PERSPECTIVE

Dynamics of the Lake Michigan food web, 1970–2000

Charles P. Madenjian, Gary L. Fahnenstiel, Thomas H. Johengen, Thomas F. Nalepa, Henry A. Vanderploeg, Guy W. Fleischer, Philip J. Schneeberger, Darren M. Benjamin, Emily B. Smith, James R. Bence, Edward S. Rutherford, Dennis S. Lavis, Dale M. Robertson, David J. Jude, and Mark P. Ebener

Abstract: Herein, we document changes in the Lake Michigan food web between 1970 and 2000 and identify the factors responsible for these changes. Control of sea lamprey (*Petromyzon marinus*) and alewife (*Alosa pseudoharengus*) populations in Lake Michigan, beginning in the 1950s and 1960s, had profound effects on the food web. Recoveries of lake whitefish (*Coregonus clupeaformis*) and burbot (*Lota lota*) populations, as well as the buildup of salmonine populations, were attributable, at least in part, to sea lamprey control. Based on our analyses, predation by salmonines was primarily responsible for the reduction in alewife abundance during the 1970s and early 1980s. In turn, the decrease in alewife abundance likely contributed to recoveries of deepwater sculpin (*Myoxocephalus thompsoni*), yellow perch (*Perca flavescens*), and burbot populations during the 1970s and 1980s. Decrease in the abundance of all three dominant benthic macroinvertebrate groups, including *Diporeia*, oligochaetes, and sphaeriids, during the 1980s in nearshore waters (≤50 m deep) of Lake Michigan, was attributable to a decrease in primary production linked to a decline in phosphorus loadings. Continued decrease in *Diporeia* abundance during the 1990s was associated with the zebra mussel (*Dreissena polymorpha*) invasion, but specific mechanisms for zebra mussels affecting *Diporeia* abundance remain unidentified.

Résumé : On trouvera ici une étude des changements dans le réseau alimentaire du lac Michigan de 1970 à 2000 et des facteurs qui en sont responsables. Le contrôle des populations de la grande lamproie marine (*Petromyzon marinus*) et du gaspareau (*Alosa pseudoharengus*), qui a débuté dans les années 1950 et 1960, a eu un impact considérable sur le réseau alimentaire. Le rétablissement des populations du grand corégone (*Coregonus clupeaformis*) et de la lotte (*Lota lota*) et l'accroissement des populations de salmonidés sont dus, au moins en partie, au contrôle de la lamproie.

Can. J. Fish Aquat. Sci. **59**: 736–753 (2002) DOI: 10.1139/F02-044

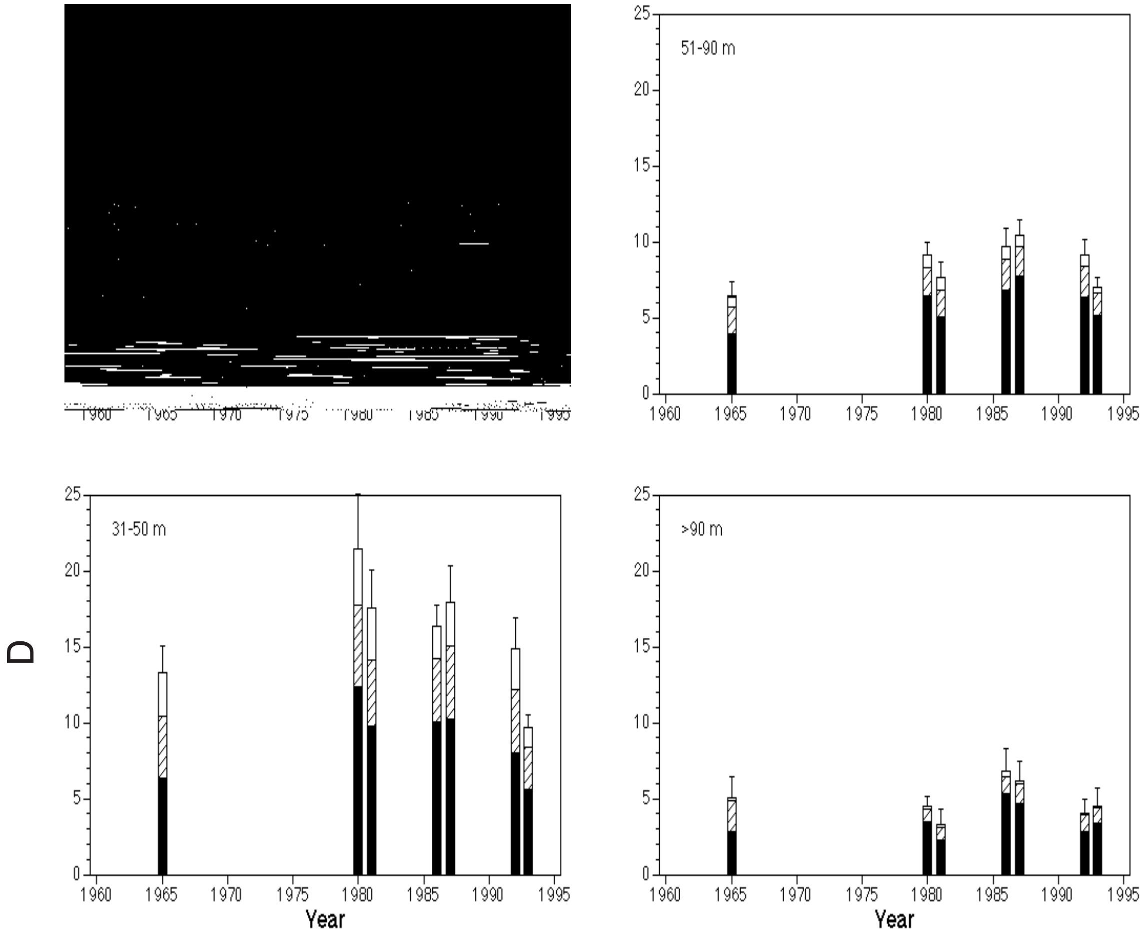
D’après nos analyses, la réduction de la densité des gaspareaux dans les années 1970 et au début des années 1980 est due principalement à la prédation par les salmonidés. À son tour, la réduction des gaspareaux a sans doute contribué au rétablissement des populations du chabot de profondeur (*Myoxocephalus thompsoni*), de la perchaude (*Perca flavescens*) et de la lotte dans les années 1970 et 1980. Durant les années 1980, la décroissance de la densité des trois groupes dominants de macroinvertébrés benthiques, *Diporeia*, les oligochètes et les sphériidés, dans les eaux côtières (≤50 m de profondeur) du lac Michigan est attribuable à une diminution de la production primaire lié à une réduction des apports de phosphore. La poursuite du déclin des densités de *Diporeia* dans les années 1990 est associée à l’invasion de la moule zébrée (*Dreissena polymorpha*

rus is also the easiest nutrient to control, primarily because phosphorus has no gaseous phase. Thus, regulation of phosphorus has been the primary management strategy for controlling eutrophication in the Great Lakes. Billions of dollars have been spent to reduce phosphorus inputs to the Great Lakes, and success has been documented in the lower Great Lakes (Johengen et al. 1994).

Phosphorus control programs substantially reduced phosphorus loadings to Lake Michigan (Fig. 1). Total annual loading decreased from over 6.5 kilotonnes (kt) in 1980 to aboutvioie et al. 1998). Diatoms have composed the bulk of the phytoplankton community during the spring isothermal mixing period since 1970.

In Lake Michigan, a deep chlorophyll layer typically forms in the upper hypolimnion and lower metalimnion during summer stratification, and this layer contributes between 5 and 10% of the annual total chlorophyll and annual primary production within the lake (Fahnenstiel and Scavia 1987*b*). Size of the deep chlorophyll layer increased between the 1970s and 1980s. This increase was attributed to greater light penetration caused by increased grazing due to increased abundance of the very large-bodied zooplankter *D. pulicaria* (Scavia et al. 1986). This change in epilimnetic zooplankton composition did not persist for more than a few years (Evans 1992), and a shift back to smaller-bodied zooplankton apparently led to a reduction in the size and concentration of the deep chlorophyll layer (Fahnenstiel and Scavia 1987*c*; G. Fahnenstiel, unpublished data).

Although a long-term series of observations on phytoplankton abundance was not available for most of the 1970–2000 time period, the available data suggested that phytoplankton abundance and production in nearshore waters of Lake Michigan have decreased during the past 30 years. Schelske et al. (1980) intensively surveyed spring TP and chlorophyll *a* concentrations in nearshore waters of the eastern side of the lake during 1972. Nearshore waters in the vicinity of the Cook Power Plant in the southeastern section of the lake was consistently sampled for chlorophyll *a* concentration during 1973–1981. Similar sampling was conducted during the recent Episodic Events – Great Lakes Experiment (EEGLE) study from 1998–2000 in the sameCookofal. thephphate s(chlorphlorphlorphlorp)F67Teoire64.2(1978tabh4h8i.8TJ To(Ev)27taaa2099i7.ted)099ted 99(obstu TD 1.6()20

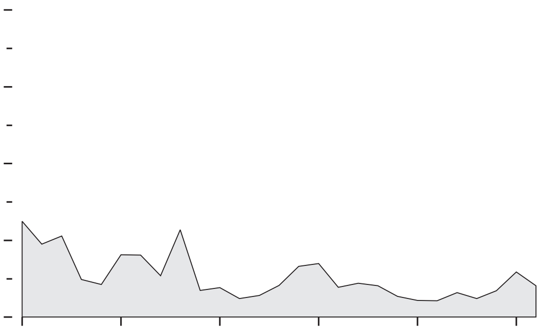


in Lake Michigan, and *Diporeia* exhibits a higher lipid content than other benthic macroinvertebrates (Gardner et al. 1985). If *Diporeia* were sufficiently reduced in abundance on a lake-wide basis, then fish heavily reliant on *Diporeia* as a food source would have to switch to other prey. Consequences of such diet switching on the growth and survival of these fishes remain unknown.

Although surveys by Nalepa (1987) and Nalepa et al. (1998) have documented changes in macroinvertebrate communities in areas deeper than 15 m, community changes have also occurred in shallower regions of Lake Michigan. The zebra mussel invasion has resulted in increased abundance of chironomids and the amphipod *Gammarus* in the shallow, rocky habitats of southern Lake Michigan (Kuhns and Berg 1999).

Dynamics of zooplankton

Long-term trends in zooplankton community structure and abundance have been documented for nearshore waters (≤50 m deep) of southeastern Lake Michigan in the vicinity of the Cook Power Plant between 1972 and 1984 by Evans and Jude (1986) and Evans (1992), and for a large portion of the offshore region (>50 m deep) during 1983–1992 by Makarewicz et al. (1995). In deeper (30- to 40-m) waters sampled by Evans and Jude (1986), summer daphnid assemblage shifted from a 1972–1976 community strongly dominated by the medium-bodied *Daphnia retrocurva* to a 1977–1981 community strongly dominated by the large-bodied *D. galeata mendotae*, to a 1982–1984 community dominated by the very large-bodied *D. pulicaria*. In contrast, *Daphnia retrocurva* dominated the daphnid community in shallower waters in the Cook Plant vicinity from 1972 to 1984. Additionally, abundance of daphnids in shallower waters was substantially higher during 1972–1980 than during 1981–1984. Evans and Jude (1986) attributed this decrease in daphnid abundance to increased predation pressure exerted by the yellow perch (*Perca flavescens*) population, which increased dramatically in size between 1980 and 1984. Evans and Jude (1986) concluded that the appearance of the very large-bodied *D. pulicaria* in the deeper waters during 1982–1984 was possibly related to a decline in alewife abundance during the 1970s and early 1980s. Wells (1970) contended that increased alewife abundance in offshore waters of Lake



Michigan during the late 1950s and early 1960s led to a shift in the size structure of the summer zooplankton community from large-bodied to small-bodied copepods and cladocerans. Evidence to support the contention that high abundance of alewives in 1966 resulted in a zooplankton community dominated by small-bodied forms was compelling; however, relatively low alewife abundance did not necessarily imply that very large-bodied zooplankters would dominate the zooplankton community (Evans 1992).

Although species composition of the crustacean zooplankton community changed considerably during 1983–1992 in offshore waters of Lake Michigan, crustacean zooplankton biomass varied without trend during that time (Makarewicz et al. 1995). Furthermore, in comparing their data with observations by Scavia et al. (1986), Makarewicz et al. (1995) concluded that crustacean zooplankton biomass during the summer in offshore waters of Lake Michigan showed no trend between 1975 and 1992. *Daphnia pulicaria* was an important constituent of the daphnid community in 1983, but subsequently declined in abundance until nearly disappearing from the lake by 1987 (Makarewicz et al. 1995). Overall, *Diaptomus* dominated the zooplankton community during 1983–1992. Increases in rotifer biomass between 1983 and 1992 were correlated with increases in unicellular algae (Makarewicz et al. 1995). Based on correlation analysis, Makarewicz et al. (1995) suggested that alewives during 1983–1992 were probably not playing a dominant role in affecting zooplankton biomass and size structure except for the size structure of calanoid copepods. However, alewife abundance remained relatively low during this time period (Fig. 4). Preliminary examination of zooplankton samples during 1994–1999 suggested that no major changes in species composition or abundance had occurred since the Makarewicz et al. (1995) study (J. Cavaletto, NOAA Great Lakes Environmental Research Laboratory, Ann Arbor, MI 48105, U.S.A., personal communication).

Invasion of Lake Michigan by the predatory cladoceran *Bythotrephes cederstroemi* in 1986 appeared to have caused some changes in zooplankton community structure (Makarewicz et al. 1995). For example, the decrease in *Daphnia retrocurva* abundance after 1986 was most likely attributable to predation by *Bythotrephes* (Lehman and Cáceres 1993).

Other than the increase in rotifer biomass between 1983 and 1992, evidence for changes in zooplankton community structure and abundance originating from bottom-up effects was not strong (Makarewicz et al. 1995). Furthermore, the issue of whether changes in top-down control from alewives or from *Bythotrephes* led to changes in phytoplankton abundance or composition remains contentious (Evans 1992; Makarewicz et al. 1998).

Abundance of *Mysis relicta*, a common prey of alewife, bloater, rainbow smelt (*Osmerus mordax*), and lake whitefish (*Coregonus clupeaformis*), in southern Lake Michigan has remained relatively stable from the 1970s through 1998 (Pothoven et al. 2000). *Mysis* is an important predator of zooplankton in Lake Michigan. Whereas micrograzers (protozoans and ciliates) are an important component of the Lake Michigan food web (Fahnenstiel et al. 1998), insufficient data are available to characterize temporal trends in their abundance or their community structure.

Dynamics of the prey fish community

Alewife

The alewife invasion during the 1940s greatly altered the fish community of Lake Michigan. Declines in abundances of emerald shiner (*Notropis atherinoides*), deepwater sculpin (*Myoxocephalus thompsoni*), yellow perch, and bloater during the 1960s have been attributed to the alewife invasion (Wells and McLain 1973). Also, alewife predation on lake trout (*Salvelinus namaycush*) fry may represent a serious impediment to lake trout rehabilitation in the lower four Great Lakes (Krueger et al. 1995).

One of the reasons for launching a major stocking program for salmon and trout in Lake Michigan in 1965 was to reduce alewife abundance, which had reached nuisance levels during the 1960s (Hatch et al. 1981; Rutherford 1997). Alewives have dominated the diet of these stocked salmonines (Stewart and Ibarra 1991; Madenjian et al.

1998*a*), and to a lesser extent, have also been eaten by burbot (Fratt et al. 1997).

Stocking of salmonines appeared to be effective in controlling alewife abundance. Alewife abundance decreased during the 1970s and early 1980s, coincident with the buildup of salmonines (Fig. 4). Alewife abundance has neither trended upward nor downward since the early 1980s, concomitant with relatively high levels of salmonine biomass within the lake. Lake-wide alewife biomass in 1973, based on bottom trawl surveys conducted by the U.S. Geological Survey (USGS) Great Lakes Science Center (GLSC), was estimated at 125 kt, whereas lake-wide biomass estimates averaged only 37 kt between 1984 and 1999 (Fig. 4*a*). Furthermore, additional GLSC trawling data indicated that the alewife decline was well underway by 1970 (Krause 1999). Although the lake-wide surveys of prey fish populations did not begin until 1973, GLSC bottom trawling was conducted at selected ports along the eastern and southern portions of the lake since 1962 (Hatch et al. 1981). Krause (1999), accounting for the reduced set of sampling locations during 1962–1972 by using a mixed model approach, estimated that lake-wide abundance of alewives in Lake Michigan was about twice as high in 1969 than it was in 1973. Further, the 1966 abundance was estimated at more than five times higher than the 1969 abundance. However, the decrease between 1966 and 1969 was partially attributable to a die-off occurring in 1967 (Brown 1972). Finally, Madenjian et al. (1986), using trend analysis, demonstrated a significant decline in alewife abundance in southeastern waters of Lake Michigan between 1973 and 1982.

Eck and Brown (1985) proposed that cold temperatures regulated alewife abundance in Lake Michigan, because a portion of the decline in alewife abundance during the 1970s and early 1980s coincided with relatively cold weather. However, 1973–1999 data for alewife abundance and temperature do not support this contention. The alewife population did not rebound even though the cold years of 1977–1982 were followed by relatively warm years of 1983 and 1985–1992 (Fig. 4*a*; T. Karl, NOAA National Climatic Data Center, Asheville, NC 28801, U.S.A., unpublished data).

bloater reproduction (Wells and McLain 1973). However, alewife abundance was relatively low during 1992–1999, when bloater year-class strength was very low. Jude and Tesar (1985) proposed that release from commercial exploitation, more than release from alewife interference, stimulated bloater recovery beginning in the late 1970s. However, exploitation rate on bloaters during the late 1980s and early 1990s was only about 1% per year, yet bloater abundance has been declining since 1989. We propose a new hypothesis to explain the pattern in bloater abundance in Lake Michigan for the past 40 years: bloater abundance in Lake Michigan follows a cycle with a period of about 30 years.

Slimy sculpin

Slimy sculpin (*Cottus cognatus*) has typically been preyed upon by juvenile lake trout in Lake Michigan, at least since the 1970s (Madenjian et al. 1998*a*). To a lesser degree, slimy sculpins are also eaten by burbot (Fratt et al. 1997). Long-term trends in slimy sculpin abundance, as determined by bottom trawl surveys, appeared to be related to changes in the spatial distribution of newly stocked lake trout. Slimy sculpin abundance decreased during the 1970s and early 1980s, remained relatively low during most of the 1980s, and then increased during the 1990s (Fig. 6). Prior to 1986, most of the lake trout stocking in Lake Michigan occurred relatively close to shore, but stocking emphasis was placed on offshore refuge areas beginning in 1986 (Holey et al. 1995). An increase in predation on slimy sculpins with increased lake trout population size during the 1970s probably caused the decrease in slimy sculpin abundance during the 1970s (Eck and Wells 1987). With the shift to predominantly offshore stocking in 1986, predation on slimy sculpins in areas of the lake trawled by USGS–GLSC likely declined, and this decline in predation allowed the increase in slimy sculpin abundance observed during the 1990s. Slimy sculpins in Lake Michigan have fed predominantly on *Diporeia* since the 1960s (Davis et al. 1997).

Dynamics of the salmonine community

Background

Stocking of salmonine fishes into Lake Michigan has had a profound effect on the lake's food web. Large-scale stocking of salmonines began in 1965, and has continued to the present. The rationale for stocking salmonines was (*i*) to control abundance of alewives, which had become a nuisance, (*ii*) to initiate a valuable sport fishery, (*iii*) to possibly initiate naturalized populations of introduced salmonines, and (*iv*) to rehabilitate the lake trout population (Holey et al. 1995; Rutherford 1997). The five species of salmonines currently stocked in Lake Michigan are lake trout, chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*), rainbow trout (*Oncorhynchus mykiss*), and brown trout (*Salmo trutta*).

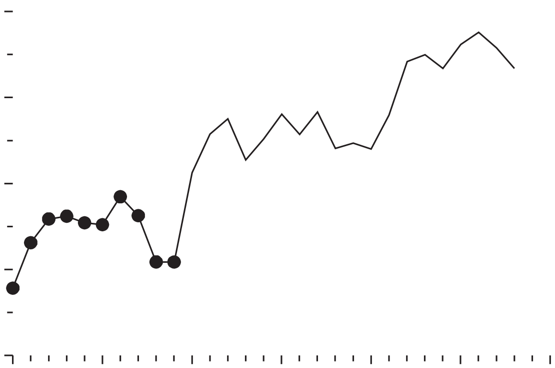
Long-term trends in biomass, production, and consumption

Lake-wide biomass and production of the five salmonine species was estimated using age-specific population models to track abundance at age over time. For all species except chinook salmon, our modeling approach was similar to the one used by Jones et al. (1993) for Lake Ontario salmonines. Using estimates of gross conversion efficiency (GCE) from bioenergetics modeling (Stewart and Ibarra 1991), lake-wide consumption of prey by salmonine populations was calculated using the production–conversion efficiency method of Ney (1990) where gross production is divided by GCE to estimate consumption. For chinook salmon, population modeling techniques outlined in Benjamin and Bence (2002) were used to estimate biomass, production, and consumption. Recruitment was quantified as the number of individuals entering the lake population, and equaled the sum of hatchery and naturally reproduced production. Salmonine stocking records have been summarized by the U.S. Fish and Wildlife Service (C. Bronte, Green Bay Fishery Resources Office, Green Bay, WI 54311, U.S.A., salmonine stocking database) and Benjamin (1998). Natural reproduction by chinook and coho salmon, as well as rainbow trout, was quantified using previously developed methods (Rutherford 1997). We assumed that natural recruitment to lake trout and brown trout populations has been negligible since 1965 (Holey et al. 1995; Rutherford 1997).

Salmonine biomass in Lake Michigan increased from 0.039 kt in 1965 to nearly 27 kt in 1986, then declined during the late 1980s, driven by a decline in abundance of chinook salmon, which has accounted for over 40% of the total salmonine biomass since 1980 (Fig. 4*b*). This decrease in chinook salmon biomass has been attributed to an outbreak of bacterial kidney disease (BKD) within the chinook salmon population (Kabre 1993). Presumably due to a decrease in BKD-induced mortality, chinook salmon biomass increased during 1994–1998, and salmonine biomass was estimated at nearly 30 kt in 1998 (Fig. 4*b*). For the most part, temporal trends in gross production mimicked trends in salmonine biomass. Annual gross production of salmonine biomass increased from 0.235 kt in 1965 to nearly 23 kt in 1998. Ratio of annual gross production to biomass (P/B) generally varied from 0.8 to 1.0.

Consumption of prey by Lake Michigan salmonines increased from only 1 kt in 1965 to 130.5 kt in 1998 (Fig. 8). Since 1977, the chinook salmon population has been responsible for approximately 50% of the consumption by salmonines (Fig. 8*a*). Most predation by salmonines in Lake Michigan has been directed at alewives (Fig. 8*b*). Alewives (both small and large sizes combined) represented, on average, 69.2% of total annual consumption from 1985 to 1998, with a maximum of 79.7% in 1998. Annual consumption of alewives by salmonines exceeded 90 kt in 1996 and 1998. Chinook salmon have been responsible for 62% of the predation on alewives by salmonines since 1980.

An important factor driving salmonine biomass and production, as well as consumption of prey by salmonines, was trends in the recruitment of young fish to the salmonine stocks. Natural recruitment of chinook salmon has increased from 1970 to the present. We estimated that annual natural recruitment of chinook salmon approached 2 million smolts during the 1990s. In some years, natural recruitment repre-



fish per 305 m of gill net during the late 1990s and a substantial proportion of these spawners was composed of fish >10 years old, yet no signs of natural recruitment have been observed (M. Toneys and P. McKee, Wisconsin Department of Natural Resources, Sturgeon Bay, WI 54235, U.S.A., unpublished data). Perhaps alewife predation on lake trout fry has also been playing an important role in suppressing natural reproduction by lake trout (Krueger et al. 1995).

Dynamics of other fish populations

Sea lamprey

Treatment of Lake Michigan tributaries, beginning in the late 1950s, with the lampricide 3-trifluoromethyl-4-nitrophenol (TFM) led to an estimated 80–90% decline in the abundance of adult sea lamprey in Lake Michigan by 1966 (Lavis et al. 2002). Lampricide treatment in streams continues to be the primary strategy for controlling the sea lamprey population in Lake Michigan.

Population sizes of spawning-phase sea lamprey in all Lake Michigan tributaries each year since 1977 have been estimated using a regression model, which incorporated relative abundance data from assessment traps in tributaries and estimates of stream discharge rates (Lavis et al. 2002). This long-term series indicates that numbers of spawning sea lampreys in Lake Michigan tributaries increased during 1977–1984, showed no trend between 1984 and 1995, and then increased again during 1995–1999. The two increases occurred primarily in northern tributaries to the lake. The first increase was attributed to an immigration of adult sea lampreys from northern Lake Huron, whereas the second increase was probably due to a decrease in sea lamprey control measures for Lake Michigan (G. Christie, Great Lakes Fishery Commission, Ann Arbor, MI 48105, U.S.A., personal communication). Lake-wide estimates of spawning sea lamprey population size ranged between 32 000 and 117 000 sea lampreys (Lavis et al. 2002).

Long-term trends for incidence of fresh sea lamprey wounds on lake trout in Lake Michigan mimicked long-term trends for sea lamprey abundance. Wounding rates in southern waters of the lake have remained nearly unchanged for the last 25 years, whereas an increase in wounding rates has been observed in northeastern waters since 1978 (Lavis et al. 2002). Overall, lamprey-induced annual mortality, estimated from wounding rate, for Lake Michigan lake trout was relatively low, averaging less than 7% for most years during 1984–1998.

Lake whitefish

Lake whitefish is the most important commercial fish in Lake Michigan. Tribal and state-licensed commercial fishers from Michigan and Wisconsin continue to exploit lake whitefish. Lake whitefish are taken in trap nets, gill nets, trawls, and pound nets.

Since 1970, annual commercial harvest of lake whitefish has more than tripled (Fig. 9), reflecting a lake-wide increase in abundance. A dramatic decline in lake whitefish abundance during the late 1950s was linked primarily with sea lamprey predation (Wells and McLain 1972). Thus, there can be little doubt that the impressive recovery of the lake whitefish population in Lake Michigan since 1970 was partially driven by sea lamprey control (Eck and Wells 1987). Stocking of lake trout also afforded extra protection from sea lamprey predation because lake trout are favored prey for sea lampreys (Wells and McLain 1972). The decrease in mean size of adult rainbow smelt during the 1970s and 1980s and decreased rainbow smelt abundance during the 1990s may have also contributed to the lake whitefish recovery because large rainbow smelt may prey upon lake whitefish fry (Wells and McLain 1973). During the last 30 years, exploitation has not impaired the ability of the adult lake whitefish population to produce large year-classes. This is true even though contemporary stocks of lake whitefish have been subjected to high exploitation rates, leading to total annual mortality that sometimes exceeded 80% (M. Ebener and J. Bence, unpublished data).

Lake whitefish size-at-age declined in Lake Michigan during the 1990s. Moreover, condition factor dropped rapidly between 1995 and 1998 (Fig. 10). Reduced growth rate during the 1990s may have resulted from density-dependent factors, as sustained high levels of lake whitefish abundance resulted in increased intraspecific competition for food resources. Other factors may also have been involved. For example, zebra mussel density increased substantially in northern Lake Michigan during the same time that lake whitefish condition declined precipitously (T. Nalepa, unpublished data). Hoyle et al. (1999) linked poor body condition of lake whitefish in Lake Ontario with zebra mussel invasion of the lake; perhaps expansion of the zebra mussel population also had a negative effect on lake whitefish condition in Lake Michigan.

Burbot

exploitation and habitat degradation (Wells and McLain 1973). During the 1990s, small populations of lake sturgeon have been associated with at least 13 tributaries (Hay-Chmielewski and Whelan 1997). With continued removal of dams on tributaries anticipated in the near future, the size of lake sturgeon population in Lake Michigan should increase as more suitable spawning habitat becomes available.

Emerald shiner

The emerald shiner (*Notropis atherinoides*) population in Lake Michigan crashed during the early 1960s, coincident with buildup of the alewife population (Wells and McLain 1973). Apparently, alewives fed on the pelagic eggs and larvae of the emerald shiner. Emerald shiner abundance has remained at very low levels during 1970–2000 (D. Jude, unpublished data; J. Dettmers, Illinois Natural History Survey, Zion, IL 60099, U.S.A., unpublished data; R. Rost, Wisconsin Department of Natural Resources, Peshtigo, WI 54157, U.S.A., unpublished data), suggesting that the relatively low alewife abundance during 1984–2000 was still sufficiently high to interfere with emerald shiner reproduction.

Round goby

The round goby, an invader from the Ponto-Caspian region, established populations in Calumet Harbor (southern Lake Michigan) and in several harbors on both the east and west sides of Lake Michigan including Milwaukee, Sturgeon Bay, Escanaba, Grand Haven, Muskegon, and Charlevoix during the 1990s (Clapp et al. 2001). Zebra mussels form a substantial portion of the diet of round gobies in the Great Lakes (C. Knight, Ohio Department of Natural Resources, Fairport, OH 44077, U.S.A., personal communication; M. Thomas, Michigan Department of Natural Resources, Mt. Clemens, MI 48045, U.S.A., personal communication). In turn, round gobies are preyed upon by several species of fish. The precipitous decline of mottled sculpin (*Cottus bairdi*) abundance in Calumet Harbor, as well as decreases in abundances of johnny darter (*Etheostoma nigrum*) and logperch (*Percina caprodes*) in Lake St. Clair, has been linked to the round goby invasion (Janssen and Jude 2001; M. Thomas, Michigan Department of Natural Resources, Mt. Clemens, MI 48045, U.S.A., personal communication). It remains to be seen whether these seemingly negative effects of round gobies on sculpins and darters will be confined to shallow and protected waters of Lake Michigan.

Lake herring

Lake herring (*Coregonus artedi*) was once a prominent member of the fish community in Lake Michigan, and the lake herring population once supported a valuable commercial fishery (Wells and McLain 1973). The crash in the lake herring population during the 1950s has been attributed to overexploitation and interference by rainbow smelt with lake herring reproduction (Wells and McLain 1973). Although there have been no signs of a lake-wide recovery, a recent increase in lake herring abundance in Grand Traverse Bay of northern Lake Michigan has been observed. Sport harvest of lake herring in Grand Traverse Bay indicated the presence of lake herring at very low levels in 1985 and 1993, but sport harvest increased three- to seven-fold during 1995–1998 compared with the 1993 harvest (G. Rakoczy, Michigan Department of Natural Resources, Charlevoix, MI 49720, U.S.A., personal communication).

Contaminants and global climate change stressors

Contaminants

The issue of contaminants acting as stressors to Great Lakes biota emerged in the 1970s (Evans 1988). Consequently, the governments of the United States and Canada negotiated the Great Lakes Water Quality Agreement in 1972, and revised this agreement in 1978. This agreement led to many remedial actions to improve the quality of Great Lakes waters. Additionally, production of polychlorinated biphenyls (PCBs) was banned, use of the pesticide DDT (1,1,1-trichloro-2,2-bis[*p*-chlorophenyl]ethane) was discontinued, and uses of the organochlorine pesticides chlordane and dieldrin were restricted in both the United States and Canada during the 1970s.

As a consequence of the abovementioned measures, concentrations of most contaminants in Lake Michigan biota decreased substantially between 1970 and 2000. For example, total PCB concentration in Lake Michigan zooplankton decreased between 1982 and 1995 (A. Trowbridge and D. Swackhamer, University of Minnesota, Minneapolis, MN 55455, U.S.A., personal communication). Total PCB concentration in *Mysis*, *Diporeia*, prey fishes, and salmonines of Lake Michigan decreased by roughly an order of magnitude between 1975 and 1995 (DeVault et al. 1996; Madenjian et al. 1998*b*, 1998*c*). During the 1970s and early 1980s, decreases were observed in total DDT, dieldrin, and oxychlordane concentrations in lake trout (DeVault et al. 1996), and in PCB, oxychlordane, DDT, and dieldrin concentrations in herring gull (*Larus argentatus*) eggs (Pekarik and Weseloh 1998). In contrast, toxaphene concentrations in lake trout did not decrease between 1986 and 1992 (DeVault et al. 1996).

Very few lake-wide temporal changes in Lake Michigan biota between 1970 and 2000 have been shown to be directly linked to stressor effects exerted by contaminants. The dramatic increase in double-crested cormorant (*Phalacrocorax auritus*) population size during the late 1980s and 1990s was due, at least in part, to the substantial reduction of contaminant levels within the lake ecosystem during the 1970s (Weseloh et al. 1995). Number of double-crested cormorant nests on islands within Lake Michigan (including Green Bay) increased exponentially from 75 nests in 1977 to 4743 nests during 1989–1990, and then to 28 158 nests in 1997 (F.J. Cuthbert, University of Minnesota, St. Paul, MN 55108, U.S.A., personal communication). Weseloh et al. (1983) documented shell thinning with high egg breakage and high egg loss (95%) with concomitant reproductive failure in Great Lakes cormorants during the early 1970s, and also reported high DDE (a metabolite of DDT) concentrations in cormorant eggs. Apparently, high concentration of DDE in the cormorants was causing eggshell thinning and reproductive failure. Increased predation by the exploding population of double-crested cormorants in Lake Michigan may have caused a reduction in abundance of sn5.6(of)-775.6(sn53o775.6(6 are not conclusive (D. Peterson, Central Michigan University, Mt. Pleasant, MI 48859, U.S.A., personal communication). To the best of our knowledge, no lake-wide temporal changes in phytoplankton communities, benthic invertebrate communities, zooplankton communities, or fish communities in Lake Michigan have been shown to be directly attributable to contaminant effects (Evans 1988). Nevertheless, contaminants may have influenced health of brown bullhead (*Ameiurus nebulosus*) populations in certain tributaries (Baumann et al. 1996).

Global climate change

An increase in atmospheric carbon dioxide enhances heat retention (Regier et al. 1990). Burning fossil fuels and changes in land use are correlated with an increase in carbon dioxide concentration in the earth's atmosphere, and therefore global climate change likely represents an anthropogenic stressor to the global environment. Although not all climatologists agree as to the nature, extent, intensity, and timing of the effects of increased carbon dioxide content in the earth's atmosphere, there is general consensus that climate warming will occur (Regier et al. 1990; Doak and Morris 1999).

Continued monitoring of prey fish populations, as well as surveillance of other components of the ecosystem, should provide further understanding of the Lake Michigan food web. Such long-term studies are especially appropriate for ecosystem manipulations (Pace and Cole 1989).

Bottom-up effects

Several changes within the Lake Michigan ecosystem during 1970–2000 may be attributable to bottom-up effects. Decline in abundance of all three dominant benthic macroinvertebrate groups, including *Diporeia*, oligochaetes, and sphaeriids, between 1980 and 1993 in nearshore (≤50 m deep) waters of Lake Michigan was believed to be chiefly due to a decrease in primary production in nearshore waters. Although long-term data for spring total phosphorus, an indicator of primary production, in nearshore waters of Lake Michigan were not available, comparison of measurements during 1998–2000 with measurements from the early 1970s suggested a decrease in primary production over this time period. In contrast, long-term data were readily available for offshore waters, and these data showed no long-term trend in primary production during 1973–1998. Similarly, abundances of the three major groups of benthic macroinvertebrates in offshore waters did not trend upward or downward during this time period. The apparent decline in primary production in nearshore waters of Lake Michigan between the 1970s and 1998–2000 was likely due to the decrease in phosphorus loadings between 1980 and 1987. The continued decrease in *Diporeia* abundance during the 1990s in nearshore waters of southern and southeastern Lake Michigan coincided with the zebra mussel invasion, although a specific mechanism whereby zebra mussels may have reduced *Diporeia* abundance remains unidentified.

Have bottom-up effects, including the apparent reduction in nearshore primary production and the continued decline of *Diporeia*, already precipitated a decrease in abundances of important fish populations in Lake Michigan? No clear effects are evident yet. The decrease in bloater abundance during the 1990s was attributed to an extended period of very low recruitment, which may be related to intraspecific mechanisms rather than bottom-up effects. Lake-wide abundances of alewife, salmonines, burbot, lake whitefish, and sculpins have not decreased during the 1990s. Even though data from Illinois waters suggested that bottom-up effects may have partly contributed to a prolonged period of low yellow perch recruitment, available data were insufficient to support the contention that a long-term decrease in zooplankton abundance was primarily responsible for the extended period of low recruitment. Rainbow smelt abundance decreased during 1992–1999; however, explanations for trends in rainbow smelt abundance, as determined by GLSC bottom trawl surveys over the past 30 years, are not obvious. Eck and Wells (1987) also experienced difficulty in interpreting long-term trends in rainbow smelt abundance.

Have these bottom-up effects already influenced growth rates or condition of Lake Michigan fishes? The decrease in lake whitefish condition between 1995 and 1998 may have been partially due to some bottom-up effects. An increase in proportion of zebra mussels or a decrease in proportion of *Diporeia* in lake whitefish diet could have led to reduced lake whitefish condition. The recent decline in alewife condition may be due to bottom-up effects. Bloater growth rate declined between 1973 and 1994, during which time the population increased tremendously in size. However, bloater growth rate has actually increased during 1994–1999, as the population has undergone a drastic decrease in size. To detect future impacts of bottom-up effects on fish populations, surveillance of fish abundance, growth rates, lipid content, and condition should be continued. Zebra mussel abundance in Lake Michigan has not yet peaked, and the quagga mussel (*Dreissena bugensis*) invasion of Lake Michigan has just begun (Nalepa et al. 2001).

Overexploitation of fish stocks

Overall, overexploitation of fish populations appeared to play a relatively minor role in shaping the Lake Michigan food web during 1970–2000. Commercial harvest of yellow perch during the 1990s may have contributed to a skewing of the sex ratio (relatively low number of female spawners), which may have contributed to prolonging the period of low recruitment to the yellow perch population. Yellow perch recruitment remained low during 1989–1997. Consequently, the yellow perch commercial fishery in Lake Michigan was closed by 1998.

Bythotrephes and round goby invasions

Although invasions by *Bythotrephes* and round goby have caused some changes to the Lake Michigan food web during the late 1980s and 1990s, the earlier invasions by sea lamprey and alewife had more serious consequences for the Lake Michigan fish community. Through predation, *Bythotrephes* may have reduced the abundance of certain smaller cladocerans. However, the impact of this reduction on the rest of the Lake Michigan ecosystem remains undepopulation associated with Lake Michigan during the late 1980s and 1990s was partially due to substantial reduction of contaminant levels within the lake ecosystem during the 1970s (Weseloh et al. 1995). To date, lake-wide consequences of this increase in cormorant abundance on the rest of the lake ecosystem remain unclear.

We were unable to attribute any of the lake-wide changes in the Lake Michigan food web between 1970 and 2000 to global climate change effects. That is not to say that global climate change has not already had some effect on the Lake Michigan ecosystem. Rather, time series for water temperature characteristics are not sufficiently long to resolve whether recent trends were part of a natural cycle or were forced by anthropogenic activity. Furthermore, insufficient data were available to identify a common long-term trend in water temperature characteristics across several locations in the lake. We would expect that ecological changes associated with global climate change would occur much more slowly than changes induced by invasions of exotic species.**fJiempeb0 -2.265i10496g1**

gan phytoplankton: primary production and growth. Can. J. Fish. Aquat. Sci. **44**: 499–508.

Fahnenstiel, G.L., and Scavia, D. 1987*c*. Dynamics of Lake Michigan phytoplankton: the deep chlorophyll layer. J. Gt. Lakes Res. **13**: 285–295.

Fahnenstiel, G.L., Krause, A.E., McCormick, M.J., Carrick, H.J., and Schelske, C.L. 1998. The structure of the planktonic food-web in the St. Lawrence Great Lakes. J. Gt. Lakes Res. **24**: 531–554.

Fitzsimons, J.D., Brown, S.B., Honeyfield, D.C., and Hnath, J.G. 1999. A review of early mortality syndrome (EMS) in Great

McQueen, D.J., Johannes, M.R.S., Post, J.R., Stewart, T.J., and Lean, D.R.S. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecol. Monogr. **59**: 289–309.

Nalepa, T.F. 1987. Long term changes in the macrobenthos of southern Lake Michigan. Can. J. Fish. Aquat. Sci. **44**: 515–524.

Nalepa, T.F., Hartson, D.J., Fanslow, D.L., Lang, G.A., and Lozano, S.J. 1998. Declines in benthic macroinvertebrate populations in southern Lake Michigan, 1980–1993. Can. J. Fish. Aquat. Sci. **55**: 2402–2413.

Nalepa, T.F., Fanslow, D.L., and Lang, G.A. 2000*a*. Trends in benthic macroinvertebrate populations in southern Lake Michigan over the past several decades. Internationale Vereinigung fÆr Theoretische und Angewandte Limnologie Verhandlungen, **27**: 2540–2545.

Nalepa, T.F., Hartson, D.J., Buchanan, J., Cavaletto, J.F., Lang, G.A., and Lozano, S.J. 2000*b*. Spatial variation in density, mean size, and physiological condition of the holarctic amphipod *Diporeia* spp. in Lake Michigan. Freshwater Biol. **43**: 107–119.

Nalepa, T.F., Schloesser, D.W., Pothoven, S.A., Horndorp, D.W., Dipf(v)2i.1(eantio-53638274)-60038274
27: