A SYNTHESIS OF ECOLOGICAL AND FISH-COMMUNITY CHANGES IN LAKE ONTARIO, 1970-2000

TECHNICAL REPORT 67

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July 2005

A Synthesis of Ecological and Fish-Community Changes in Lake Ontario, 1970-2000

by

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TABLE OF CONTENTS

Abstract

We assessed stressors associated with ecological and fish-community changes in Lake Ontario since 1970, when the first symposium on Salmonid Communities in Oligotrophic Lakes (SCOL I) was held (J. Fish. Res. Board Can. 29: 613-616). Phosphorus controls implemented in the early 1970s were undeniably successful; lower food-web studies showed declines in algal abundance and epilimnetic zooplankton production and a shift in pelagic primary productivity toward smaller organisms. Stressors on the fish community prior to 1970 such as exploitation, sea lamprey (*Petromyzon marinus*) predation, and effects of nuisance populations of alewife (*Alosa pseudoharengus*) were largely ameliorated by the 1990s. The alewife became a pivotal species supporting a multi-million-dollar salmonid sport fishery, but alewife-induced thiamine deficiency continued to hamper restoration and sustainability of native lake trout (*Salvelinus namaycush*). Expanding salmonine populations dependent on alewife raised concerns about predator demand and prey supply, leading to reductions in salmonine stocking in the early 1990s. Relaxation of the predation impact by alewives and their shift to deeper water allowed recovery of native fishes such as threespine stickleback (*Gasterosteus aculeatus*) and emerald shiner (*Notropis atherinoides*). The return of the Lake Ontario ecosystem to historical conditions has been impeded by unplanned introductions. Establishment of *Dreissena* spp. led to increased water clarity and increased vectoring of lower trophic-level production to benthic habitats and contributed to the collapse of *Diporeia* spp. populations, behavioral modifications of key fish species, and the decline of native lake whitefish (*Coregonus clupeaformis*). Despite reduced productivity, exotic-species introductions, and changes in the fish community, offshore *Mysis relicta* populations remained relatively stable. The effects of climate and climate change on the population abundance and dynamics of Lake Ontario fish were unknown at the time of SCOL I, but a temperature-time series begun in the late 1950s in the Kingston Basin has since provided evidence of climate warming and associated fish-community changes. We should expect ecological surprises in the coming decades that will challenge scientists and fishery managers especially as they face new exotic species, climate warming, and escalating stakeholder demands on the resource. Continuous long-term ecological studies were critical for interpreting changes in Lake Ontario's fish community over the past three decades and will be essential in the future for both scientific understanding and management of the fishery.

Introduction

The Laurentian Great Lakes have been subject to accelerated ecological change since the arrival of European settlers 250 years ago. Lake Ontario and other Great Lakes ecosystems experienced numerous stresses including overfishing, colonization by exotic species, cultural eutrophication, and contaminant discharge leading to degradation in water quality, loss and change of habitat, and the decline of native-fish communities in the 1950s and 1960s. By the 1970s, Lake Ontario's major native-fish stocks had been pushed to near extinction (Christie 1972). Atlantic salmon (*Salmo salar*), deepwater sculpin (*Myoxocephalus thompsoni*), lake trout (*Salvelinus namaycush*), burbot (*Lota lota*), and coregonines (*Coregonus* spp.) had all disappeared or had seriously declined in abundance, while non-native fish such as alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*), and white perch (*Morone americana*) proliferated. Overfishing and sea lamprey (*Petromyzon marinus*) predation were also destabilizing factors in the Lake Ontario fish community. Sea lamprey predation on salmonids and burbot likely increased as the number of dams in the Lake Ontario watershed decreased and acted in concert with commercial fishing to virtually eliminate large piscivores (Christie 1972). Cultural eutrophication, a major destabilizing force on the Lake Ontario ecosystem from the 1940s to the 1970s, led to nuisance algal blooms and water-quality deterioration (Vollenweider 1968; Hurley 1970; Schelske 1991).

The sequence of events that led to a deterioration of habitat and fish stocks throughout the Great Lakes, including Lake Ontario, led to two important milestones. The first was the 1972 Great Lakes Water Quality Agreement (GLWQA) (International Joint Commission 1988) between the United States and Canada, which resulted in controls and permissible phosphorus loadings to each of the Great Lakes and marked a new era of ecosystem management and recovery. Implementation of this agreement led to a decrease in phosphorus concentrations in all the Great Lakes, including Lake Ontario, and to a process termed oligotrophication. The second was the 1971 symposium on Salmonid Communities in Oligotrophic Lakes (SCOL I) (Loftus and Regier 1972), which yielded new insights about anthropogenic stressors on fish communities in Great Lakes ecosystems. SCOL I was an important milestone in the advance of Great Lakes science and was an important stimulus leading to a broader thrust in thinking about fish and fisheries within the context of a lake ecosystem.

Christie (1972) synthesized long-term fish-community changes in Lake Ontario and examined abiotic and biotic stressors from the 1800s to 1970 to assess shifts in fish-stock abundance. The lesson learned from Christie's analysis was that, while sea lamprey predation, overfishing, and water quality were identified as primary destabilizing factors in the Lake Ontario fish community, there was a need to understand how the food web functioned. During the 1980s and 1990s, an understanding of the Lake Ontario food web increased, and it was realized that exotic fishes, particularly alewife, played a much larger role in the destruction of the original fish community than was previously believed (O'Gorman and Stewart 1999; Ketola et al. 2000). In addition, now there is a greater appreciation for the significant role humans play as a driving force in shaping the ecosystem and its food web. Attempts to restore the Lake Ontario ecosystem to historical conditions over the past 30 years through active management to reduce phosphorus, restore native species, and control sea lamprey have been impeded by anthropogenic impacts associated with exotic-species invasions, habitat modification, and climate change.

In this paper, we build upon the scientific understanding of SCOL I through assessment of the dynamics of the Lake Ontario food web from 1970 through 2000. We hypothesize that, while oligotrophication has driven the recovery process of the Lake Ontario ecosystem, the lake will not return to historical conditions but rather will take a new path in response to unplanned exotic-species introductions. Our approach was to analyze long-term data on the Lake Ontario food web and to examine driving forces that were responsible for ecological and especially fishery changes in the lake since 1970. We examine the impact of stressors associated with nutrient abatement, exotic-species introductions, and fish management on fish communities and speculate on the future of the Lake Ontario ecosystem. In our synthesis and integration of links across trophic levels, we acknowledge the importance of concurrent scientific reviews in *The State of Lake Ontario: Past, Present, and Future* edited by M. Munawar (2003). This book originated from a symposium jointly sponsored by the International Association of Great Lakes Research and the Aquatic Ecosystem Health and Management Society. The present paper forms part of the proceedings of a workshop convened at the University of Toronto at Mississauga, May 18-20,

2000. The workshop was sponsored by the Great Lakes Fishery Commission (GLFC) to revisit Great Lakes ecosystem change three decades since the SCOL I Symposium at Geneva Park, Ontario, in July 1971 and for which the proceedings were subsequently published as a special issue of the Journal of the Fisheries Research Board of Canada (Volume 29, Number 6, June 1972). A condensed version of the present paper has been published in the Canadian Journal of Fisheries and Aquatic Sciences (Mills et al. 2003).

The Lake Ontario Ecosystem

Lake Ontario (Fig. 1) ranks as the 17th largest lake in the world with a surface area of 18,960 km² (Beeton et al. 1999). The lake's watershed is dominated by forests (49%) and agriculture (39%), and 7% of the basin is urbanized (Stewart et al. 1999). Approximately 6 million people live in the watershed with nearly 70% residing in the Province of Ontario. The maximum depth of Lake Ontario's main basin is 244 m and the relatively shallow Kingston Basin with its numerous embayments, peninsulas, and islands accounts for more than 50% of the lake's shoreline. A total of 86% of Lake Ontario's inflow comes from the upper Great Lakes via the Niagara River.

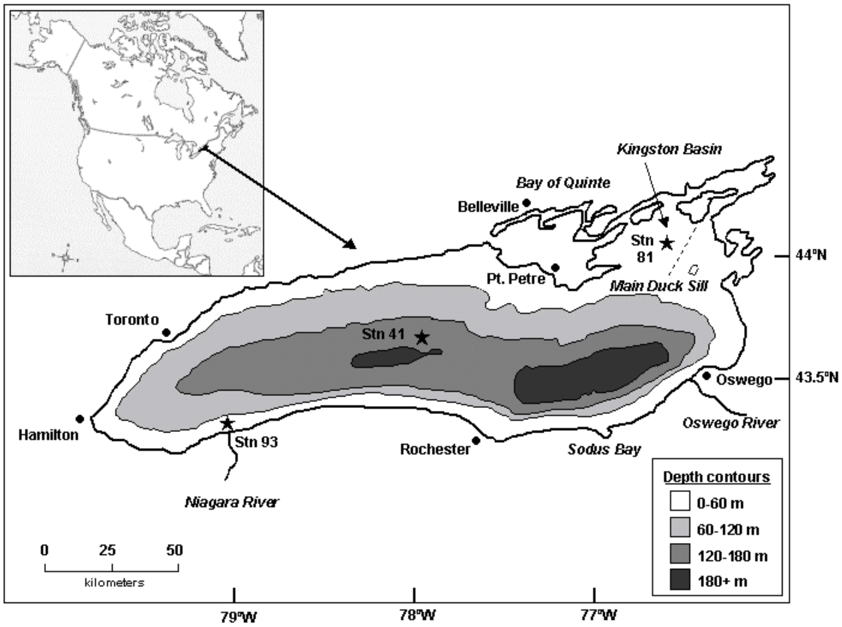


Fig. 1. Bathymetric map of Lake Ontario showing long-term sampling locations (★).

Understanding the Lake Ontario ecosystem requires knowledge of habitat use and spatial-temporal distributions of organisms. Short-term, spatially comprehensive studies in the 1960s and 1980s revealed spatial gradients throughout Lake Ontario of temperature and nutrients and of community structure of phytoplankton and zooplankton (Patalas 1969; Munawar and Nauwerck 1971; Neilson and Stevens 1987). Although much is known about the offshore waters of Lake Ontario, the dynamics in the offshore (>30-m depth) habitat are not necessarily reflective of nearshore (<30-m depth) and embayment (morphologically semi-isolated from the main lake) habitats (Gregor and Rast 1982; Rand et al. 1995). Embayments have higher levels of phosphorus and chlorophyll and warm faster in springtime than nearshore and offshore habitats (Hall et al. 2003). In contrast, the nearshore has a more disturbed physical regime associated with wave activity. Further, the coefficient of variation of density of organisms such as zooplankton declines with distance from shore (Johannsson et al. 1991).

Since the late 1960s and early 1970s, the Lake Ontario ecosystem has been subject to numerous socio-political influences, management actions, and unplanned events that have been crucial to understanding ecosystem changes over the last three decades (Table 1). Pivotal events for Lake Ontario initially consisted of management actions taken to remediate anthropogenic abuses to the aquatic ecosystem and to restore a balanced fish community. The first year of what were to become annual releases of Pacific salmon (*Oncorhynchus* spp.) to reduce alewife and create a recreational fishery was 1968. Large-scale management activities accelerated through the 1970s with the signing and implementation of binational agreements to reduce phosphorus loading to the lake, the initial treatment of streams flowing into Lake Ontario to kill larval sea lamprey, and the start of annual releases of hatchery-reared lake trout for population restoration. The pivotal event for the ecosystem in the 1990s, however, was not a planned, science-based, management action but rather the unintentional establishment and proliferation of a suite of exotic species from Eurasia that gained entry to the Great Lakes through transoceanic shipping.

Table 1. Management actions, socio-political influences, and unplanned events that have been pivotal to understanding ecological changes in the Lake Ontario ecosystem since 1968.

Year	Pivotal event	Citation
1968	First annual release of Pacific salmon for alewife control and recreational fishing	Owens et al. 2003
1970	Canada limits phosphates in detergents	Stevens and Neilson 1987
1971	First treatment of Canadian tributaries to Lake Ontario with lampricide	Pearce et al. 1980
1972	New York limits phosphates in detergents	Stevens and Neilson 1987
1972	U.S./Canada Great Lakes Water Quality Agreement sets in motion programs to control phosphorus discharges	Stevens and Neilson 1987
1972	First treatment of New York tributaries to Lake Ontario with lampricide	Pearce et al. 1980
1973	First annual release of hatchery-reared lake trout for population restoration	Elrod et al. 1995
1974	Twenty-two cormorant nests of Little Galloo Island	Weseloh and Ewins 1994
1982	First record of fry produced in Lake Ontario by hatchery- reared lake trout	Marsden et al. 1988
1983	Last record of bloater in Lake Ontario	Owens et al. 2003
1989	First record of zebra mussel (*Dreissena polymorpha*)	T. Schaner, OMNR, Glenora Fisheries Station, Picton, ON
1991	First record of quagga mussel (*D. bugensis*)	Mills et al. 1993
1992	Start of *Diporeia* spp. collapse	Lozano et al. 2001
1993	Start of annual, successful reproduction by hatchery-reared lake trout	O'Gorman et al. 2000
1995	First record of blueback herring (*Alosa aestivalis*)	Owens et al. 1998
1996	First record of *Echinogammarus ischmus*	Dermott et al. 1998
1998	First record of *Cercopagis pengoi*	MacIsaac et al. 1999
1998	First record of round goby (*Neogobius melanostomus*)	Owens et al. 2003

Nutrient Dynamics and Oligotrophication

Because phosphorus was identified as the culprit leading to eutrophication of the Great Lakes, the historic GLWQA of 1972 (revisited in 1978 and amended in 1987) resulted in the implementation of management policies for phosphorus. This phosphorus control program was an undeniable success (Millard et al. 2003). Phosphorus loading to Lake Ontario declined by nearly 50% from a peak of 15,036 $t•y^{-1}$ in 1969 to 7,410 $t•y^{-1}$ in 1981, close to the loading target of 7,000 $t•y^{-1}$ established by the GLWQA. This recovery period (12 years) was consistent with early phosphorus models (Thomann et al. 1977; Chapra and Sonzogni 1979) that suggested the response time for Lake Ontario to achieve target concentrations of phosphorus would range from 8 to 22 years. Reductions in phosphorus in the open waters of Lake Ontario were well documented from lakewide surveillance (Surveillance Program, Environment Canada, Burlington, Ontario) and long-term sampling programs (Lake Ontario Bioindex Project, Fisheries and Oceans Canada, Burlington, Ontario) at Stations 41 (mid-lake) and 81 (Kingston Basin) (Fig.1) (Millard et al. 2003). The Surveillance Program cruises examined lakewide water-quality changes (since the early 1970s), while the Lake Ontario Bioindex Project (1981-1995) examined the lower-level trophic response to reduced phosphorus loading. Spring total phosphorus (TP) concentrations declined by over 50% from 20-25 $µg•L^{-1}$ in the early 1970s to 9.9 $µg•L^{-1}$ (just below the target concentration of 10 $µg•L^{-1}$) by 1986. During 1986-1993, TP concentrations fluctuated within ± 0.5 $µg•L^{-1}$ of the target. Similar patterns of decline were observed for soluble reactive phosphorus (SRP): levels peaked at 15.3 $µg•L^{-1}$ in 1973 and then dropped to less than 5.0 $µg•L^{-1}$ by the 1990s (Fig. 2a).

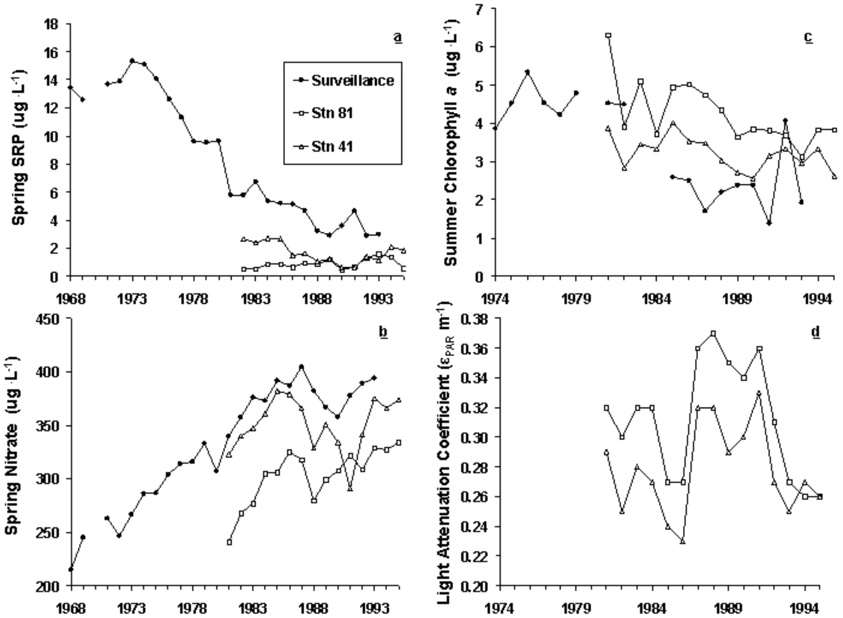


Fig. 2. Long-term trends in: a) mean spring soluble reactive phosphorus (SRP), b) mean spring nitrate, c) mean summer chlorophyll *a*, and d) seasonal mean light attenuation coefficients at Bioindex Stations 41 and 81 and for surveillance cruises in Lake Ontario during 1968-1995. The line for surveillance chlorophyll data is discontinuous because no data are available for 1980, 1983, and 1984. Surveillance SRP and nitrate (N) data are discontinuous because no data are available for 1970-1971.

In contrast to phosphorus, silica concentrations exhibited no long-term changes in the open waters of Lake Ontario (Johannsson et al. 1998; Millard et al. 2003) whereas nitrate concentrations increased significantly. Seasonal nitrate maxima occur during spring and have been used to assess long-term nitrate trends (Millard et al. 2003). Nitrate concentrations increased significantly over the long term, with the most rapid increase occurring from 1968 to 1987 (Fig. 2b). Mean spring concentrations increased from 215 µg•L^{-1} in 1968 to about 400 µg•L^{-1} by the late 1980s but leveled off during the 1990s (Lean 1987; Stevens and Neilson 1987; Neilson et al. 1994). Lean

(1987) concluded that the increase in nitrate was associated with higher loading from the watershed and was not associated with reduced algal demand because the nitrate increase occurred prior to implementation of phosphorus control. Millard et al. (2003) showed that the rate of nitrate increase paralleled nitrogen-fertilizer use in the Great Lakes basin and mirrored the observed Lake Ontario mid-lake increase up to the mid-1980s and the more recent stable period in the 1990s.

Ratios of nitrogen to phosphorus (N:P) in the early 1970s (Stevens and Neilson 1987) were in the range (16:1) where nitrogen and phosphorus might have co-limited phytoplankton growth (Forsberg et al. 1978; Rhee and Gotham 1980; Vincent 1981; Nicholls and Carney 1986). However, a steady increase in nitrate and decrease in TP over the last two decades elevated the N:P ratio to in excess of 50:1 (Johannsson et al. 1998) such that Lake Ontario is now more P-limited than N-limited (Forsberg et al. 1978; Vincent 1981) for at least three months during the summer in the open, deep waters of the lake (Lean et al. 1987; Millard et al. 1996a). The shallow Kingston Basin is P-limited for a much longer period than the offshore habitat (Millard et al. 1996a) because spring water-column light intensities can exceed growth-limiting levels at full-vertical mixing in this part of the lake but not in the offshore (Millard et al. 1996a).

Diatoms are important food for zooplankton and macroinvertebrates like *Mysis relicta* and *Diporeia* spp. (hereafter, diporeia as a common name); diatom biomass has not declined significantly over the long term in mid-lake, but spring diatom biomass has declined in the Kingston Basin since the establishment of dreissenid mussels (Johannsson et al. 1998; Millard et al. 2003). Diatoms have a spring requirement for silica, typically depleting surface waters of this nutrient during late spring and early summer as thermal stratification is established and the photosynthetic light supply becomes less of a growth-limiting factor (Schelske et al. 1986; Millard et al. 1996b). Diatom abundance peaks in the spring in Lake Ontario (Millard et al. 1996a; Johannsson et al. 1998; Millard et al. 2003). With the onset of thermal stratification, however, diatoms sink rapidly out of the water column and are relatively scarce during the rest of the season. In Great Lakes waters, an inverse relationship generally exists between peak mean-spring diatom biomass and minimum silica concentration (Schelske et al. 1986). This diatom-silica interaction has been evident in mid-lake Lake Ontario through the 1980s and was more notable at mid-lake and in the Kingston Basin in the 1990s with diatoms showing a general decline and silica increasing.

Phytoplankton Community Composition and Primary Production

Phytoplankton-biomass and species-composition data based on lakewide surveys are scarce (Munawar and Munawar 2003). Surveys were conducted in various seasons in only three years: 1970, 1978, and 1990. A comparison of 1970 (high phosphorus; pre-dreissenids) data with 1990 (low phosphorus; post-dreissenids) indicated that mean algal biomass in the spring increased considerably in 1990 (dominated by diatoms) (Munawar and Munawar 2000) (Fig. 3). On the other hand, mean phytoplankton biomass decreased in the fall of 1990 (dominated by Chlorphyceae, Cryptophyceae, and diatoms), possibly in response to phosphorus declines and/or the onset of the establishment of dreissenids in eastern Lake Ontario. Comparison of 1970 data (Vollenweider et al. 1974; Munawar and Munawar 1996) with 1990 data (Munawar and Munawar 2003) indicated considerable change in phytoplankton composition. Predominant eutrophic diatom and Cyanophyta species had either been replaced by oligotrophic (Chrysophyceae and Diatomeae) species or occurred in very low numbers.

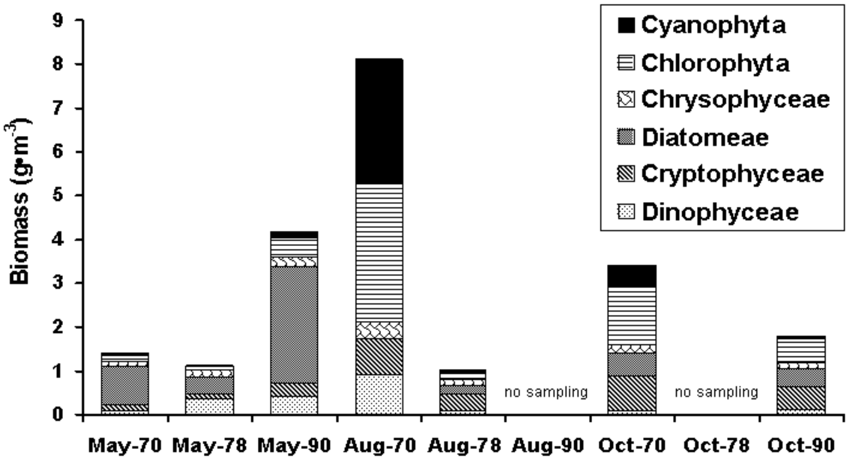


Fig. 3. Mean phytoplankton biomass and taxonomic composition in Lake Ontario on a lakewide basis at 30-35 stations during May, August, and October of 1970 (13 cruises), 1978 (8 cruises), and 1990 (3 cruises). Data modified from Munawar and Munawar (2003).

Lake Ontario's oligotrophication is also supported by other structural changes recorded in the size composition of phytoplankton. Size-fractionated primary production was determined in Lake Ontario for several years in the 1990s, under the auspices of the Lake Ontario Trophic Transfer (LOTT) binational project (Munawar and Munawar 2003), according to the procedures described by Munawar and Munawar (1996). Estimates of spring, summer, and fall primary-production size-fractionated for picoplankton (<2 µm), nanoplankton (2-20 µm), and netplankton (>20 µm) during 1990-1997 reflect a period of increasing *Dreissena* colonization and post-nutrient abatement. Size-fractionated primary-production estimates from 1990-1997 showed that most production was associated with the smaller-sized nano- and picoplankton. This shift reflects a major change from the eutrophic period of the early 1970s, which was a time when netplankton likely contributed most of the production (Vollenweider et al. 1974).

Summer phytoplankton growth in Lake Ontario has probably always been phosphorus limited, even at the higher concentrations prior to phosphorus control (Lean et al. 1987; Millard et al. 1996a). Algal biomass, as indicated by summer chlorophyll, however, did not respond immediately to reduced phosphorus loadings and concentrations. Lakewide chlorophyll did not decline until the early 1980s when a decrease of about 2 µg•L^{-1} was observed between 1982 and 1985 (Stevens and Neilson 1987; Millard et al. 2003) (Fig. 2c); chlorophyll remained at these lower levels (1.5-2.5 µg•L^{-1}) between 1985 and 1993. Although significant declines were observed between 1981 and the early 1990s in particulate organic carbon and nitrogen during the stratified period in both the main lake and Kingston Basin, significant declines in chlorophyll in the 1990s were only observed in the Kingston Basin (Johannsson et al. 1998; Millard et al. 2003). Summer chlorophyll concentrations declined at Station 81 from maxima of 5.0-6.0 µg•L^{-1} in the early to mid-1980s to 3.5-4.5 µg•L^{-1} through the late 1980s and 1990s. In the Kingston Basin, spring (pre-stratified) chlorophyll levels exhibited a significant decline in more recent years (1987-1995), particularly after 1992, despite stable TP concentrations (Millard et al. 2003). Similar declines in spring chlorophyll concentrations had been observed earlier (1982-1984) in both the main lake and Kingston Basin. The significance of the chlorophyll decline in the 1990s was its occurrance in the Kingston Basin and not in the offshore waters of the open lake.

Studies of primary production (PP) have been used to assess the response of the phytoplankton community to decreasing phosphorus loads over the last 30 years (Table 2). We have chosen to present areal primary production integrated over longer time periods (annual or seasonal). Studies by Gloschenko et al. (1974) in 1970 and those conducted in 1972-1973 during the International Field Year for the Great Lakes (IFYGL) (Stadelmann et al. 1974) were done before implementation of phosphorus control. The Lake Ontario Nutrient Assessment Study (LONAS) provided seasonally intensive sampling along a mid-lake transect in 1982 (Lean et al. 1987), and studies by Millard et al. (1996b) and others encompassed years between 1987 and 1992. In general, studies have characterized ecosystem productivity with seasonal or annual PP (g•C•m^{-2}) and have correlated changes, both decreasing (Millard and Johnson 1986) and increasing (Goldman 1981; Goldman and DeAmezaga 1984), with phosophorus loading. Millard et al. (1996b) measured photosynthesis during May to October at two stations in Lake Ontario during 1987-1992 and reanalyzed the IFYGL data collected in 1972. Their analysis suggested that seasonal photosynthesis (1 May-31 October) declined by 30% coincident with the decline in phosphorus concentrations in Lake Ontario for the period 1972-1992. The decline in photosynthesis, however, was not proportional to the 50% decline in phosphorus concentrations because of the positive compensating effect increased light penetration has on depth of photosynthesis. A further decrease in light attenuation followed zebra mussel (*Dreissena polymorpha*) establishment. Seasonal mean attenuation coefficients for photosynthetically available radiation (400-700 mm)•(ε_{PAR} m^{-1}) decreased significantly at mid-lake and in eastern Lake Ontario in the early 1990s (Fig. 2d). At station 81, ε_{PAR} declined 25% from a seasonal mean of about 0.35 m^{-1} in 1991 to 0.26 m^{-1} in 1994-95, which equates to a deepening of the euphotic zone of about 5 m. Despite this increase in light penetration, areal photosynthetic rates likely have not been maintained at the same levels observed prior to dreissenid invasion. The potential for photosynthesis in the light-limited part of the water column to offset the negative impacts of reduced algal biomass on areal photosynthetic rates is limited without drastic increases in photosynthesis per unit biomass (Millard and Sager 1994; Fahnenstiel et al. 1995). Although compensatory effects preventing a decline in areal photosynthesis after the introduction of zebra mussels have been observed in Oneida Lake, New York (Idrisi et al. 2001), the algal biomass decline there was only 35% and was accompanied by an increase in photosynthesis per unit biomass.

Table 2. Studies of seasonal (1 May-31 Oct) areal primary production in Lake Ontario since 1970.

Study	Station	Year	Primary Production (g C m^{-2})
Gloschenko et al. (1974)	Lakewide	1970	170[a]
Stadelmann et al. (1974), IFYGL	19	1972-1973	191[b]
Lean et al. (1987), LONAS	403	1982	75[b]
Millard et al. (1996a), Bioindex	81	1987-1995	142[c]
	41	1987-1995	137[c]
S. Millard, unpubl. data	Lakewide	1990-1996	97-137
S. Millard, unpubl. data	Kingston Basin E2	1993-1994, 1998	99

[a] Estimate is for April-December. Reduce by 10-20% for comparison to other studies.

[b] See Millard et al. (1996a) for details of how published IFYGL value was corrected.

[c] Values differ slightly from those in Tables 4 and 9 in Millard et al. (1996a) because three additional years of data included.

An understanding of the Lake Ontario food web in 1970 did not include knowledge of the microbial food web (MFW), which includes bacteria, heterotrophic nano-flagellates, ciliates, nanoplankton, and picoplankton (Munawar et al. 2003). The MFW is now considered an essential pathway of energy transfer to zooplankton (Munawar and Munawar 1999) and fish. Heterotrophic flagellates and bacteria are active in biodegradation of organic material that regenerates mineral substances that are then used by unicellular autotrophs (Blackburn et al. 1997). In turn, flagellates are consumed by microzooplankton such as ciliates (10-80 µm). With the shift toward a more oligotrophic state over the past 30 years, the plankton community has shifted toward autotrophic nano- and pico-plankton with a tight coupling between heterotrophic nanoflagellates (HNF) and bacteria and with bacteria numbers increasing when predation pressure from HNF declines (Munawar et al. 2003). Although data are lacking, we speculate that the microbial loop is more important now than it was in the 1970s when nutrient levels and algal productivity were higher.

Secondary Producers and Consumers: Links to Fish

Zooplankton

Zooplankton Community Composition

Surprisingly, the Lake Ontario zooplankton community was not studied until 1967 when whole-lake and large-scale studies were initiated (Patalas 1969; McNaught and Buzzard 1973; Czaika 1974; Watson and Carpenter 1974). At that time (1967-1972), the zooplankton community was dominated by small cladocerans and cyclopoid copepods, primarily *Diacyclops thomasi* (formerly *Cyclops bicuspidatus thomasii*), *Tropocyclops extensus* (formerly *T. prasinus mexicanus*), *Bosmina* spp. (*B. leideri* and *B. freyi* formerly known as *B. longirostris* (De Milo 1993)), and *Daphnia retrocurva*. Mesotrophic and eutrophic zooplankton species such as *Eubosmina coregoni* and *Ceriodaphnia lacustris* were present regularly, while *Chydorus sphaericus*, *Eurytemora affinis*, *Acanthocyclops vernalis*, *Leptodora kindtii*, and *Mesocyclops edax* were seen only occasionally (Patalas 1972; Balcer et al. 1984; Makarewicz 1993; Johannsson et al. 1998). This community remained intact through the 1980s (Johannsson 1987; Taylor et al. 1987; Johannsson et al. 1991).

Nutrients and Zooplankton Production

Changes in the nutrient status of Lake Ontario since the 1970s were expected to impact the zooplankton community through changes in abundance, biomass and production, and community composition. The response of the zooplankton community to declines in phosphorus levels occurred primarily in abundance, biomass, and productivity. Total zooplankton summer density and production declined significantly between 1981 and the early 1990s in the main lake, along the south shore, and in the Kingston Basin (Johannsson et al. 1991; Makarewicz et al. 1995; Johannsson et al. 1998; Johannsson 2003) (Fig. 4a). Epilimnetic zooplankton production (15 June-31 October) in Lake Ontario decreased from the early to mid-1980s (Fig. 4b) and paralleled the decline in concentrations of total phosphorus (Johannsson 2003). In mid-lake, zooplankton production declined from 17-42 g dry wt•m^{-2}•season^{-1} during 1981-1985 to 8-19 g dry wt•m^{-2}•season^{-1} during 1986-1995. Epilimnetic zooplankton production in the Kingston Basin declined from 28-52 g dry wt•m^{-2}•season^{-1} during 1981-1984 to 7-13 g dry wt•m^{-2}•season^{-1} during 1993-1995. Johannsson (2003) ruled out fish predation in favor of nutrient decline as the driving force leading to lower zooplankton production in the lake in the 1980s and early 1990s.

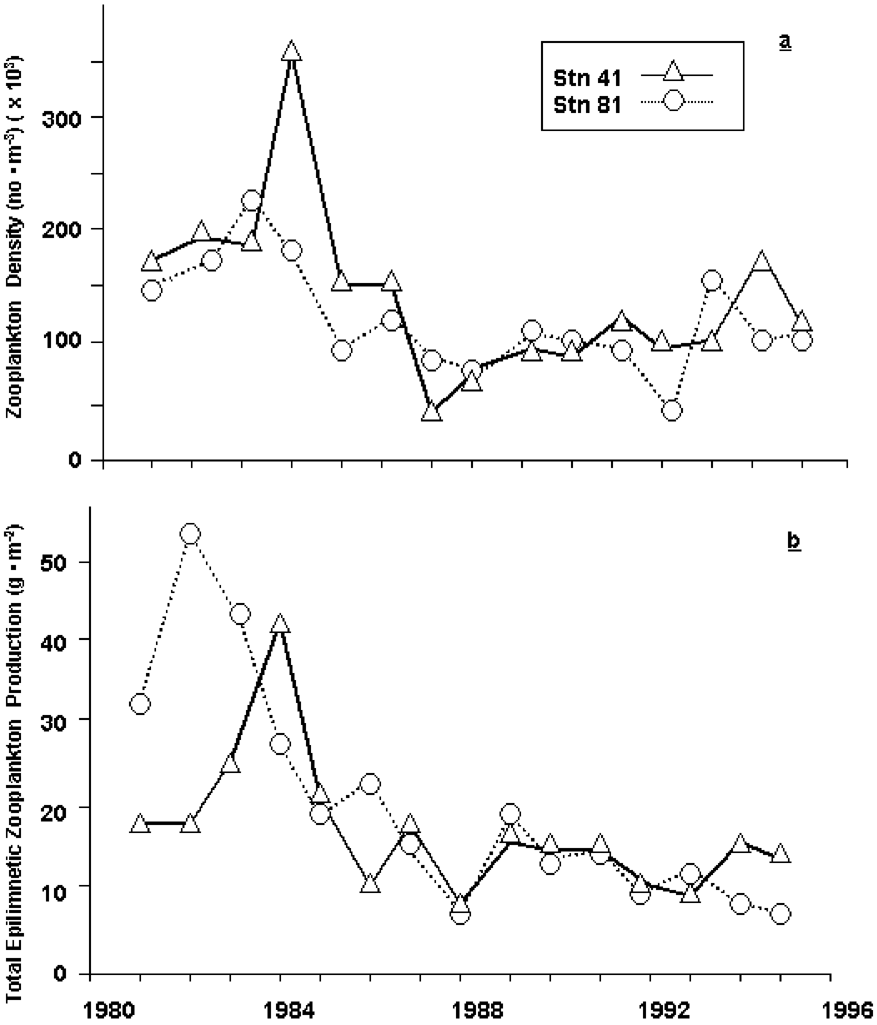


Fig. 4. Trends in a) total zooplankton density during the stratified period and b) total epilimnetic zooplankton production in Lake Ontario between 15 June-31 October, 1981-1995. All estimates based on samples collected from either the top 20 m or the epilimnion of Lake Ontario, whichever was shallower, at Stations 41 and 81 of the Bioindex Program.

Epilimnetic zooplankton production can account for 80% of total zooplankton production (excluding *Mysis relicta*) in mid-lake waters of Lake Ontario (Kuns and Sprules 2000). Therefore, declines of 50% in epilimnetic zooplankton production may reduce growth and biomass of planktivorous fish populations. In Lake Ontario, alewife and *Mysis relicta* are the predominant planktivores (Rand et al. 1995; Gal et al. 1999). Yearling growth (i.e., production) of alewife is positively linked to epilimnetic zooplankton abundance (O'Gorman et al. 1997).

Only small changes in zooplankton community composition were observed as phosphorus levels declined in Lake Ontario. *Chydorus sphaericus* disappeared in the mid-lake and Kingston Basin in the early 1990s, and *Ceriodaphnia lacustris* declined in abundance and was not observed in the mid-lake in 1995 (Johannsson 2003).

Zooplanktivory

Zooplankton, with their intermediate position in the food web, reflect the combined impacts of nutrient reduction (bottom-up) and fish predation (top-down) (McQueen et al. 1986, 1989). In the late 1960s-early 1970s, Lake Ontario lacked top predators, and planktivorous alewife dominated the fish community (Christie 1974). The impact of planktivory since 1970, particularly by alewife, was significant and structured the zooplankton community toward small species (e.g., *Bosmina* spp.). Zooplankton are the principal food of juvenile and adult alewife (Mills et al. 1992; Urban and Brandt 1993), which were responsible for >96% of the predation on zooplankton by Lake Ontario fish as late as 1990 (Rand et al. 1995). Alewife abundance declined 42% from the early 1980s to the early 1990s (O'Gorman et al. 2000), and subtle changes in the zooplankton community coincided with this decline. The relative production of *Daphnia* spp. increased from <15% (1981-1985) to 30-50% (1986-1995) of total zooplankton production (Johannsson 2003). The abundance of summer cyclopoid copepods (1987-1995 in the mid-lake) and of total zooplankton (in the spring during 1981-1995) increased (Johannsson et al. 1998). An increase in abundance of larger species in the late 1980s and early 1990s coincided with the decline in adult alewife. August mean cladoceran length was larger in 1990-1991 than in the late 1980s (Makarewicz et al. 1995; Johannsson 2003). Decreases in planktivory should have led to detectable increases in zooplankton productivity; however, zooplankton production did not increase significantly during 1987-1995 (Johannsson et al. 1998; Johannsson 2003).

Exotics

Two exotic spiny-tailed cladocerans and the veliger larvae of *Dreissena* spp. (Schaner 1991) have been added to the Lake Ontario zooplankton community since 1970. The cladoceran *Bythotrephes longimanus* (formerly known as *B. cederstroemi*) was first seen in 1982 (Fricker and Abbott 1984), and *Cercopagis pengoi* was first observed in 1998 (MacIsaac et al. 1999). Both *B. longimanus* and *C. pengoi* are predators on other zooplankton. Recent evidence by Benoit et al. (2002) indicates that *C. pengoi* feeds on small copepods and *Bosmina*, likely causing decreased juvenile copepod production through direct predation and a shift of copepod vertical distribution to deeper, colder waters. Interestingly, *B. longimanus* has only been observed in Lake Ontario in 1987 and 1994 (primarily in the fall), while *C. pengoi* has been observed lakewide since 1998 (highest densities in August and September) (Makarewicz et al. 2001). At present, *B. longimanus* has little impact on the food fish. *Cercopagis pengoi*, on the other hand, is very abundant in the summer, although its impact on fish is unknown.

Habitat

Our understanding of the dynamics and linkages of zooplankton to other trophic levels now includes information on spatial gradients among habitats associated with depth, distance from shore, degree of isolation from the open lake, and physical processes (e.g., mixing, currents, and upwellings) (Taylor et al. 1987; Johannsson et al. 1991; Hall et al. 2003). The density of zooplankton in surface waters does not necessarily change from nearshore to offshore; however, areal abundance increases with the addition of the meta- and hypo-limnion and their associated zooplankton communities. Zooplankton-community structure changes in springtime with distance from shore; more rapid warming of embayment and nearshore waters promote earlier development of warm-water zooplankton species. Consequently, planktivory by adult alewife and age-0 fish occurs earlier in embayments than in the nearshore or offshore. *Daphnia* spp. populations are suppressed in early July in embayments before they develop in the offshore (Hall et al. 2003). Zooplankton species diversity is also higher in nearshore and embayment habitats than in offshore habitats due to the addition of littoral species. Zooplankton density is more variable in nearshore habitats than offshore habitats most likely because of physical disturbances associated with upwellings, currents, and wind-generated wave activity (Johannsson et al. 1991).

Mysis relicta—the "Krill" of Lake Ontario

Mysis relicta is abundant in Lake Ontario, is part of both the benthic and pelagic food webs, and has food habits and migration patterns similar to those of euphausiids in the oceans (Grossnickle 1982; Beeton and Bowers 1982). In many respects, mysids can be considered the "krill" of the Great Lakes and Lake Ontario.

Mysids reach a length of 25 mm and exhibit remarkable diel migrations (as much as 100 m) from deep water to feed on hypolimnetic and metalimnetic zooplankton during the night (Gal et al. 1999). Abundant populations have been known since the 1960s to inhabit the deep waters of Lake Ontario (Christie 1972; Carpenter et al. 1974; Shea and Markarewicz 1989; Johannsson 1992, 1995). Mysids avoid light levels comparable to about 10^{-4} lux in Lake Ontario (Gal et al. 1999); at early dawn, the animals migrate back to deeper waters to avoid predation from visually feeding fish. They spend the day on the lake bottom but have been collected above the bottom (110-130 m) during the day where water depths are greater than 140 m.

Mysid density decreases with decreasing depth from 100 m to the shallow nearshore (Johannsson 1992, 1995), which is a pattern attributed to higher fish predation in the nearshore and a tendency to migrate to deeper, colder waters. In the offshore, abundance in the water column is lower in the spring than in the summer and fall, probably due to a larger proportion of mysids remaining on the bottom at night in the spring (Johannsson et al. 2003). Mysid production also increases with increasing depth. Shea and Makarewicz (1989) calculated production to be 0.13 g dw•m^{-2}•7 month^{-1} at a 35-m depth increasing to 1.23 g dw•m^{-2}•7 month^{-1} at a 100-m depth. A whole-lake study conducted in 1990 found that most mysid production occurred at depths of 100-150 m. Areal production decreased rapidly at depths <100 m, increased gradually with depth at depths >100 m, and reached a maximum of 5.96 g dw•m^{-2}•y^{-1} in regions >200-m depth (Johannsson 1995).

The abundance of *Mysis* has not changed in Lake Ontario since the mid-1980s. Average annual density (1984-1995) in open waters (Station 41) varied from 200-540 ind•m^{-2} with no significant trends (Johannsson et al. 2003). Corresponding biomass values range from 0.8-2.2 g dw•m^{-2} (assuming an average weight of 4 mg dw per individual). Mysid production (at Station 41), on the other hand, can be significantly reduced when consumption by alewife is high, and ranged from 1.90 g dw•m^{-2}•y^{-1} in 1984 to 4.88 g dw•m^{-2}•y^{-1} in 1995 (Johannsson et al. 2003). Mysid production strongly reflects the survivorship of larger-sized individuals; a small increase in survivorship may not be detectable in abundance but will be detectable in production. The mean weight of a mysid from April to October has generally increased as predation by alewife decreased (Johannsson et al. 2003).

Mysids are omnivores (Grossnickle 1982) and show marked seasonality in their diet. Johannsson et al. (2001) estimated that 50% of their energy in May was from diatoms and 50% from zooplankton in summer nearly 100% was from zooplankton, and in fall >80% was from zooplankton. The remaining diet consisted of amphipods and diatoms. Smaller mysids are more herbivorous, but they do consume small cladocerans, cyclopoids, and rotifers (Johannsson et al. 2001). There is little evidence of mysids feeding on sediments in Lake Ontario even though they may do so in other lakes (VanDuyn-Henderson and Lasenby 1986). As predators, mysids select cladocerans over copepods, probably due to the slower escape response of cladocerans (Cooper and Goldman 1980; Nero and Sprules 1986). *In situ* experimental estimates of daily feeding rates of *Mysis relicta* range from 2-39% (depending on body size) of their body weight per day (Cooper and Goldman 1980; Bowers and Vanderploeg 1982; Nero and Sprules 1986).

Mysids are important prey for rainbow smelt, alewife, and young piscivores in Lake Ontario (Mills et al. 1992). Rainbow smelt depend more on mysids than do alewife, and their diet is often dominated by mysids (Urban and Brandt 1993). Mills et al. (1992) found that mysids were eaten primarily by alewife in the spring and fall when the thermocline was less pronounced. Mysids could contribute up to 30-40% by weight of the alewife diet at those times. This difference in diet between rainbow smelt and alewife is likely the consequence of the smelt's ability to feed more efficiently on larger food particles and of the greater spatial overlap that exists between mysids and smelt than between them and alewife. Mysids are also eaten by benthic fish and are a predominant October diet item of slimy sculpins (*Cottus cognatus*) (Owens and Weber 1995).

Benthic Macroinvertebrate Fauna

The status of the Lake Ontario benthic-macroinvertebrate community has changed dramatically since 1970. Benthic invertebrates in the food web serve the critical function of providing energy to higher trophic levels and are affected by water column productivity, settling organic matter, and sediment texture. For example, the cold-water amphipod diporeia relies heavily on newly settled organic matter during spring diatom blooms (Gardner et al. 1989), whereas oligochaetes feed deeper in the sediments on older, buried organic material and bacteria (Brinkhurst and Chua 1969; Matisoff et al. 1999). Densities of invertebrates in Lake Ontario tend to be greatest where nutrient levels and the flux of organic matter are high. These locations include Toronto Harbour, the Niagara River, the Genesee River near Rochester, and the shallow Kingston Basin near the St. Lawrence River (Fig. 1). The benthic-macroinvertebrate community also serves as an important environmental barometer because it is sensitive to water-quality conditions. During the period from the 1960s to the 1970s when water-quality degradation persisted in Lake Ontario, macrobenthos populations declined (Nalepa 1991; Barton and Anholt 1997). With mandated binational programs to improve water quality in Lake Ontario in the 1980s and 1990s, expectations were high that the benthic community would benefit greatly from these efforts. Unfortunately, the effects of toxic contaminants in sediments persist in Lake Ontario. Nalepa and Thomas (1976), Golini (1979), and Barton and Anholt (1997) have all found the pollution-sensitive diporeia rare at sites near the mouth of the Niagara River. Such scarcity has been attributed to high loadings of chlorinated hydrocarbons from industries (Durham and Oliver 1983; Nalepa 1991). Besides toxic contaminants, biological pollution associated with unexpected introductions has continued to impact Lake Ontario's benthic food web.

Zebra and Quagga Mussels

One of the most significant changes in the benthic macrofauna of Lake Ontario has been the establishment of two species of *Dreissena*. The zebra mussel was first detected in the lake in 1989, and, by 1991, the quagga mussel (*D. bugensis*) was observed coexisting with the zebra mussel (Griffiths et al. 1991; Mills et al. 1993). South-shore studies between 1992 and 1995 showed that total dreissenid biomass had increased and areas of the lake bottom that had been dominated by zebra mussels in 1992 were dominated by quagga mussels in 1995 (Mills et al. 1999). In 1992, zebra mussel biomass exceeded quagga mussel biomass at all depths from 15 to 75 m. By 1995, zebra mussel biomass exceeded quagga mussel biomass only at 15 m, and at all other depths 51-88% of the dreissenid biomass consisted of quagga mussels.

The dramatic increase in *Dreissena* spp. populations was associated with a loss of larger-sized fingernail clams, *Sphaerium* spp., (mainly *S. corneum* and *S. nitidum*) (Fig. 5). October biomass of inshore *Sphaerium* spp. decreased from 828 mg•m^{-2} in 1991 to zero in 1995, a collapse likely due to competition with *Dreissena* spp. for food and space. Only the smaller, subsurface-feeding *Pisidium* spp. remained after 1994. Numbers of the shallow-water amphipod *Gammarus fasciatus* increased between 1990 and 1995 subsequent to the establishment of *Dreissena* spp. *Gammarus fasciatus* benefited from increased structural complexity associated with mussel colonies and increased energy transfer to the benthos through pseudofecal deposition (Bruner et al. 1994; Dermott et al. 1993; Stewart and Haynes 1994; Haynes et al. 1999). However, *Gammarus fasciatus* may be replaced by the newly established amphipod *Echinogammarus ischnus*. By 1996, *E. ischnus* was present at the mouth of the Niagara River where it displaced *G. fasciatus* (Dermott et al. 1998). *Echinogammarus ischnus* is now common at rocky, shallow sites in Lake Ontario including Hamilton Harbour in the west, Sodus Bay in the southeast (C. Mayer, Department of Biology, Syracuse University, Syracuse, New York, personal communication), and the Bay of Quinte in the northeast (RD, personal observation).

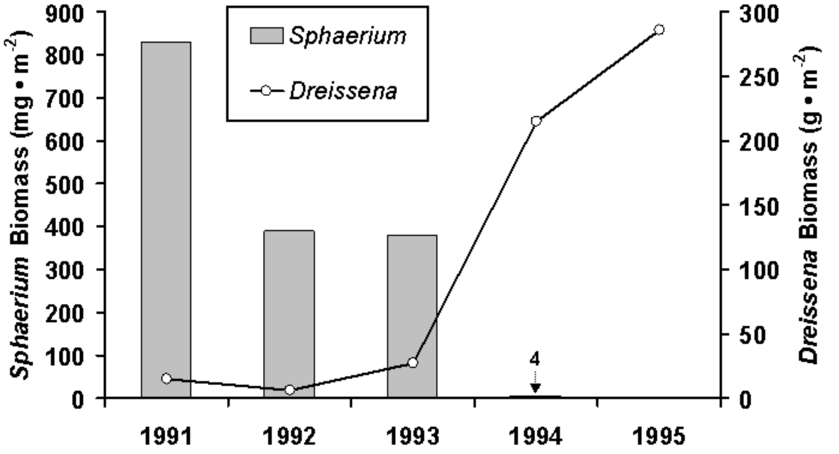


Fig. 5. Shell-free dry-weight biomass in October of *Sphaerium* spp. and *Dreissena* spp. at a sandy-silt inshore site (Stn. 93) in Lake Ontario, 1991-1995.

Colonization of the lake by dreissenids has likely decreased crustacean zooplankton production, particularly in nearshore regions. In Lake Erie, dreissenid mussels suppressed zooplankton production by reducing pelagic primary production and by competing for production both as adults in shallow regions and as veliger larvae in the water column (Johannsson et al. 2000). Similar processes undoubtedly are occurring also in Lake Ontario.

Diporeia

Historically, diporeia, the burrowing amphipod, was most abundant at depths of 30-60 m (Sly and Christie 1992) and represented 60-80% of benthic biomass in Lake Ontario (Johannsson et al. 1985). Accordingly, this organism has been a critically important food source for lake whitefish (*Coregonus clupeaformis*, hereafter, whitefish) (Hoyle et al. 2003) and sculpins (Owens et al. 2003). In the Kingston Basin, density of diporeia increased during 1983-1989 and reached 16,000 m^{-2} in 1989 (Fig. 6). Dry-weight biomass ranged from 2.3-3.0 $g{\bullet}m^{-2}$ before 1985 (Johannsson et al. 1985; Dermott and Corning 1988) and peaked at 5.0 $g{\bullet}m^{-2}$ in 1988. A rapid population increase of diporeia between 1987 and 1989 in offshore waters (Stn. 41) was in synchrony with similar events in the Kingston Basin (Stn. 81) and in the Bay of Quinte (Dermott 2001).

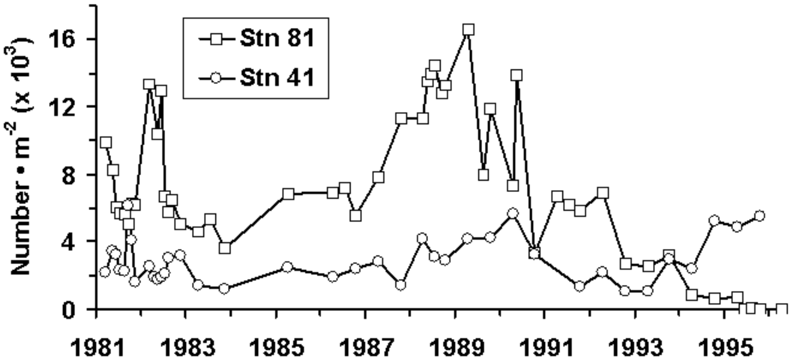


Fig. 6. Density of the amphipod *Diporeia* spp. at Bioindex Stations 41 (offshore, Fig. 1) and 81 (Kingston Basin) in Lake Ontario, 1981-1996.

Diporeia density in the Kingston Basin (at depths <35 m) plummeted to <4 m^{-2} by October 1995 and to zero in April 1996 (Fig. 6). In October 1995, diporeia were no longer present in the Bay of Quinte or along Lake Ontario's southeast shore at depths <50 m (Dermott 2001; Dermott and Munawar 2001). Lozano et al. (2001) observed also a significant decline in diporeia density during 1972-1997 at depths of 12-88 m. A zone of low diporeia density (<4 individuals•m^{-2}), encompassing a significant portion of soft sediment habitat in Lake Ontario currently extends to 26 km offshore and as deep as 160 m (Lozano et al. 2001). This reduction of diporeia numbers is expected to have a significant impact on the fish that depend on these organisms for their growth and survival.

Other Macrobenthos

Oligochaeta and Sphaeriidae (exclusively *Pisidium lilljeborgi*, *P. nitidium*, and *P. conventus*) biomass was relatively stable in offshore (Stn. 41) habitat in the 1980s (Fig. 7). Mean Oligochaeta biomass increased from 105 mg•m^{-2} (dry weight) during 1981-1989 to 210 mg•m^{-2} during 1990-1995, but *Pisidium* biomass remained stable averaging 2.3 and 2.2 mg•m^{-2} during those periods. In the Kingston Basin, total benthic biomass decreased during 1967-1985 (Johnson and McNeil 1986; Nalepa 1991). Oligochaeta and Sphaeriidae biomass in the Kingston Basin (Stn. 81) greatly increased during 1985-1990 (Fig. 7). Recent studies by Lozano et al. (2001), however, revealed that densities of Oligochaeta and Sphaeriidae at 10-35 m in 1997 were significantly lower than in 1964 or 1972. Biomass of Oligochaeta and Sphaeriidae in mid-lake (1993-1995) exhibited increases similar to diporeia (Fig. 6), which suggests that these benthic macroinvertebrates responded to similar environmental conditions.

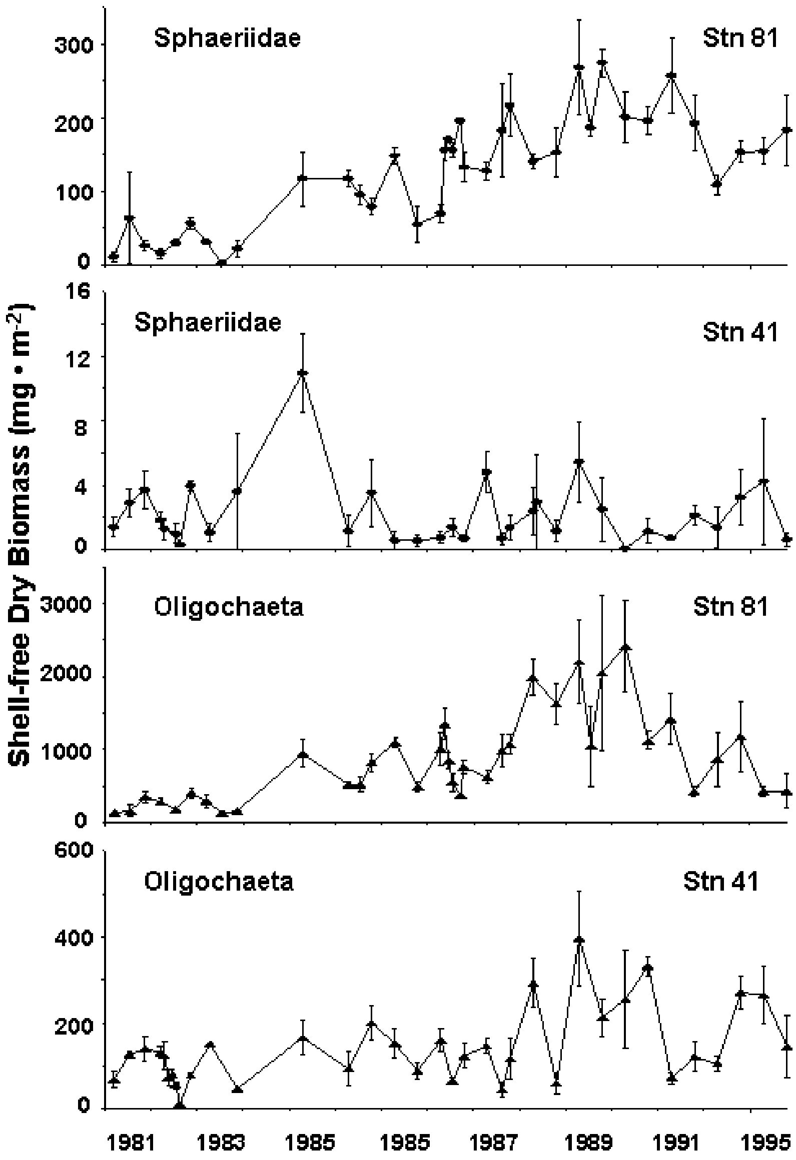


Fig. 7. Shell-free dry-weight biomass (mg•m^{-2}) of Sphaeriidae and Oligochaeta at Bioindex Stations 41 and 81 in Lake Ontario, 1981-1995. Error bars are ±1 S.E.

The inshore macrobenthos community has undergone further change with the establishment of the exotic New Zealand mud snail (*Potamopyrgus antipodarum*). This parthenogenic snail was first observed 1 km offshore in western Lake Ontario in 1991 (Zaranko et al. 1997) and reached a density of 8300 m^{-2} in October 1995. The snails *Amnicola* spp. and the *Valvata* spp. have now been replaced by the New Zealand mud snail.

The Forage Fish Community

In the 1970s and early 1980s Lake Ontario's offshore fish community was dominated by non-native planktivores (alewife and rainbow smelt) and a native benthivore, slimy sculpin (Owens et al. 2003). By the 1990s, exotic planktivore and slimy sculpin populations had declined, but native fishes such as threespine stickleback (*Gasterosteus aculeatus*) and emerald shiner (*Notropis atherinoides*) became more common.

Alewife

In the Canadian waters of the Kingston Basin, a 3-year running average of trawl catches of age-1 and older alewife showed two features that were apparent in the gillnet series of Christie et al. (1987a): a minor peak in abundance in the mid-1970s and a low abundance in the late 1970s (Fig. 8a). A mass mortality of alewife during the winter of 1976-1977, precipitated by unusually cold temperatures, depressed alewife numbers during the late 1970s (O'Gorman and Schneider 1986; Bergstedt and O'Gorman 1989; Ridgway et al. 1990). Following the 1976-1977 mass mortality, bottom trawl catches showed alewife numbers increasing in both the Kingston Basin (Fig. 8a) and U.S. waters (Fig. 8b). Population trends in the two areas differed subtly during the 1980s and more sharply during the 1990s. In the 1980s, the numbers of alewife in the Kingston Basin during summer gradually rose, whereas numbers of alewife in U.S. waters of the lake in spring slowly declined. In the early 1990s, alewife numbers increased sharply in the Kingston Basin but remained stable in U.S. waters. By the late 1990s, alewife numbers were at very low levels in both of these regions of the lake.

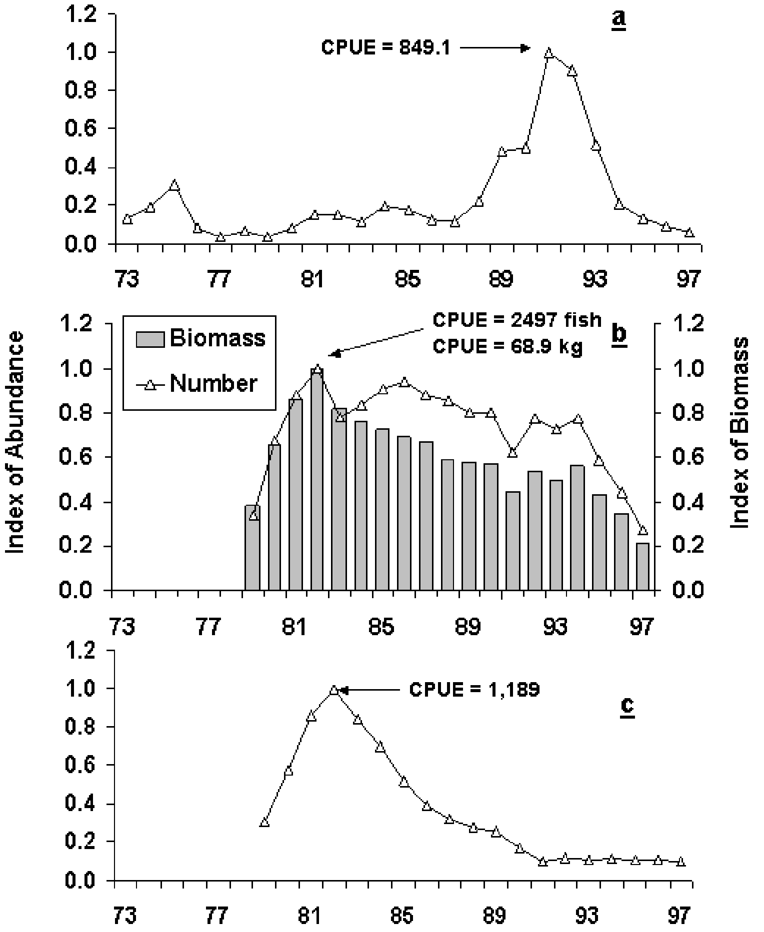


Fig. 8. Indices of relative abundance of alewives in Lake Ontario: a) yearling and older caught in deep water, 0.5-nm trawl hauls during May-August, 1972-1998, at six sites in Canada's waters of the Kingston Basin. Index is a 3-year running geometric mean standardized to the indicated maximum CPUE (Casselman and Scott 2003); b) yearling and older caught in trawl tows of 10-min duration in late April-early May, 1978-1998, in U.S. waters of Lake Ontario. Index is a 3-year running mean standardized to the indicated maximum (stratified) CPUEs; and c) >164-mm total length in U.S. waters of Lake Ontario, 1978-1998. Abundance is shown as a 3-year running mean standardized to the indicated maximum CPUE.

The occasional divergence in alewife population trends in two geographic regions of the lake was understandable considering the large inter-annual variation in over-summer survival of sexually immature age-1 alewife and their seasonal bathymetric distribution of alewife. Survival of age-1 alewife was inversely related to the number of age-2 and older alewife (O'Gorman et al. 1987), and most mortality apparently occurred before mid-summer (Johannsson and O'Gorman 1991). Therefore, numbers of age-1 alewife in the lake differed sharply between the early-spring assessment in U.S. waters and the summer assessment in the Kingston Basin. Most alewife retreat to depths of 35-110 m in winter (Bergstedt and O'Gorman 1989), and, as nearly all of the Kingston Basin is <40-m deep, alewife are largely absent at that time. Consequently, the Kingston Basin, Bay of Quinte, and upper St. Lawrence River must be repopulated each summer by alewives that migrate from overwinter habitats in the deep waters of the lake's main basin. Inter-annual differences in the proportion of the population migrating to the Kingston Basin would result in different population estimates in U.S. and Canadian eastern waters. The peak in abundance in the 1990s in the Kingston Basin indicates changes related to migrations between onshore and offshore areas and to variations in spawning runs into the Bay of Quinte. This increase in Kingston Basin abundance represents real changes, which were confirmed by gillnet catches and changes in the diets of lake trout and walleye (*Sander vitreus*). A dramatic abundance decline in the main lake followed dreissenid colonization in the early 1990s (O'Gorman et al. 2000). Heavy predation was undoubtedly one factor causing a reduction in alewife numbers in the main lake during the late 1990s, but, perhaps, more important was the absence of a strong year-class during 1992-1997. The waning population of alewife posed a new problem for fishery managers. Because the alewife fueled an economically important recreational fishery, managers recognized that they must conserve the diminished population to preserve the recreational trout and salmon fishery.

Alewife biomass declined more sharply than the numbers of alewife in U.S. waters during the 1980s (Fig. 8b). The discrepancy between numbers and biomass was due initially to a decline in body condition of fish following the peak in numbers in the early 1980s. Mean weight of a 165-mm total length (TL) alewife in spring predicted from length-weight regressions averaged 35.1 g in 1978-1980, 30.8 g in 1981-1983, and 28.3 g in 1984-1986. Population biomass continued to decline more rapidly than numbers in the mid and late 1980s as numbers of large alewife (>164-mm TL) declined faster than the total number (Fig. 8c). From the 1982 peak, numbers of large alewife declined 48% by 1985 and 83% by 1990, whereas total numbers declined 27% by 1985 and 43% by 1990. The smaller numbers of large alewife were caused by the combined effects of heavy predation by expanding populations of salmon and trout (Brandt 1986; Jones et al. 1993; Rand et al. 1995) and slower growth of alewife after sexual maturity (O'Gorman et al. 1997).

Alewife are both the primary prey of salmonines and important predators on zooplankton (Morsell and Norden 1968; Urban and Brandt 1993; Mills et al. 1995), larval fish (Brandt et al. 1987; Krueger et al. 1995; Mason and Brandt 1996), and macrozooplankton (*Bythotrephes* and *Mysis*) (Mills et al. 1992). Strong links were evident among zooplankton stocks, juvenile alewife abundance and growth, and growth of young salmonines. O'Gorman et al. (1987) found that first-year growth of coho salmon (*Oncorhynchus kisutch*) was not dependent on size at release but was related to the biomass of age-0 alewives, whereas second-year growth of coho salmon was dependent on the biomass of age-1 alewife (O'Gorman et al. 1987). Growth of age-1 alewife was dependent on zooplankton density and the numbers of age-0 alewife competing for zooplankton (O'Gorman et al. 1997).

Rainbow Smelt

Rainbow smelt are the second-most-abundant open-water fish in Lake Ontario (Casselman and Scott 2003) and are predators on and competitors with other pelagic fishes such as alewife. Age-1 and older rainbow smelt feed on a variety of food resources including zooplankton, non-native macrozooplankton (e.g., *Bythotrephes*), macroinvertebrates (e.g., mysids and diporeia), and larval and juvenile fish (O'Gorman 1974; Mills et al. 1995). Numbers and biomass of rainbow smelt fluctuated widely and without trend in U.S. waters of Lake Ontario during 1978-1998 (Fig. 9a). In U.S waters, biomass peaked in the early 1980s, whereas numbers peaked in the late 1980s; similar trends occurred in eastern Canadian waters (Casselman and Scott 2003). In the early 1990s, biomass and numbers reached lows about 75% below the peaks of the 1980s. The discrepancy in peaks of biomass and numbers was due to high numbers of large rainbow smelt (>149 mm TL) in the early 1980s (Fig. 9b). Numbers of large rainbow smelt, however, had dropped by about 85% by the mid-1980s and remained low thereafter. Christie et al. (1987a), Casselman and Scott (1992), and Owens et al. (2003) all considered size-selective predation by salmonids as the most plausible explanation for the loss of larger rainbow smelt.

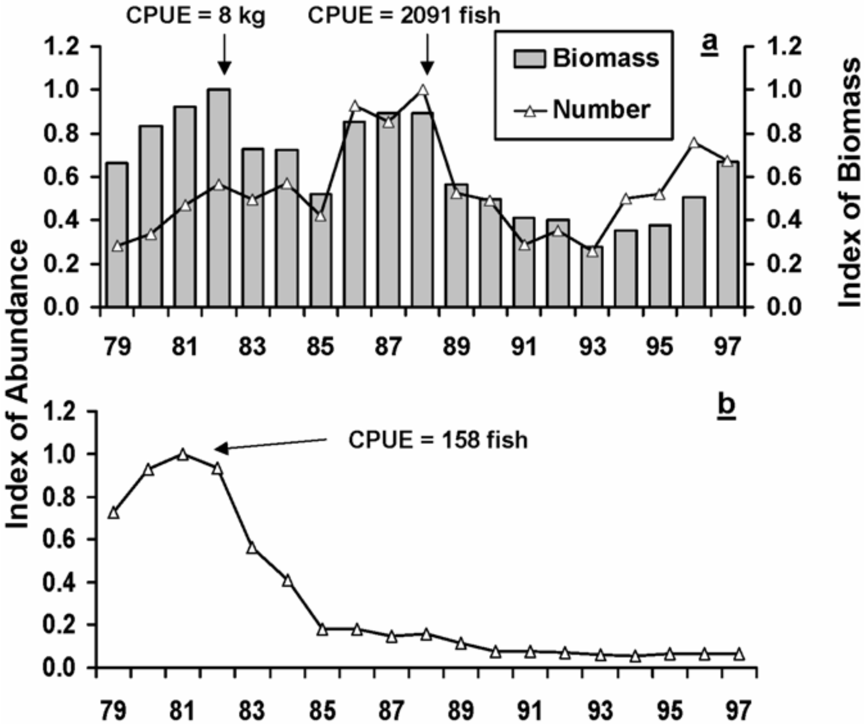


Fig. 9. Indices of relative abundance of rainbow smelt caught in trawl tows of 10-min duration in late May-early June, 1978-1998 in U.S. waters of Lake Ontario. Indices are 3-year running means standardized to the indicated maximum (stratified) CPUE. Panel a shows indices for age-1 and older rainbow smelt, and panel b shows indices for rainbow smelt >149-mm total length.

Slimy Sculpin

Slimy sculpin are important in the diet of lake trout (Elrod and O'Gorman 1991). Along the south shore, the number of slimy sculpin fell sharply between fall 1982 and fall 1984 due to predation by stocked juvenile lake trout (Owens and Bergstedt 1994). Numbers slowly rose during 1984-1991, declined abruptly in 1992, and remained low during 1993-1998 in both U.S. and Canadian waters (Casselman and Scott 2003; Owens et al. 2003). The 1992 decline in overall numbers was due entirely to the collapse of the dense population of poor condition, slow-growing fish in the southeast corner of the lake at depths >70 m (Owens and Weber 1995; Owens and Noguchi 1998). Owens et al. (2003) hypothesized that the decline of slimy sculpin was due to reductions in productivity resulting from nutrient abatement and from reductions in diporeia populations, an important food, brought on by dreissenid colonization.

Deepwater Coregonids

Three species of deepwater coregonids were present in Lake Ontario in the 1960s (Todd and Smith 1992), but none persisted past the mid-1980s. In 1964, Wells (1969) reported catching bloater (*Coregonus hoyi*), *C. reighardi*, and *C. kiyi* in experimental gillnets along the south shore, but he noted that all were extremely scarce. In the synoptic survey of 1972, only one deepwater coregonid (bloater) was caught in northwestern Lake Ontario (Owens et al. 2003). The next documented catch was in 1983. No deepwater coregonids were caught during 1984-1998 despite widespread, multi-season assessment trawling in southern and eastern waters.

Deepwater Sculpin

Deepwater sculpin, once abundant in the deeper waters of the main basin (Dymond et al. 1929), were not reported in southern Lake Ontario during 1943-1971. Christie (1973) reported that the last specimen identified from northern Lake Ontario was taken in 1953. The synoptic survey of 1972 failed to collect deepwater sculpin in the southern part of the lake, but a few were taken in the northern part of the lake (Casselman and Scott 2003; Owens et al. 2003). Deepwater sculpin were listed by Crossman and Van Meter (1979) as being present in 1972-1975, although they noted that they were extremely rare and considered endangered. After 1972-1975, deepwater sculpin were not reported until 1996, when one was caught in an Ontario Ministry of Natural Resources (OMNR) trawl. Thereafter, a few were taken near the mid-lake in the northeast (Casselman and Scott 2003), and one was caught off the southwestern shore in 1998—the first sighting of this formerly abundant fish in U.S. waters since 1942. The reappearance of deepwater sculpin in Lake Ontario was the last in a series of changes in the open-water fish community that followed dreissenid colonization, increased water quality, and the shift of rainbow smelt and alewife to deeper water in the early 1990s (O'Gorman et al. 2000).

The Salmonid Fish Community

Chinook salmon

Resumption of chinook salmon (*Oncorhynchus tshawytscha*) stocking in Lake Ontario by New York state in 1969 and by the Province of Ontario in 1971 followed a 35-year hiatus (Parsons 1973; Kocik and Jones 1999). Despite failed early introductions in Lake Ontario, remarkable angling returns from Lake Michigan following introductions of Pacific salmon caused renewed interest in the other Great Lakes including Lake Ontario (Kocik and Jones 1999). The combination of 1) angler preference for large, fast-growing chinook salmon; 2) the preference by chinook salmon for alewife as prey; and 3) the comparably lower hatchery-production costs of chinook salmon all led to chinook salmon becoming the key player in the species mix of the fish community. By 1982, chinook salmon was the principal salmonid predator in Lake Ontario and represented between 32% and 54% of annual stocking during 1982-1999.

Predation by chinook salmon on alewife was so effective that fishery managers became concerned that predator demand might outweigh prey supply. Because of their high abundance and fast growth, chinook salmon accounted for an estimated two-thirds of lakewide predator demand for alewife (Jones et al. 1993). Consequently, management of predator demand required modification of chinook salmon stocking levels, but, because of the popularity of this species in the recreational fishery, lowering stocking levels was controversial. As a result, chinook salmon stocking received considerable binational attention and public scrutiny (Kocik and Jones 1999; O'Gorman and Stewart 1999; Stewart et al. 1999). Stocking peaked in 1984 at 4.2 million fish and ranged from 3.2-3.6 million fish during 1985-1992. Chinook salmon stocking was reduced substantially in 1993-1994 based on a management review in 1992 (O'Gorman and Stewart 1999) and ranged from 1.5-1.7 million fish annually during 1994-1996. Due to stakeholder demand and a second management review (Stewart et al. 1999), stocking was increased slightly in 1997 and has ranged from 2.0-2.2 million fish annually during 1997-1999.

Lake Trout

Lake trout had declined to virtual extinction in Lake Ontario by the 1950s (Christie 1973). Hatchery-reared lake trout stocked in the Kingston Basin during 1953-1964 survived well to lengths of 38-45 cm (Pearce et al. 1980), but few survived to sexual maturity because of harvest by commercial gillnets and predation by sea lamprey (Christie 1973, 1974). Control of sea lamprey began in 1971 (Elrod et al. 1995), and lake trout stocking was renewed in 1973 with the goal of restoring a self-sustaining population (Schneider et al. 1983). Lake trout stocking increased from 66,000 fish in 1973 to 1.9 million fish in 1985 and was maintained above 2.0 million fish annually until 1992. Changes in stocking policy aimed at reducing predation on alewife (O'Gorman and Stewart 1999; Stewart et al. 1999) resulted in reductions in lake trout stocking beginning in 1993 to 0.9-1.1 million fish annually. Management efforts to minimize mortality from sea lamprey, anglers, and commercial fishers, and the shift in stocking to mostly Seneca strain (a strain with a higher survival rate than other strains) all contributed to a rebuilt, but hatchery-origin lake trout population (Marsden et al. 1989; Elrod et al. 1995; Schneider et al. 1998).

Rainbow Trout

Rainbow trout (*O. mykiss*) have long been naturalized in Lake Ontario (MacCrimmon and Gots 1972) and support an important sport fishery. Despite tributary spawning runs of wild rainbow trout in the 1970s, stocking increased from 107,000 fish in 1972 to 1.1 million fish by 1980. During 1981-1999, stocking ranged from 570,000 to 1.3 million fish annually, which comprised 6% to 23% of the total salmonids stocked. Compared to other introduced salmonids, stocking rates of rainbow trout have received less scrutiny. Encouragement of wild rainbow trout production has recently been established as a management goal (Stewart et al. 1999); however, no specific stocking policies to support this goal have been developed. Much of the annual variation in rainbow trout spawning runs has been the result of the stocking of a diversity of life stages (spring fingerlings, fall fingerlings, and yearlings) with widely varying survival.

Brown Trout

Self-sustaining stream-resident stocks of brown trout (*Salmo trutta*) occur in the Lake Ontario watershed, but few wild fish currently exist in the main body of the lake (Bowlby 1991). Stocking of brown trout accelerated along with other salmonid stocking during the 1970s and 1980s and reached a peak of 0.9 million fish in 1991. During 1992-1999, stocking remained relatively unchanged, ranging from 585,000 to 672,000 fish annually.

Coho Salmon

Much of the initial excitement and development of a salmon fishery in Lake Ontario was attributed to the introduction of coho salmon (Scott and Crossman 1999; Kocik and Jones 1999). Both New York's and Ontario's renewed interest in salmonid introductions began with initial stockings of coho salmon in 1968 (New York) and 1969 (Ontario). Coho salmon dominated the Province of Ontario's stocking program until 1979. Peak stocking years for coho salmon were 1988 (879,000 fish) and 1992 (829,000 fish). Coho salmon stocking was discontinued for economic reasons by the Province of Ontario from 1992 to 1996 but was resumed in 1997 due to strong public demand. From 1997-1999, the numbers of coho salmon stocked in New York and Ontario waters combined have ranged from 196,000 to 360,000 fish annually.

Atlantic Salmon

The extirpation of Atlantic salmon in Lake Ontario has been well documented (Ketola et al. 2000). Efforts in the recent past (post-1970) have been directed toward the feasibility of reestablishing this once-abundant fish. Stocking began in 1987 when the Province of Ontario introduced 1,000 fall fingerlings into Wilmot Creek. From 1988 to 1995, between 28,000 and 76,000 spring yearlings and fall fingerlings were stocked into Canadian streams. During 1996-1999, the Province shifted to fry, stocking from 121,000 to 249,000 annually. Both landlocked and anadromous strains of Atlantic salmon have been stocked.

In New York state, the Atlantic salmon program evolved from an emphasis on rehabilitation to a trophy sport fishery (Abraham 1988). Beginning in 1996, the U.S. Fish and Wildlife Service initiated small-scale stockings to investigate survival and growth. The first stockings (post-1970) of Atlantic salmon by New York were in 1983, and from 1983 to 1990 stocking ranged from 25,000 to 53,000 fish. From 1991 to 1999, stocking varied from 98,000 to 302,000 yearlings and fingerlings annually

Other Fish of Interest

American Eel

American eels (*Anguilla rostrata*) have shown extreme dynamics in abundance over the past four decades—increasing to record-high levels from the 1960s through the 1980s and decreasing abruptly to very-low levels in the late 1990s. Recruitment to the Upper St. Lawrence River-Lake Ontario stock has virtually ceased. The cause of the collapse is unclear, although human-induced mortality (from exploitation and hydroelectric turbines), habitat loss (dam construction), and climate change (changes in oceanic currents and temperatures) are likely important (Casselman 2001).

Walleye, Yellow Perch, and Smallmouth Bass

The walleye is an important predator in the inshore fish community of eastern Lake Ontario. Walleye reached record-low levels in the early 1970s and record-high levels in the Bay of Quinte in the early 1990s. The walleye resurgence began with an extremely large year-class in 1978 following a winterkill of its larval predators, alewife and white perch, which succumbed to the severe winters of 1976-1977 and 1977-1978 (Casselman and Scott 2003). In the late 1980s and early 1990s, the walleye population of the Bay of Quinte shifted toward the outer bay as spawning runs of alewife, an important prey species for walleye, diminished. Although large-sized walleye are known to migrate seasonally between the Bay of Quinte and eastern Lake Ontario, this shift, along with increased abundance, was associated with dispersal out of the lower Bay of Quinte altogether and into eastern Lake Ontario. Dispersal of walleye accelerated in the early 1990s in association with the progressively increasing water transparency caused by dreissenid colonization (Casselman and Scott 2003). In the mid-1990s, walleye abundance increased in New York’s waters of the eastern basin. An increase in walleye abundance was also seen in the Upper St. Lawrence River and likely reflected a dispersal from the Bay of Quinte. As walleye abundance decreased in the upper Bay of Quinte, yellow perch (*Perca flavescens*) abundance increased substantially throughout the bay at a time when this species was generally decreasing in the eastern basin of Lake Ontario.

Yellow perch were at record-high levels in northeastern Lake Ontario in the late 1970s and early 1980s but declined precipitously in the mid-1980s. Among the many factors associated with these dynamics were the massive winterkill of alewives (significant predators on yellow perch larvae (Mason and Brandt 1996)) in the late 1970s and their strong rebound in the 1980s. A shift in alewife distribution toward deeper water in the early 1990s boosted yellow perch reproductive success but double-crested cormorant (*Phalacrocorax auritus*) predation increased thereafter and appears to be responsible for decreased yellow perch abundance in eastern Lake Ontario in recent years (Burnett et al. 2002). Likewise, the smallmouth bass (*Micropterus dolomieu*) population that was at record-high levels of abundance in the late 1970s through the early 1990s reached record-low levels in the late 1990s. This decrease was associated with increased cormorant predation in both U.S. and Canadian waters (Casselman et al.

2002; Lantry et al. 2002). Also, smallmouth bass year-class strength may have been dampened by several extremely cold summers in the early 1990s, especially 1992, following the Mount Pinatubo eruption of 1991 (Hoyle et al. 1999; Casselman et al. 2003). Although weather conditions were especially favorable for recruitment in the late 1990s, particularly in the extremely warm summers of 1995 and 1998, smallmouth bass abundance has not resurged.

Blueback Herring

Two juvenile blueback herring (*Alosa aestivalis*) were caught in Lake Ontario in October 1995, the first and only record of this anadromous marine clupeid in the Great Lakes. The fish were caught within 20 km of the confluence of the Oswego River with Lake Ontario. The only other record was the observation of large numbers of juveniles in the Oswego River in 1994 (Owens et al. 1998).

Lake Herring

Remnant populations of lake herring (*Coregonus artedii*) persist in Lake Ontario. Lake herring are not abundant in any region of the lake but are encountered more frequently in the Kingston Basin and near Sodus Bay (Owens et al. 2003). In 1996, morphologically different lake herring were caught in very-deep water (139 m) (Casselman and Scott 2003), suggesting that two different populations may live in the lake.

Threespine Stickleback, Emerald Shiner, and Burbot

The recent emergence of native fishes such as threespine stickleback, emerald shiner, and burbot reflects a significant change in the Lake Ontario fish community. Owens et al. (2003) suggested the seminal event that allowed these native fishes to reproduce successfully was a relaxation of predation on their larvae that resulted from the change in distribution of alewife to deeper water in spring. In 1994, threespine sticklebacks were abundant and remained so through 1998 after being absent to rare in survey catches during 1979-1993 (Owens et al. 2003). In 1996, emerald shiners were commonly caught in assessment trawls, and in 1997-1998 they were abundant. In contrast, during 1978-1995, emerald shiners were absent or rare in 15 years, common in two years, and abundant in only one year. Numbers of burbot caught in gillnets set in U.S. waters increased sharply during 1996-1998.

Round Goby

Round gobies (*Neogobius melanostomus*) were first observed in western waters in 1998 and in the Bay of Quinte in 1999. The current extent of the goby population in western Lake Ontario is not known, but sightings have been reported between St. Catherines and Hamilton, including Hamilton Harbour. In eastern Lake Ontario, gobies can now be found in most of the Bay of Quinte and east as far as Kingston and the mouth of the St. Lawrence River. A single report from the Presqu'ile area suggests that the eastern population is spreading westward along the northern shore of the lake. The population density of gobies has not been estimated, but beach seine hauls made two years after the first sighting at the same location in the Bay of Quinte yielded more gobies than all other species combined. In western Lake Ontario, densities of gobies in experimental lake trout egg nets were as high as 117 individuals$\cdot$m^{-2} (JDF, personal observation).

Cormorants

Double-crested cormorants were first observed in Canadian waters of Lake Ontario in 1938 and in New York waters in 1945 (Weseloh and Ewins 1994). Breeding numbers remained low until the late 1970s due mainly to contamination of Lake Ontario by organochlorine compounds, particularly DDE (dichlorodiphenyldichloroethylene), which resulted in severe thinning and breakage of eggshells and reproductive failure (Weseloh et al. 1983; Weseloh 1987). Reduced contaminant levels, an abundant food supply (primarily alewife), and their protected status in both the U.S. and Canada led to a dramatic resurgence of double-crested cormorants in the 1980s and 1990s. Population trends have been particularly well documented for Little Galloo Island (LGI) in eastern Lake Ontario (Fig. 10). The number of nests occupied by cormorants on LGI increased from 22 in 1974 to over 8,000 in 1996. Nest counts on LGI decreased for the first time in 15 years in 1993 and 1994, rebounded in 1995, and continued to increase through 1996. Thereafter, nest counts declined in response to intensive human activity associated with population assessments and, eventually, control. In contrast, other Lake Ontario cormorant populations have continued to increase.

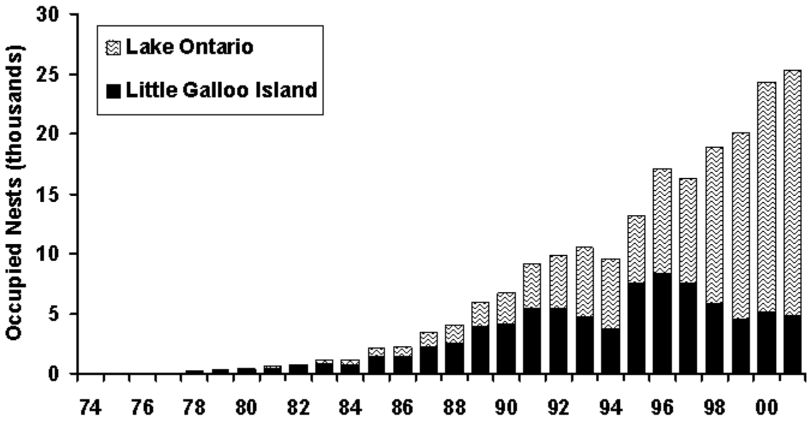


Fig. 10. Numbers of double-crested cormorant nests on Little Galloo Island (dark shading) and elsewhere (light shading) in Lake Ontario, 1974-2001 (Weseloh and Ewins 1994; D. Weseloh, Canadian Wildlife Service, 4905 Dufferin Street, Downsview, Ontario, M3H 5T4, and G. Mazzocchi, New York State Department of Environmental Conservation, 317 Washington Street, Watertown, New York, 13601, personal communications).

Years in which alewife abundance was high were also years when reproductive output and post-fledging survival of double-crested cormorants was high (Weseloh and Ewins 1994). In 1994, the population of cormorants declined likely because the alewife population declined. Although cormorants seemingly have had little overall effect on the alewife population, studies in U.S. waters of the Eastern Basin indicated adverse effects on smallmouth bass (Schneider et al. 1999; Lantry et al. 2002) and yellow perch (Burnett et al. 2002).

Fisheries Management and the Rise and Fall of Native Species

The decades just prior to the 1970s saw population collapses of many native species that comprised the historical fish community (Christie 1972). Fishery managers recognized the numerous stresses on the fish community and instituted new measures to set the stage for the recovery process. The most notable actions were sea lamprey control (Pearce et al. 1980), quotas to regulate commercial fishing effort, and stocking of salmonid predators to control exotic prey fish (Christie et al. 1987b). Further control measures were instituted including efforts to minimize loadings of mercury, chlorinated hydrocarbons (DDT and PCBs), and municipally produced phosphorus (Minns et al. 1986). The full effects of these initiatives on Lake Ontario fish would not be known until the 1980s and 1990s.

In the early 1970s, efforts to control alewife, establish a sport fishery, and restore lake trout led to an acceleration of stocking of fish predators including lake trout; brown trout; rainbow trout; and Atlantic, chinook, and coho salmon. Limited stocking of kokanee salmon (*Oncorhynchus nerka*) during 1965-1972 was not successful and was discontinued in 1973 (Pearce et al. 1980). Initially, stocking failed to produce significant fisheries due to high sea lamprey-induced mortality (Pearce et al. 1980). Sea lamprey control was initiated in 1971, and, by the mid-1980s, stocks of lake trout, brown trout, chinook salmon, and coho salmon all responded positively to reduced numbers of sea lamprey. These successes led to new management questions: 1) what is the most suitable fish species mixture for the lake, and 2) what level of stocking is necessary to maintain a balance between predator demand and prey supply.

Enhanced survival of trout and salmon led to an expansion of hatchery-stocking programs in both New York and Ontario and the dawn of a massive recreational fishing industry (O’Gorman and Stewart 1999). Pacific salmonines played a pivotal role in the transformation of the recreational fishery. As the salmonid fishery expanded with the onset of accelerated stocking (beginning in 1980), and the potential for record fishery yields was imminent, management concerns emerged about the sustainability of the salmonid fishery in the face of a waning alewife population (Kocik and Jones 1999; O’Gorman and Stewart 1999). By the mid-1980s, New York state and the Province of Ontario agreed to limit stocking to 8 million salmonids annually (Fig. 11) (Kerr and Le Tendre 1991). Concerns about salmonid predator demand and prey supply were rekindled in the early 1990s (Jones et al. 1993). By 1993, salmonid stocking levels were reduced to 4.5 million and have been maintained at between 4 and 5.5 million annually (Fig. 11). These efforts to build the Lake Ontario fishery resulted in a multi-million-dollar recreational fishing industry (O'Gorman and Stewart 1999). Total annual expenditures by anglers participating in Lake Ontario's recreational fisheries were $53 million (Canadian) for Ontario in 1995 (Department of Fisheries and Oceans 1997) and $71 million (U.S.) for New York in 1996 (Connelly et al. 1997).

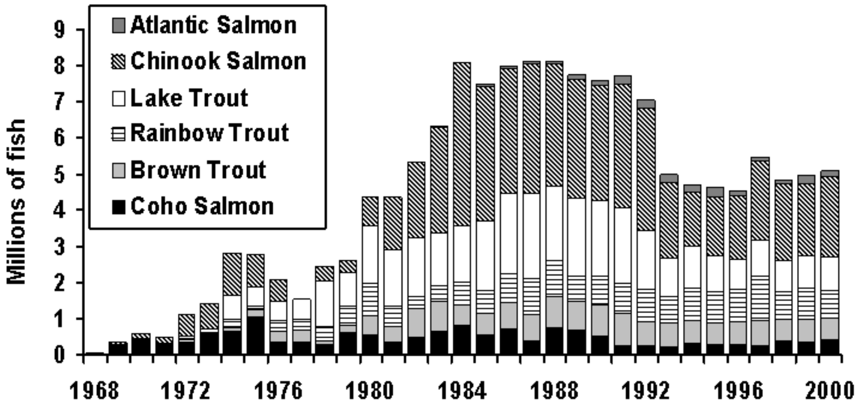


Fig. 11. Numbers of coho salmon, brown trout, rainbow trout, lake trout, chinook salmon, and Atlantic salmon stocked in Lake Ontario, 1968-2000 (excludes fish stocked at a weight <1 g).

Exploitation by Anglers

The salmonid fishery in Lake Ontario produced exceptional fishing effort and harvest by anglers. Harvest also reflected angler preferences–chinook salmon were most sought, followed in decreasing order by rainbow trout, lake trout, brown trout, and coho salmon (Stewart et al. 2003) (Fig. 12). Harvest rate and effort declined from 1985 to 1995 following the reduction in salmonid stocking in the mid-1980s. By 1995, fishing effort was about half the 1990 peak, and harvest declined by over two-thirds for all species from 1985 to 1995. For example, chinook salmon harvest declined from a high of 224,000 in 1986 to 53,000 by 1995 (Fig. 12) with 58% of the decline occurring in New York waters. During 1985 to 1995, total effort for all species in the offshore fishery ranged from 2.2-4.4 million angler-hours with 70% of the fishing effort occurring in New York waters (Stewart et al. 2003).

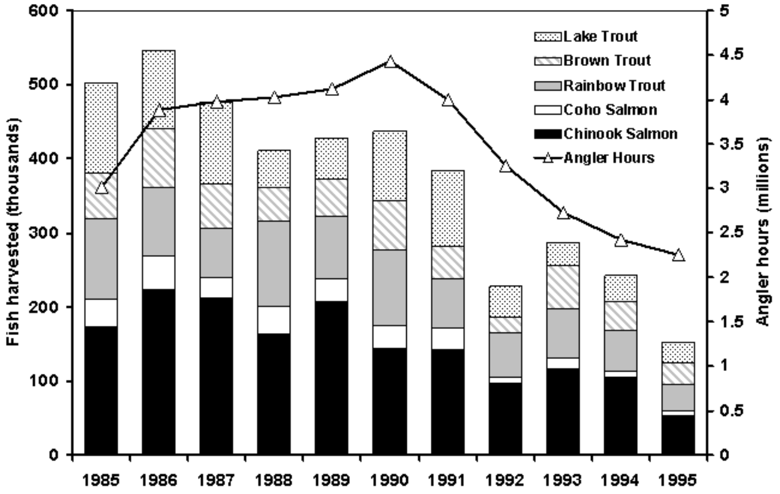


Fig. 12. Harvest (number of fish) of lake trout, brown trout, rainbow trout, coho salmon, and chinook salmon and effort by anglers (hours) in Lake Ontario, 1985-1995.

Lake Trout

Restoration programs have resulted in an increase in hatchery-reared lake trout in the Kingston Basin (Casselman et al. 1999) and U.S. waters (Elrod et al. 1995; O'Gorman et al. 1998). Relative abundance of yearling and older lake trout in the Canadian waters of the Kingston Basin increased in the 1980s, peaked in 1991, and then declined to levels similar to those in the 1980s (Fig. 13). In U.S. waters, abundance of immature fish peaked in 1983 and remained at relatively high levels throughout much of the 1980s before declining to low levels in the early 1990s (Fig. 14). Abundance of mature fish rose rapidly during 1980-1986 and remained high through 1998.

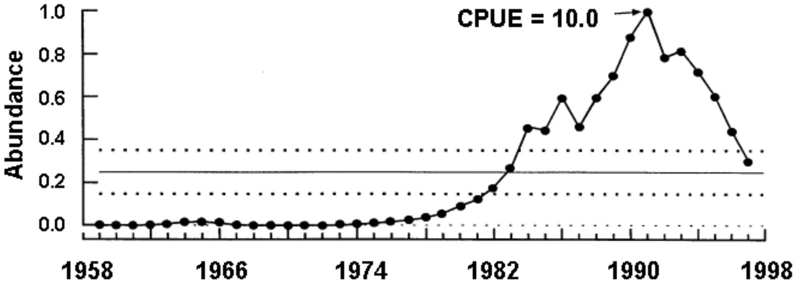


Fig. 13. Indices of relative abundance of lake trout (yearling and older) caught in deepwater sets of multi-mesh gill nets in May-August, 1958-1998, at six sites in the Kingston Basin of Lake Ontario. Index is a 3-year running geometric mean standardized to the maximum indicated CPUE. Mean and 95% confidence limit are solid and dark dotted lines, respectively. Zero is demarcated by a light dotted line (Casselman and Scott 2003).

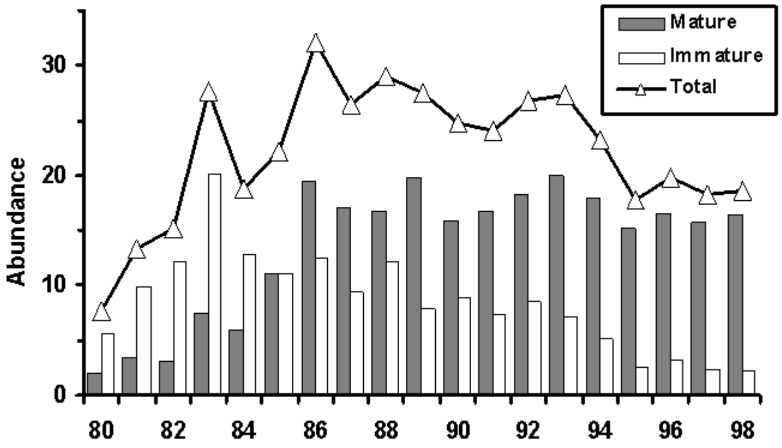


Fig. 14. Abundance of immature and mature lake trout from U.S. waters of Lake Ontario, 1980-1998. Abundance is the CPUE from joint New York State Department of Environmental Conservation and U.S. Geological Survey September gillnet surveys. CPUE is the mean catch from 10-17 random stations per year. At each station four nets were set parallel to contours, one at the 10ºC isotherm and the other three at 10-m successively deeper depths (Elrod et al. 1995; O'Gorman et al. 1998).

Despite seemingly adequate numbers of mature lake trout during much of the 1980s and early 1990s (Selgeby et al. 1995), naturally produced fish were not found except for fry captured on spawning shoals (Marsden et al. 1988; Casselman 1995; Elrod et al. 1995; Krueger et al. 1995). The failure of hatchery-origin fish to reproduce was puzzling because many of the environmental factors thought to contribute to reproductive failure of lake trout had been remediated and overall ecosystem quality had improved (Fitzsimons et al. 2003). Levels of contaminants of great concern for lake trout fry and adults declined in the 1970s and 1980s (Walker et al. 1991; Fitzsimons 1995; Guiney et al. 1996; Huestis et al. 1996). Contaminant levels in lake trout eggs were below those known to cause acute toxicity although the potential for sublethal effects continued (Fitzsimons 1995). High nutrient levels (Nicholls and Hopkins 1993) and excessive periphyton growth no longer caused low oxygen levels in interstitial spaces on spawning reefs where eggs incubate (Sly 1988). Alewife, however, were thought to impede the resurgence of lake trout because of their ability to exert heavy predation pressure on lake trout fry (Jones et al. 1995; Krueger et al. 1995; Fitzsimons et al. 2002) and to induce mortality of fry through thiamine deficiency (known as Early Mortality Syndrome (EMS)) caused by a maternal diet of alewife (Fitzsimons et al. 1999). EMS-induced mortality of newly hatched fry ranged from 50% to 75% in naturally deposited eggs on a spawning reef in western Lake Ontario during 1992-1999. During this same period, thiamine levels in eggs appeared, based on a sampling of adults adjacent to this same reef, to be declining. Although reduced thiamine levels and EMS are not sufficient to completely inhibit recruitment, sublethal effects resulting from thiamine deficiency may pose a significant bottleneck. Nevertheless, naturally produced age-1 and older lake trout of the 1993-1998 year-classes were found in low numbers throughout U.S. waters of the lake (O’Gorman et al. 1998; Owens et al. 2003). Reasons for the abrupt shift from consecutive years of reproductive failure to consecutive years of limited reproductive success are not clear. The shift coincided with a peak in potential egg deposition (BFL and RO, unpubl. data) and a change in the spring distribution of alewives toward deeper water and away from nearshore lake trout nursery areas (O’Gorman et al. 2000).

Recoveries of wild lake trout past the fry life stage were sporadic prior to 1993 and consisted of a few adults, whose scales and otoliths showed in-lake paternity, and several yearlings collected in OMNR index trawling (Casselman 2000). During 1993-1999, 140 young native trout were collected in U.S. waters and 15 in Canadian waters (O'Gorman et al. 1998; Casselman 2000). Year-class composition was similar for the U.S. and Canadian catches.

Lake Whitefish

Historically, whitefish were an important component of the Lake Ontario commercial fishery and an abundant species in the cold-water fish community of the eastern region of the lake. Most of the commercial harvest was taken from the Kingston Basin where two major spawning stocks existed: the bay stock that spawned in the Bay of Quinte and the lake stock that spawned along the south shore of Prince Edward County, Ontario. By the mid-1960s, these two stocks and the fishery they supported collapsed (Christie 1968); only small populations persisted into the late 1960s and 1970s. Bottom trawling surveys indicated that age-0 whitefish production began to increase in the late 1970s (lake stock) and early 1980s (bay stock). By 1986, the production of significant numbers of age-0 fish was higher, as reflected by especially large year-classes in 1987, 1991, 1992, 1994, and 1995. Catches of age-1+ whitefish (mixed stocks) increased throughout the 1980s and early 1990s in the Kingston Basin (Fig. 15).

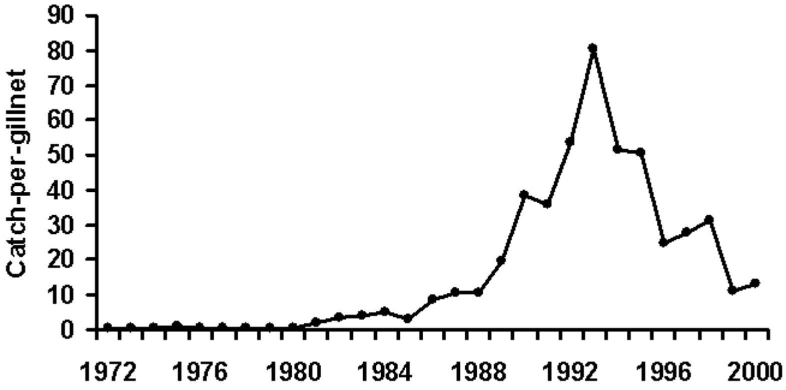


Fig. 15. Catch per gillnet (sum of catch adjusted to 100 m of each mesh size, 3.8- to 15.2-cm stretched measure) of age-1 and older whitefish in the Kingston Basin of Lake Ontario, 1972-2000.

Rehabilitation of lake trout in the late 1970s contributed to reductions in the alewife and rainbow smelt populations that may have indirectly impacted whitefish. Casselman and Scott (1992) showed that 94% of the variance in the catch of whitefish from the mid-1970s to the early 1990s was explained by the catch of lake trout four years earlier. Catches of large rainbow smelt were negatively correlated with the abundance of lake trout four years earlier and explained 70% of the variance. Hence, rainbow smelt abundance was negatively associated with whitefish abundance. These associations were strong, suggesting that large rainbow smelt have a direct effect on survival of larval whitefish.

Cold falls and winters followed by warm summers and reductions in the abundance of large rainbow smelt were associated with a substantial whitefish resurgence in the late 1970s and early 1980s (Casselman et al. 1996). By the early 1990s, whitefish stocks had recovered to historically high levels of abundance and a large spawning stock had accumulated (Casselman et al. 1996; Casselman 2000). Whitefish abundance peaked in the early 1990s but decreased rapidly after 1992. The demographics of the whitefish population also changed after 1992. Before 1994, the youngest fish caught on spawning shoals were age-3, whereas, after 1994, the youngest fish were age-5 or age-6. Mean age of fish in the harvest increased from ages 5-6 in 1994 to ages 8-9 in 1999.

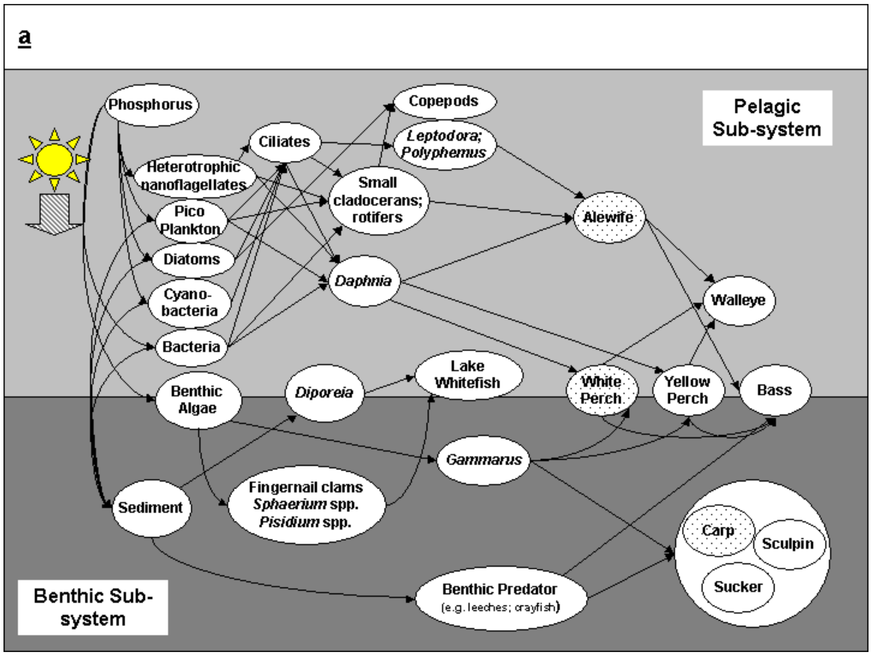
The deepwater amphipod diporeia has been an important food item of whitefish in Lake Ontario (Ihssen et al. 1981). No diporeia were found in whitefish stomachs in 1998.

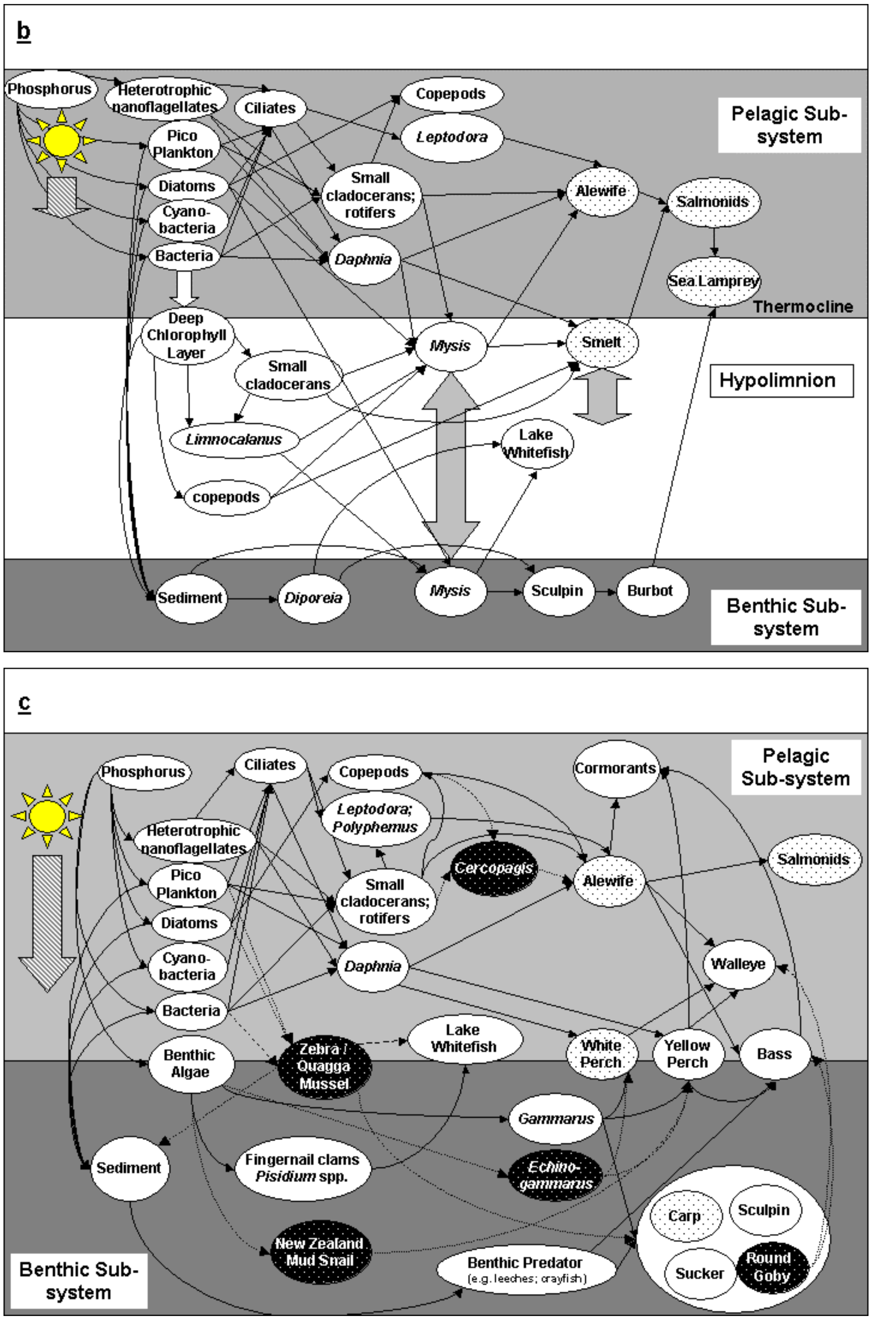
With the collapse of this important food resource by the mid-1990s in the Kingston Basin, whitefish shifted to other prey items, notably small (2-7 mm TL) dreissenid mussels, *Pisidium* spp., and *Sphaerium* spp. Dreissenid mussels consumed by whitefish were small (95% of mussels were 2-7 mm TL). A dramatic decline in whitefish condition was associated with the shift in diet to a predominance of dreissenids (Hoyle et al. 2003).

The Lake Ontario Food Web

Ecological changes in the Lake Ontario food web have been dramatic since SCOL I (Fig. 16). In the 1950s and 1960s, pessimism prevailed among Great Lakes scientists and managers as depreciation of the fish communities and degradation of water quality proceeded unabated. By 1970, lake trout populations were extirpated, the few remaining salmonids were riddled with sea lamprey wounds, cultural eutrophication resulted in excessive algal growth and low water clarity, proliferation of alewife led to intense zooplanktivory and a predominance of small cladocerans and cyclopoid copepods, and only a remnant population of whitefish persisted (Fig. 16a, b). In ensuing years, oligotrophication drove the recovery process, and the food web was altered greatly (Fig.16c, d). By 2000, sea lamprey predation no longer plagued salmonids and burbot, exotic alewife supported a recreational fishery for Pacific salmon, and the invasion of *Dreissena* spp. fostered new trophic interactions. The microbial food web including bacteria, ciliates, heterotrophic nano-flagellates, and picoplankton was identified as an essential pathway of energy transfer to zooplankton. Food-web changes were most evident in nearshore areas: diporeia disappeared; six new invasive species were established (*Cercopagis pengoi*, *Dreissena polymorpha*, *D.*

bugensis, *Neogobius melanostomus*, *Potomopyrgus antipodarum*, and *Echinogammarus ischnus*); large fingernail clams (*Sphaerium* spp.) disappeared; double-crested cormorant populations greatly expanded; and water clarity increased dramatically. *C. pengoi* proliferated in late summer and early fall in offshore waters, and densities of quagga mussels exceeded those of zebra mussels at depths >15 m along the southern shore of the lake. Despite these changes, omnivorous *Mysis relicta* populations remained relatively stable, coupling the benthic and pelagic food webs.




b
Phosphorus
Heterotrophic nanoflagellates
Ciliates
Copepods
Leptodora
Pelagic Sub-system
Pico Plankton
Diatoms
Cyano-bacteria
Bacteria
Small cladocerans; rotifers
Alewife
Salmonids
Daphnia
Sea Lamprey
Thermocline
Deep Chlorophyll Layer
Mysis
Smelt
Small cladocerans
Hypolimnion
Limnocalanus
Lake Whitefish
copepods
Sediment
Diporeia
Mysis
Sculpin
Burbot
Benthic Sub-system
c
Phosphorus
Ciliates
Copepods
Cormorants
Pelagic Sub-system
Leptodora; Polyphemus
Heterotrophic nanoflagellates
Cercopagis
Alewife
Salmonids
Pico Plankton
Small cladocerans; rotifers
Diatoms
Cyano-bacteria
Daphnia
Walleye
Bacteria
Lake Whitefish
Zebra / Quagga Mussel
White Perch
Yellow Perch
Bass
Benthic Algae
Gammarus
Sediment
Fingernail clams Pisidium spp.
Echino-gammarus
Carp
Sculpin
New Zealand Mud Snail
Sucker
Round Goby
Benthic Sub-system
Benthic Predator (e.g. leeches; crayfish)

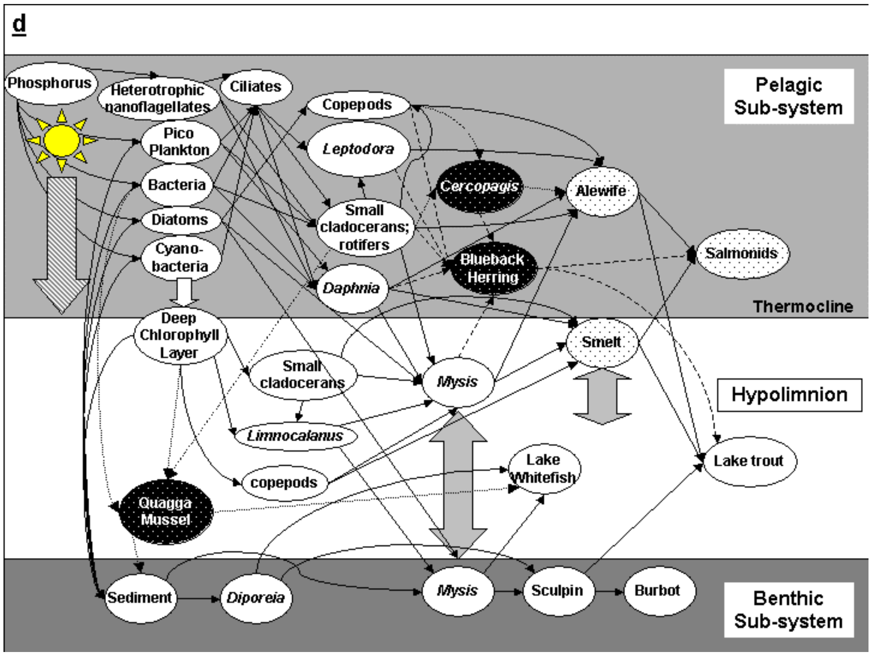


Fig. 16. The food web of Lake Ontario in nearshore (a, c) and offshore (b, d) habitats in 1970 (a, b) and 2000 (c, d). Thin solid arrows indicate the direction of energy flow; thin, dashed arrows represent energy flow to and from exotic species introduced since 1970; wide, gray bi-directional arrows represent migration through the water column; and wide, striped uni-directional arrows represent the relative depth of light penetration. All exotic species are stippled with those that arrived post-1970 shown against a dark background. Predator-prey interactions involving larval fish are not depicted.

Climate Change and the Lake Ontario Ecosystem

The effects of climate and climate change on population abundance and community dynamics of Lake Ontario fish were unknown at SCOL I because historical time-series data were lacking. Most of the time series that were rigorous and community-based were initiated in the late 1950s. For example, community-based sampling of eastern Lake Ontario and the Bay of Quinte was initiated in the late 1950s such that they were little more than a decade old when reviewed in SCOL I (Christie 1972). The maturity of these data sets today has provided the scope and precision necessary to quantify effects of climate change (Casselman 2000).

Long-Term Temperature Trends

Mid-summer (July and August) surface-water temperatures over the past 60 years averaged 23.2°C with an average annual variability of more than 3.5°C (Casselman 2002). From 1987-1991, summers were especially warm with four of the five years being well above average. Warm years were synchronous with the strongest El Niño events, and cold years were synchronous with the strongest La Niña events. The one notable exception was the cold summer of 1992 that occurred during an El Niño period (1991-1995) and was a result of the June 1991 eruption of Mount Pinatubo in the Philippines (Nicholls et al. 1996). Volcanic ash from the eruption circled the northern hemisphere and produced a global cooling effect throughout 1992, which affected open-water conditions in Lake Ontario into 1993 and 1994 (Casselman et al. 1999). Seven of the 10 years from 1956 to 1965 were below average and were related to the La Niña events of 1956-1957 and 1965.

Water temperatures in the Bay of Quinte during April-September increased significantly after 1950. Water temperatures increased 1.1°C after 1950 and reached record-high levels in the late 1990s. This overall trend matches predictions of global climate change (Nicholls et al. 1996). December water temperatures describe late-fall thermal conditions and reflect winter severity. For the Lake Ontario ecosystem, the temperatures during December are especially important for understanding changes in fish populations (Casselman 2002). Early winter conditions affect spawning and the period of most rapid egg and fry development in native salmonids (lake trout, lake herring, and whitefish). Further, December water temperatures correlate with winter severity, which is known to affect important prey and larval fish predators such as alewife (O’Gorman et al. 1987) and white perch (Hurley 1986).

Winter Kills of Thermally Ill-Adapted Exotics

The effects of global climate on the Lake Ontario fish community have been most obvious in the winter-kill dynamics of alewife. Substantial winter kills occurred during the severe winters of 1976-1977 and 1977-1978, resulting in the lowest abundance of alewife since 1972 (Hurley 1986; O'Gorman and Schneider 1986; O'Gorman et al. 1987; Ridgway et al. 1990; Casselman and Scott 2003) (Fig. 17). Subsequent to the mass mortality of alewife following severe winters, growth of survivors increased (O'Gorman and Schneider 1986). White perch also experienced mass mortality in the severe winters of 1976-1977 and 1977-1978 (Minns and Hurley 1986). White perch are important predators on larval walleye; with white perch numbers depressed, larval walleye survival was substantially enhanced, and a major year-class was produced in the Bay of Quinte in 1978 (Casselman and Scott 2003).

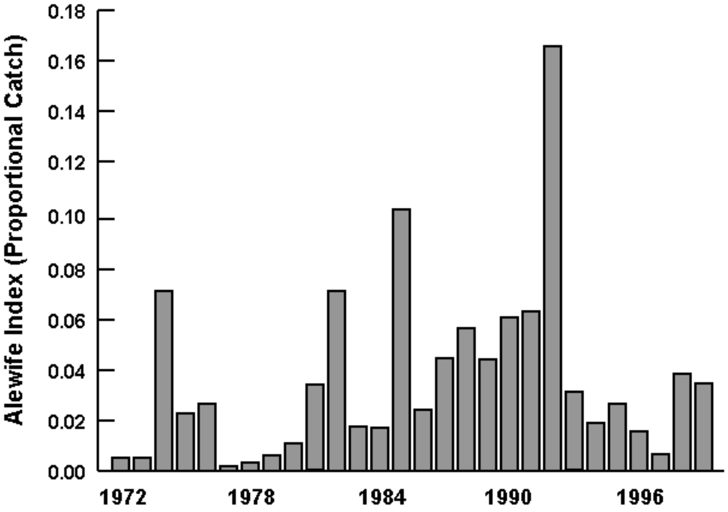


Fig. 17. Indices of proportional abundance of alewife (yearling and older) caught in May-August, 1972-1999, in bottom trawls and multi-mesh gillnets at six standard deepwater sites in the Kingston Basin of Lake Ontario used for long-term community indexing (Casselman and Scott 1992; Casselman et al. 1999).

Recruitment of Spring-Spawning Species

Although survival of alewife can be negatively affected by severe winters, warm springs can enhance recruitment of species such as northern pike (*Esox lucius*) (Casselman and Lewis 1996), smallmouth bass (Hoyle et al. 1999), and yellow perch (JMC, unpubl. data). Year-class strength of alewife produced by emigrants spawning in the Bay of Quinte is positively correlated with May water temperatures (Fig. 18) (Casselman 2000). The relationship does not appear to be linear, however, because when temperatures are either extremely low or extremely high, age-0 alewife abundance deviates from the trend. The strongest alewife year-classes appear to be produced at intermediate temperatures. Temperature effects are likely complex, but alewife recruitment and abundance are temperature-related.

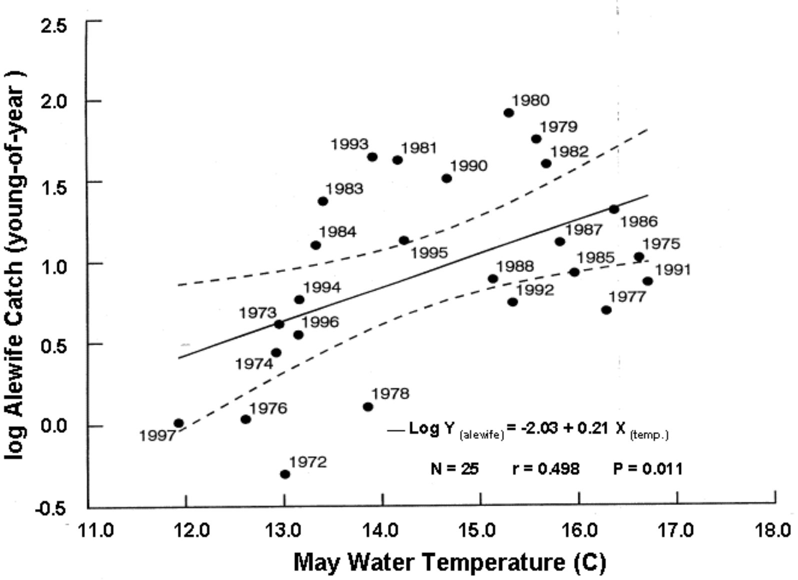


Fig. 18. Relation between the logarithm of the summer (August-September) catch of age-0 alewife per trawl haul in the Bay of Quinte and spring (May) water temperatures in Lake Ontario, 1972-1997. Regression equations, correlation coefficient, and probability level are shown. Dashed, curved lines delineate the 95% confidence limits (Casselman 2000).

The effects of climate and temperature on year-class strength of many fish species are becoming increasingly well documented (Casselman 2002). For cool- and warm-water fish, the effects of climate and temperature are usually correlated with either spring or summer temperatures or with the length of the growing season. Generally, warmer conditions produce stronger year-classes of warm-water species. In contrast, extremely warm summers, as exemplified by those of 1973 and 1975 in eastern Lake Ontario, can be too warm for cool-water species such as northern pike (Casselman and Lewis 1996).

Recruitment of Fall-Spawning Species

Spring water temperatures are usually positively related to year-class strength and productivity of spring-spawning species, whereas fall water temperatures are likely negatively related to year-class strength of fall-spawning, cold-water species (Casselman 2000, 2002). Cold falls and severe winters, which in Lake Ontario hamper thermally ill-adapted exotic species such as alewife and white perch, have a positive effect on year-class strength of salmonids. The resurgence of whitefish in Lake Ontario in the late 1970s and early 1980s likely resulted from an abnormally cold fall and winter in 1976-1977 (Casselman et al. 1996; Hoyle et al. 1999). Year-class distributions from spawning whitefish in 1988 and 1990 indicated that the resurgence in the late 1970s coincided with a substantial contribution from the 1977 year-class. Remarkably, remnants of two other strong, older year-classes, the 1962 and 1967, were also present in 1988 and 1990 and were major contributors to the 1977 year-class. All three strong year-classes, 1962, 1967, and 1977, hatched in winters so cold that alewife suffered winter mortality the following spring. In fact, spawning temperatures in the fall of 1976 were colder than in any other year during the past 25 years.

Discussion

Fisheries exploitation, introductions, and eutrophication were highlighted in SCOL I as factors contributing to the degradation of Great Lakes fish communities. The sea lamprey and alewife were recognized as particularly important predators impacting the Lake Ontario fish community (Christie 1972; Christie et al. 1987b). Since 1970, negative effects of exploitation of native fishes, eutrophication, sea lamprey, and alewife have been largely ameliorated, thereby contributing greatly to the restoration of the Lake Ontario ecosystem. The new establishment of non-native species, however, continues to hamper goals to restore Lake Ontario’s historical fish communities by causing irreversible ecological effects.

Managers of the Lake Ontario ecosystem in the late 1960s and early 1970s recognized that water-quality degradation was so extreme that the lake environment had to be changed. Results of ecological studies indicated that eutrophication could be reversed through mandated controls on phosphorus loading to the lake (Neilson and Stevens 1987). The GLWQA signed by the U.S. and Canada in 1972 provided the backdrop for a reduction in total phosphorus levels in offshore waters of Lake Ontario to a target level of 10 $\mu g \bullet L^{-1}$ and set the stage for oligotrophication. Skeptics predicted that environmental change was either irreversible or would take decades. But Lake Ontario (and Lake Erie) responded soon after remedial measures were put in place. At the time of the GLWQA, however, the connection between phosphorus supply and higher trophic-level production, especially to fish, was not understood. Subsequently, scientists realized the need for long- and short-term studies that focused on food-web linkages, and managers recognized their value in decision making. Scientists and managers would take longer to acknowledge that the issues of water quality and fisheries production were linked.

Control of the sea lamprey was effective in improving the survival of salmonid piscivores in Lake Ontario, and advances in fish-culture technology led to the establishment of large populations of salmonid predators that effectively controlled alewives. With an expanding salmonid predator population, fishery managers were forced to address ecological issues related to food availability, habitat, genetics, pathogens, and exotics, as well as the concerns of stakeholders.

Fishery managers hoped that the path to recovery of the Lake Ontario ecosystem following the 1950s and 1960s would be a return to historical conditions. Early signals were consistent with these expectations. For example, nuisance algal blooms declined dramatically in response to nutrient abatement and re-established native species such as lake trout responded positively to sea lamprey control (Elrod et al. 1995). Further, structural changes in the size and species composition of phytoplankton indicated a shift from a eutrophic to an oligotrophic community, and, in association with this change, smaller-sized organisms contributed more to primary productivity (Munawar and Munawar 2003; Munawar et al. 2003). The recovery of Lake Ontario would take a new ecological path—one that would be markedly influenced by unplanned introductions. Restoration of lake trout, for example, would be hampered by a thiamine deficiency of fry brought about by their parents feeding on exotic alewife (Fitzsimons et al. 1999). Whitefish populations would no longer thrive because of the loss of their preferred food—the native amphipod diporeia. The lesson of the last three decades has been clear: the trajectory of the recovery process of the Lake Ontario food web has taken new and unpredicted ecological paths.

Restoration of Great Lakes fish communities has often been considered a signal of a healthy ecosystem. Re-establishment of the bloater in Lake Ontario would satisfy those who desire an ecosystem that supports a self-reproducing, diverse fish community. Historically, bloaters migrated in close association with their migrating prey, *Mysis relicta*. Mysids are abundant in Lake Ontario's abyss; their offshore biomass may exceed that of alewife and rainbow smelt combined (Johannsson et al. 2003). The lack of a significant deepwater predator for mysids is a missing link in the Lake Ontario food web—a link that limits movement of energy in the offshore pelagia. Evidence of improved environmental conditions, reduced alewife and rainbow smelt densities, and an abundant offshore mysid population in Lake Ontario would seemingly provide a window of opportunity to re-establish bloaters. The collapse of diporeia populations, however, eliminated the likelihood of fully restoring bloaters because, in Lake Michigan, diporeia was the most important food (followed closely by *M. relicta*) in bloater diets (Wells and Beeton 1963). Although competition with dreissenids for food is suspected as the cause of the loss of diporeia, other factors such as disease(s) from pathogens are also possible. If mysid populations collapse, restoration of bloater would likely be impossible.

Concerns about the roles played by persistent organic contaminants in the demise of lake trout in Lake Ontario and in their marginally successful rehabilitation have persisted for decades (Zint et al. 1995; Cook et al. 1997). The suspected historical effects of contaminants on lake trout cannot yet be definitively determined because the appropriate analytical methods for their detection are recent. Nevertheless, new methodologies and assessment techniques (Cook et al. 1997) now permit more definitive statements regarding the current potential of contaminants to block fish reproduction (Fitzsimons 1995). The historical effects of contaminants on lake trout and other fish species will continue to be explained in the coming decades. Although lake trout fry are highly sensitive to dioxin and dioxin-like chemicals, residue levels are now below those associated with acute toxicity. The synergistic effects of other organo-chemicals on newly discovered phenomena such as diet-induced thiamine deficiency (Fisher et al. 1996; Fitzsimons et al. 1999) in fish are unknown and need to be explored.

One of the most dramatic changes in the Lake Ontario ecosystem since SCOL I was improved water clarity resulting from both oligotrophication and the invasion of dreissenids. Increased water clarity has resulted in far-reaching trophic interactions that could only be determined from understanding the whole food web. For example, following establishment of dreissenid mussels, increased water clarity may have caused alewife, rainbow smelt, and age-2 lake trout to shift to deeper water (O'Gorman et al. 2000). The outcome of this shift is unclear currently but this behavior modification will increase predation on *M. relicta*.

Zebra mussel-induced water-clarity changes likely redirected energy produced nearshore to benthic habitats and perhaps made them more vulnerable to invasion by non-native species. So far, *Echinogammarus ischnus*, the New Zealand mud snail, and the round goby have become established in nearshore benthic habitat during the 1990s (Fig. 16c). Round gobies will likely play a special role in the coming decades as a benthic prey and an important energy vector between *Dreissena* spp. and predaceous fishes, especially with the current declines in diporeia and slimy sculpin. Gobies, however, are unlikely to replace slimy sculpin as the preferred prey of juvenile lake trout during thermal stratification because the bathymetric distributions of the two species differ—gobies are on the bottom above the thermocline and juvenile lake trout are well below the thermocline. If gobies migrate to greater depths in the fall as thermal stratification weakens, they likely will provide food for juvenile and adult lake trout and in so doing would partially fill the functional role of slimy and deepwater sculpins. Interestingly, questions regarding future food-web scenarios in Lake Ontario will most likely involve organism functionality, as discussed by Eshenroder and Burnham-Curtis (1999). For example, does it matter whether lake trout feed on gobies or sculpin if these benthic fishes serve similar functional roles in the food web?

M. relicta, in contrast to zooplankton, diporeia and alewife, have exhibited little response to oligotrophication, increased water clarity, and top-down effects of fisheries management. Mysid production, however, has increased, possibly a result of declining numbers of larger alewife that feed on them (Johannsson et al. 2003). This low-level response of mysids could be due to their migration patterns and their use of the largest habitat, by volume (the hypolimnion), in the lake. These factors minimize predation on mysids by visually feeding fish. In addition, omnivory allows mysids to switch to algae or detritus if their primary prey, zooplankton, declines in abundance. For alewife, the primary forage fish in the lake, the principal role of mysids may be one of energy storage (Johannsson et al. 2003). Metalimnetic zooplankton production can be stored as mysid biomass and fed on by alewife from fall through spring when the distributions of the two species overlap. The availability of mysids could have significant implications for growth, gonad development, and overwinter survival of alewife.

Moving into the Future

The post-1970 era provided assurance to skeptics that environmental change in the Lake Ontario ecosystem associated with chemical pollution was reversible. In contrast, environmental change associated with biological pollutants such as invasive species is likely irreversible. Once established, exotics rarely disappear, although their role in the food web may change significantly with time. For example, the role of the alewife has shifted over the last six decades from a nuisance species to a pivotal species that supports a multi-million-dollar salmonid sport fishery (O'Gorman and Stewart 1999). Ironically, although environmental conditions have greatly improved in Lake Ontario and the other Great Lakes during the last three decades, this period has coincided with an acceleration in the establishment of new exotics (Mills et al. 1993; Ricciardi 2001). Global transport of organisms associated with shipping and the establishment of organisms from far-away places such as the Black, Caspian, and Baltic Seas were unheard of in the decades prior to 1970. Although the intent of the GLWQA was "to restore and maintain the chemical, physical, and biological integrity of Great Lakes waters," release of untreated waters from the ballast tanks of ocean-going vessels into the Great Lakes was not considered within the Agreement. We recommend that future policy makers institute measures to reduce the risk of introducing new biological pollutants to Lake Ontario and the other Great Lakes.

Over the last two decades, Lake Ontario has experienced significant reductions in phosphorus with a concomitant shift toward oligotrophy and a dramatic increase in water clarity resulting from both nutrient reduction and proliferation of filter-feeding *Dreissena* spp. Macroinvertebrate activity increased since the invasion of *Dreissena* spp. (Stewart and Haynes 1994), light penetration increased, benthic-feeding round gobies became established, and benthic algae such as *Cladophora* reached nuisance levels (Charles O'Neill, New York Sea Grant, Brockport, New York, personal communication). We suggest that these events are in response to greater light penetration and reflect a redirection of energy production from pelagic to benthic habitat. We contend that the combined effects of oligotrophication and dreissenid-induced modifications will favor benthic over pelagic energy pathways, particularly in nearshore areas and bays. We expect that this shift in the direction of energy flow will have dramatic ecological consequences for the lake by favoring colonization of bottom-dwelling organisms, promoting fish communities that make efficient use of benthic habitat, and enhancing growth of benthic algae and submersed aquatic vegetation. Thus, we expect benthification to be coupled with the oligotrophication of Lake Ontario.

We expect that future global warming will lead to increasing water temperatures in Lake Ontario and thereby affect the dynamics between fishes and their habitats. The impacts (both positive and negative) of global warming on fish species will depend on species-specific thermal requirements and changes in thermal habitat. Rising temperatures associated with seasonal climate events could positively affect salmonids by increasing the habitat volume for cold-water species in well-oxygenated lakes like Lake Ontario (Magnuson et al. 1990). On the other hand, increasing water temperatures in late fall and early winter may negatively affect fish survival and emergence, notably of lake trout and whitefish (Casselman 1995). At the same time, increasing water temperatures could result in stronger year-classes of warm-water species such as smallmouth bass (Casselman et al. 2002) and alewife.

The initial introduction of salmonids into the Great Lakes was, in part, an attempt to control alewife but focused quickly on developing a multi-million-dollar recreational fishing industry (O'Gorman and Stewart 1999). The strategy for rehabilitation of lake trout, and later Atlantic salmon, in Lake Ontario had strong scientific and ecological underpinnings (Elrod et al. 1995; Schneider et al. 1983). The overwhelming desire of stakeholders to have a recreational fishery made up of both native and exotic salmonids, however, has been the driving force of fishery management. Consequently, the current Lake Ontario fish community comprises a mix of exotic species that have no evolutionary sympatry. In addition, the number of salmonids and their top-down influence on fish communities (Christie et al. 1987a; McQueen et al. 1989) is regulated largely through stocking. As a result, conventional ecological paradigms are difficult to apply, and descriptions of historical fish-community structures are not useful for either understanding or predicting species interrelationships or equilibrium states (Christie et al. 1987b; Eshenroder and Burnham-Curtis 1999). Managers of the Lake Ontario fishery resource will be challenged in the coming decades as the ecosystem changes and will need to rely more on tools such as ecological modeling and risk assessment to gain insights into possible outcomes and consequences of management decisions.

As we move into the future, managers will continue to struggle with the sustainability of fishery resources. Some will argue for maximum utilization of fishery resources, and others will be more concerned with restoration of native-species assemblages. Regardless of which fish community is preferred, understanding how fish integrate into the Lake Ontario food web and respond to environmental change has become embedded into the thinking of managers and scientists alike. The Lake Ontario ecosystem and its stakeholders have and will continue to profit from this philosophy in the coming decades. The Lake Ontario food web and energy partitioning within it have become more complex, particularly in nearshore waters. Understanding ecological processes involving benthic and pelagic food-web pathways and their linkages to fish will continue to challenge both scientific understanding and a desire to manage large-lake ecosystems. Challenges for scientists, managers, and stakeholders in the coming decades will be monumental, because expectations will be hampered by ecological surprises resulting from anthropogenic forces such as climate change and species invasions. We hope that society will invest in the future of Lake Ontario and the other Great Lakes because they are among the greatest natural resources on earth.

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