Among the lakes dominated by Chinook salmon, Chinook salmon appears to be the least food limited in Lake Ontario. Thus, our analyses suggest that risks of events associated with predator food limitation, such as a salmon die-off, are probably less in that lake than in Lakes Huron and Michigan. Even in Lake Ontario concerns regarding over abundance of salmonines have been expressed, leading to reductions in salmonine stocking (Jones et al. 1992; Lange et al. 1995; Rand and Stewart 1998a, 1998b). Szalai (2003) found in her analyses for Lake Michigan that only when lake-wide abundances of all piscivores were reduced to levels that generally allowed near maximal Chinook salmon growth could the risk of alewife population collapse and high Chinook salmon mortality be substantially reduced. Thus, relatively low stocking and high alewife densities may be necessary to manage primarily for a large and consistent Chinook salmon fishery. This appears to be incompatible with levels of piscivory associated with the rehabilitated lake trout stocks seen in Lake Superior during the late-1990s (see also discussion in Bence et al. 2008). Management that limits predator abundance to sustain Pacific salmon stocks will likely keep Great Lakes ecosystems from experiencing the same level of top-down influence that might be expected from lake trout recovery like that seen in Lake Superior.

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Appendix. Methods used to estimate prey biomass density in Lake Ontario during 1997-2002.

Distributions of numbers of targets identified by hydroacoustic gear were summarized for the epilimnion, metalimnion, and hypolimnion. All targets greater than -58 dB in the hypolimnion were assumed to be age-1 or older rainbow smelt. Metalimnion and hypolimnion targets were grouped into three dB categories, and the distribution was separated into three normal modes using least-squares to estimate parameters of the three normal distributions. Targets in the largest mode were assumed to be age-1 or older alewife. For age-1 and older alewife and age-1 and older rainbow smelt in the hypolimnion, numbers were converted to biomass based on the average mass of age-1 and older fish in that stratum for that year. Targets in the second mode were treated as planktivores of unknown species. We calculated mass associated with targets in each dB category under the assumption that targets were alewife or rainbow smelt and averaged these results. Relationships used to convert target strength to mass were: rainbow smelt, Total length = 1.09 * Fork length, mass (g) = 0.0000026(fork length (mm)^{3.219}), target strength (dB) = 19.9 * log₁₀(total length(cm)) - 67.7; alewife, Total length = 1.146 * Fork length, mass (g) = 0.0000057(fork length (mm)^{3.144}), target strength (dB) = 6.98 * log₁₀(mass(g)) - 50.07.

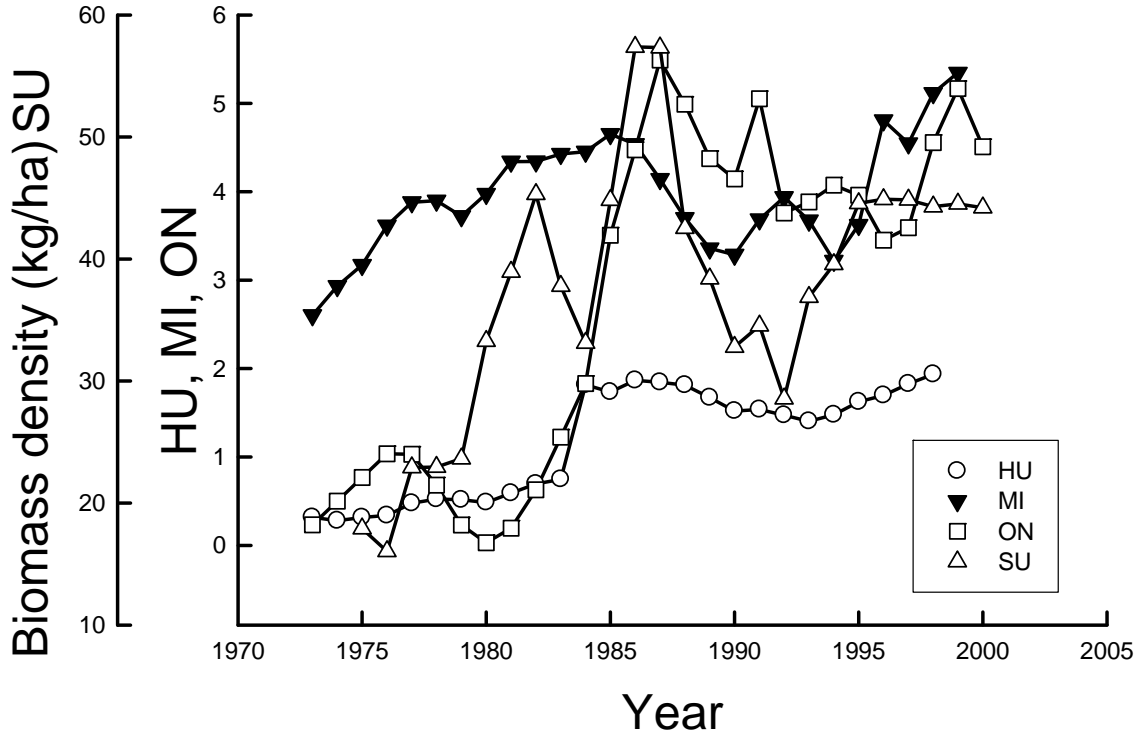


Figure 1. Estimates of biomass density (kg/ha) of lake trout and Chinook salmon combined in Lake Michigan (MI), the main basin of Lake Huron (HU), Lake Ontario (ONT), and eastern Lake Superior (SU) during 1972-2000. Estimates were based on age-structured stock assessment models (Lake Michigan: Szalai (2003), Madenjian et al. (2002); Lake Huron: Dobiesz (2003), Dobiesz et al. (2005); Lake Ontario: unpublished analysis; Lake Superior: 1836 treaty water assessments with methods as described by Bence and Ebener (2002) and expanded to account for siscowet as described by Bence et al. (2003)).

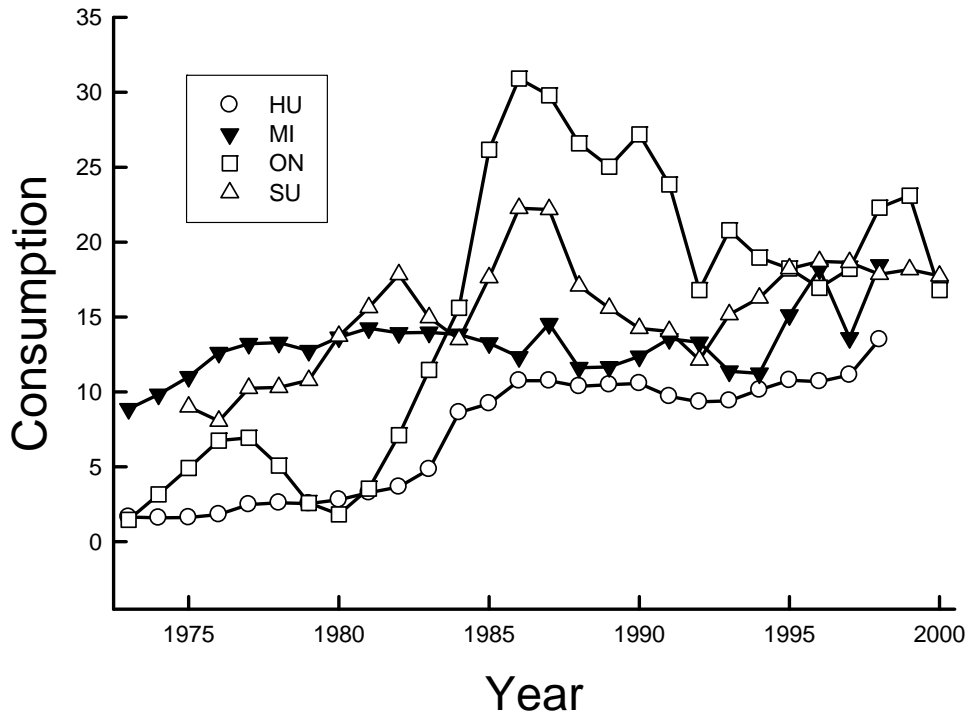


Figure 2. Estimates of consumption (kg/(ha-yr)) of prey fish by lake trout and Chinook salmon combined in Lake Michigan, the main basin of Lake Huron, Lake Ontario, and eastern US waters of Lake Superior during 1972-2000. Estimates were based on age-structured stock assessment models as in Figure 1 and application of a production/conversion efficiency approach to convert predator growth into consumption (Dobiesz 2003; Szalai 2003).

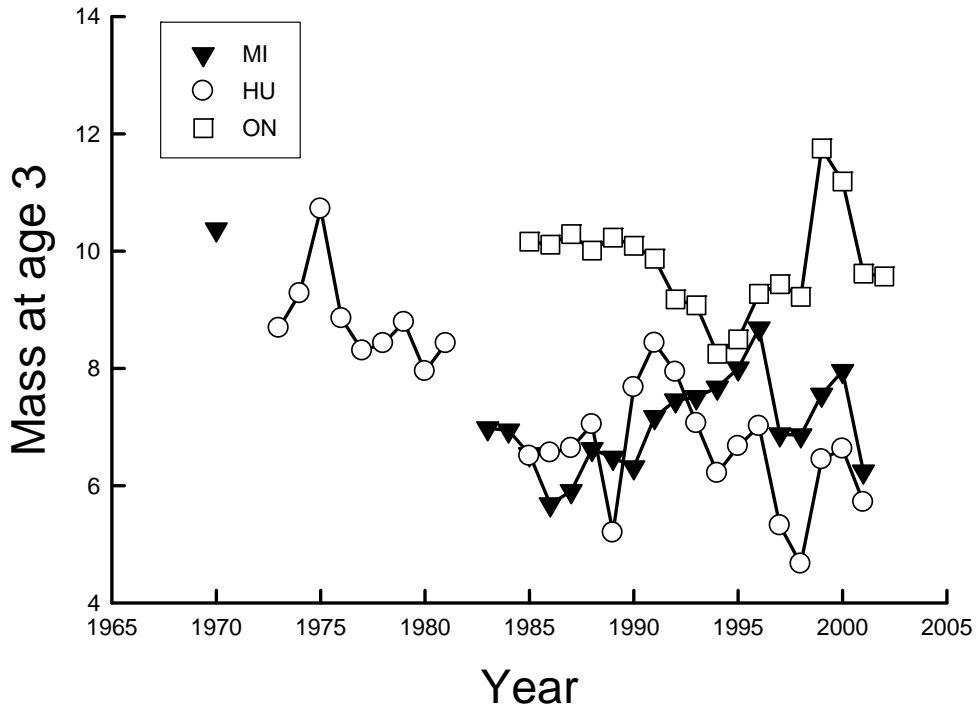


Figure 3. Chinook salmon mass at age 3 (kg) in samples from the late summer and fall recreational fisheries of Michigan’s waters of Lakes Michigan and Huron (aging by scales) and Lake Ontario (decomposition of size compositions and application of a mass-length relationship) during 1970-2000.

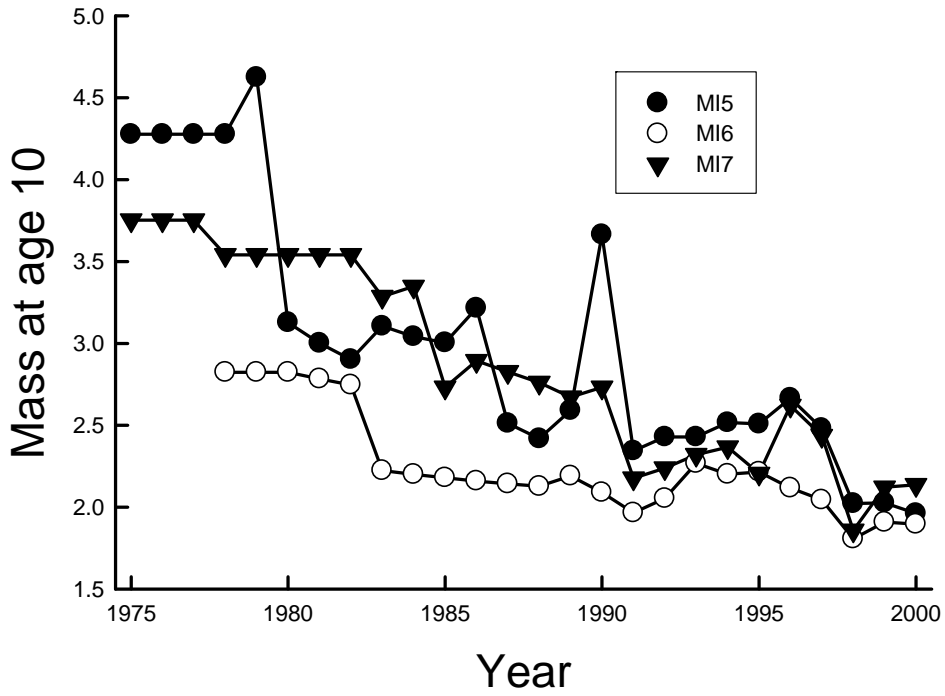


Figure 4. Lake trout mass at age 10 (kg) for three management areas (MI5, MI6 and MI7) in eastern US waters of Lake Superior. Estimates of mean mass-at-age based on Michigan DNR spring gill-net surveys, compiled for stock assessments (Bence and Ebener 2002) during 1975-2000.

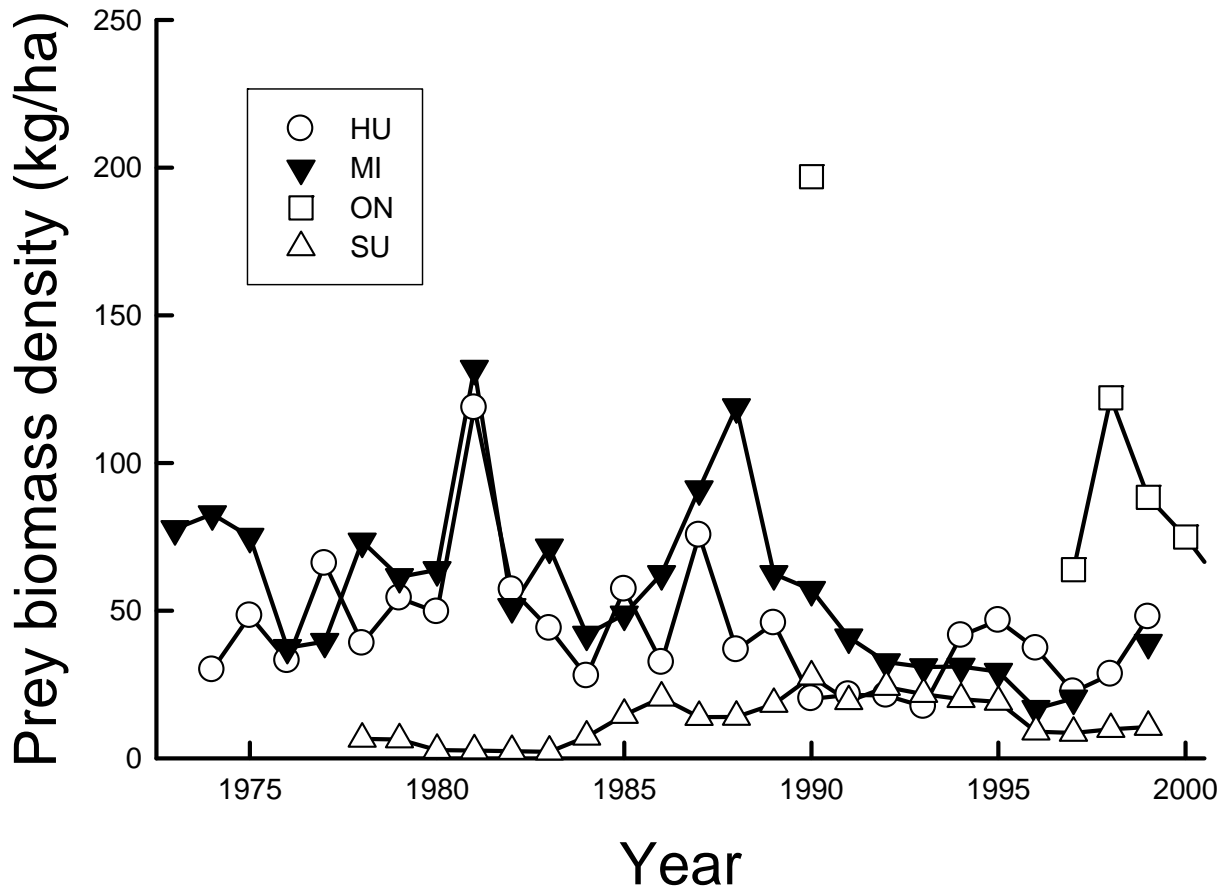


Figure 5. Prey fish biomass density (kg/ha) for Lakes Superior, Huron, Michigan, and Ontario during 1973-2000. For Lakes Michigan and Huron, prey fish biomass density is the total of age-0 bloater, alewife, and rainbow smelt in the fall in Great Lakes Science Center surveys, adjusted for catchability of different prey fish types based on hydroacoustic estimates during 1992-1996. Lake Ontario values are from a fall 1990 hydroacoustic survey estimate of all forage fish from Mason et al. (2001), and unpublished estimates from a OMNR/NYDEC survey during 1997-2000 (See appendix). Estimates for Lake Superior are based on unadjusted swept area estimates calculated from a bottom trawl survey (Bronte et al. 2003).

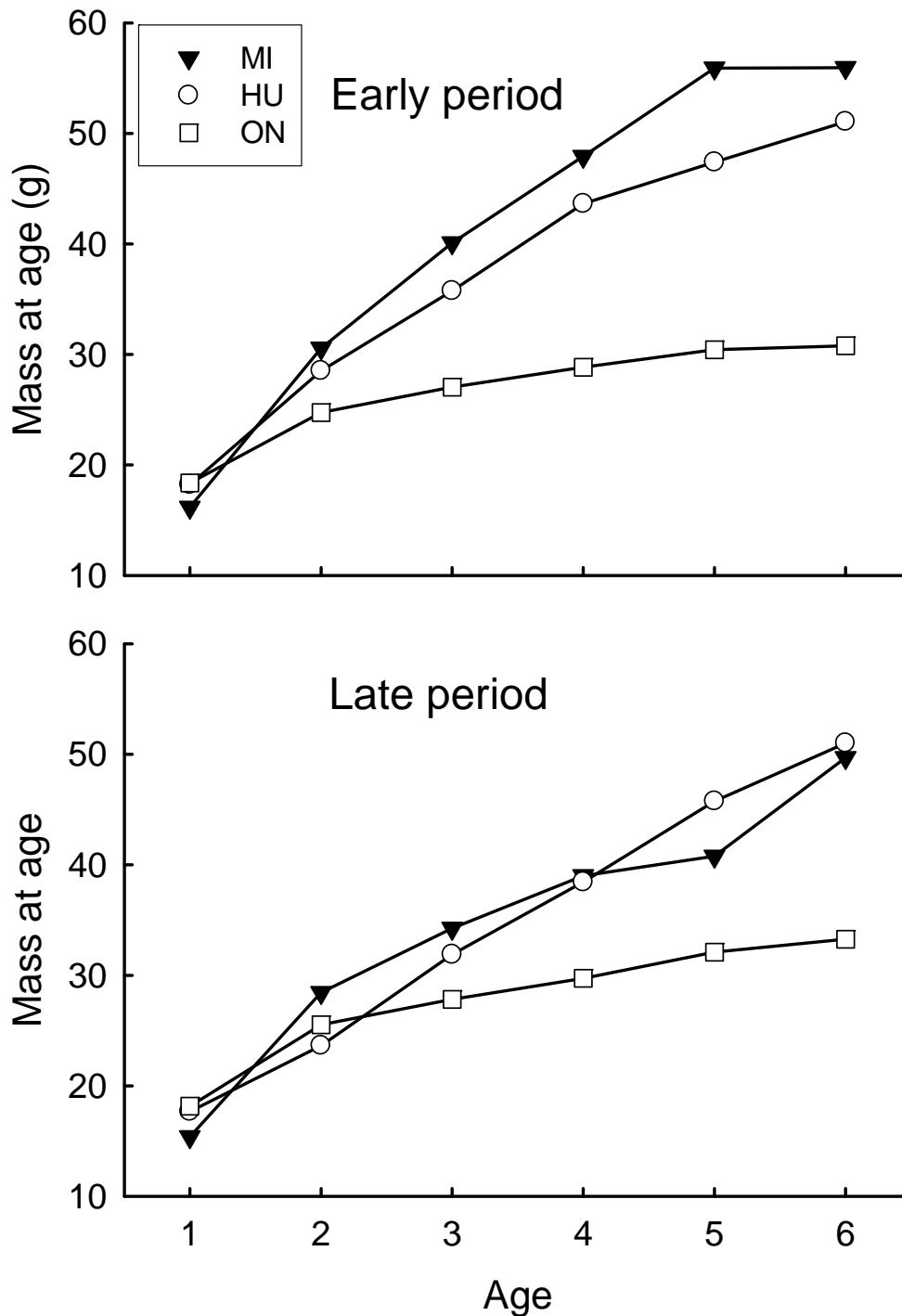


Figure 6. Alewife mass-at-ages 1-6 in the fall for Lakes Michigan (MI), Huron (HU), and Ontario (ON) averaged over “early” (E) year classes from 1983 through 1986 and “late” (L) year classes from 1996 through 1999. Values are from USGS trawl surveys in fall on Lakes Michigan and Huron and spring and fall surveys on Lake Ontario. Mass-at-age was estimated from mean length-at-age and a length-mass relationship. Mean length-at-age was determined from observed length compositions and age-length keys. For Lake Ontario, fall trawl data was limited, so mean length at age $t+1$ in the spring was used as an estimate of mean length at age t in the fall of the previous year. Fall data were used to derive mass-length conversions, which differed between spring and fall.

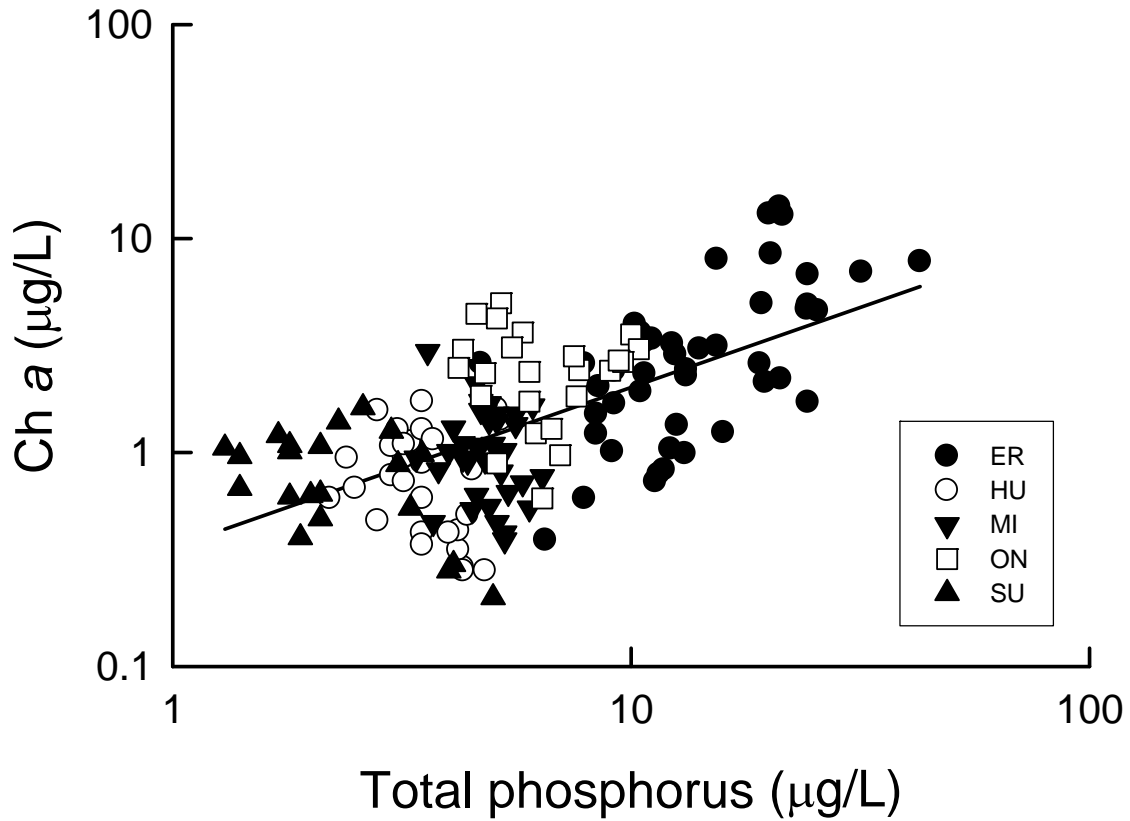


Figure 7. Relationship (log-log scale) between summer chlorophyll-*a* concentration (Ch-*a*) and spring total phosphorus concentration (TP) for 1983 through 2002, based on Great Lakes National Program Office program data. ER, HU, MI, ON, SU indicate observations from Lakes Erie, Huron, Michigan, Ontario and Superior, respectively. All values are averaged by basin for each year (three basins in ER and SU; two basins in HU, MI and ON). Ch-*a* values are epilimnetic; TP values are from the upper 20 m.

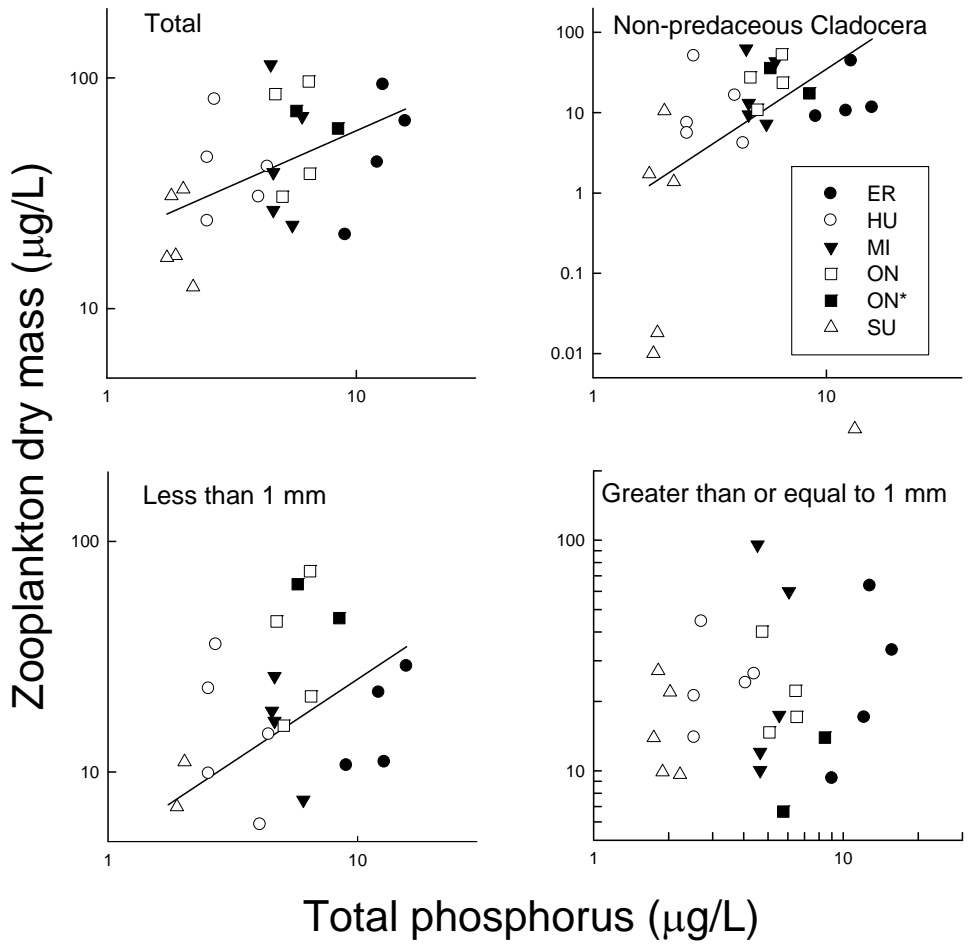


Figure 8. Relationship (log-log scale) between crustacean summer zooplankton biomass (dry mass per volume basis) and spring total phosphorus concentration (TP) for total, small (< 1 mm), large (≥ 1 mm), and cladocerans (excluding predators). Solid lines indicate regression fits to data. One zero for a Lake Superior Cladocera observation was replaced by 0.01. ER, HU, MI, ON, SU indicate observations from Lakes Erie, Huron, Michigan, Ontario and Superior, respectively. ON* indicate observations from Lake Ontario in 1990-1991.