PERSPECTIVE / PERSPECTIVE

Ecology of the Lake Huron fish community, 1970–1999[1]

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Abstract: We review the status of the Lake Huron fish community between 1970 and 1999 and explore the effects of key stressors. Offshore waters changed little in terms of nutrient enrichment, while phosphorus levels declined in inner Saginaw Bay. Introduced mussels (*Dreissena* spp.) proliferated and may have caused a decline in *Diporeia* spp. This introduction could have caused a decline in lake whitefish (*Coregonus clupeaformis*) growth and condition, with serious repercussions for commercial fisheries. *Bythotrephes*, an exotic predatory cladoceran, and other new exotics may be influencing the fish community. Sea lampreys (*Petromyzon marinus*) remained prevalent, but intensive control efforts on the St. Mary's River may reduce their predation on salmonines. Overfishing was less of a problem than in the past, although fishing continued to reduce the amount of lake trout (*Salvelinus namaycush*) spawning biomass resulting from hatchery-reared fish planted to rehabilitate this species. Massive stocking programs have increased the abundance of top predators, but lake trout were rehabilitated in only one area. Successful lake trout rehabilitation may require lower densities of introduced pelagic prey fish than were seen in the 1990s, along with continued stocking of hatchery-reared lake trout and control of sea lamprey. Such reductions in prey fish could limit Pacific salmon (*Oncorhynchus* spp.) fisheries.

Résumé : Nous faisons le point sur l'état de la communauté de poissons du lac Huron de 1970 à 1999 et nous étudions les effets des principaux facteurs de stress. Les eaux du large ont connu peu de changement en ce qui a trait à l'enrichissement en nutriments, alors que les concentrations de phosphore ont diminué dans la baie de Saginaw intérieure. Les moules introduites (*Dreissena* spp.) ont proliféré et ont peut-être causé un déclin de *Diporeia* spp. Cette introduction peut avoir causé une diminution de la croissance et de la condition du corégone de lac (*Coregonus clupeaformis*), ce qui a eu des répercutions graves sur les pêches commerciales. *Bythotrephes*, un cladocère prédateur exotique, et d'autres espèces exotiques nouvelles peuvent peut-être influencer la communauté de poissons. Les grandes lamproies marines (*Petromyzon marinus*) restent présentes, mais des efforts considérables de contrôle dans la rivière

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St. Mary's peuvent avoir réduit leur prédation sur les salmoninés. La surpêche est un problème moins important que par le passé, bien que la pêche ait continué de réduire la biomasse des reproducteurs chez le touladi (*Salvelinus namaycush*) provenant des élevages en pisciculture et ensemencés pour la réhabilitation de l'espèce. Des programmes d'empoissonnements massifs ont accru l'abondance des prédateurs supérieurs, mais le touladi n'a été réhabilité que dans une région. Le succès de la réhabilitation du touladi exigera peut-être des densités d'introduction de poissons pélagiques plus faibles que dans les années 1990, tout en maintenant l'empoissonnement de touladis élevés en pisciculture et le contrôle des grandes lamproies marines. De telles réductions des poissons proies pourraient limiter les pêches des saumons du Pacifique (*Oncorhynchus* spp.).

[Traduit par la Rédaction]

Introduction

The watershed of the Laurentian Great Lakes encompasses over 750 000 km^2, each of the five Great Lakes ranks among the largest 17 in the world, and Lake Huron has the world's fourth largest surface area. The water bodies that comprise Lake Huron (the main basin, the North Channel, and Georgian Bay) are partially separated by Manitoulin Island and the Bruce Peninsula (Fig. 1). Saginaw Bay is a large, shallow enbayment of the main basin. Lake Huron is connected to Lake Michigan by the Straits of Mackinac and also receives outflow from Lake Superior through the St. Mary's River. The lake is generally characterized as oligotrophic.

The Great Lakes experienced substantial anthropogenic ecological change, including changes to nutrient concentrations, habitat, and species diversity. By the 1960s, these changes had substantially degraded the Great Lakes for human use, including reductions in the abundance of fishable populations. The 1971 Salmonid Communities of Oligotrophic Lakes (SCOL-1) symposium was aimed at describing changes in the lakes: identifying the effects of cultural eutrophication, fishery exploitation, and fish introductions and predicting future responses (Loftus and Regier 1972). The 1972 and 1978 Great Lakes Water Quality Agreements (GLWQA) between Canada and the United States were directed specifically at reducing nutrient and contaminant loads.

By the start of the 1970s, the Lake Huron fish community was highly disturbed (Berst and Spangler 1972). Lake trout (*Salvelinus namaycush*), once the dominant predator, was nearly extirpated with only two extant, localized populations remaining, both in Georgian Bay. Burbot (*Lota lota*), another important native predator, had declined in abundance. Populations of lake herring (*Coregonus artedi*), lake whitefish (*Coregonus clupeaformis*), and bloater (*Coregonus hoyi*) were greatly reduced in abundance and in their contributions to the fisheries. Other deepwater ciscoes (*Coregonus* spp.) were greatly reduced in abundance or extirpated (Eshenroder and Burnham-Curtis 1999). Major stressors identified as the root causes of these changes were commercial fishing and the invasion of the sea lamprey (*Petromyzon marinus*).

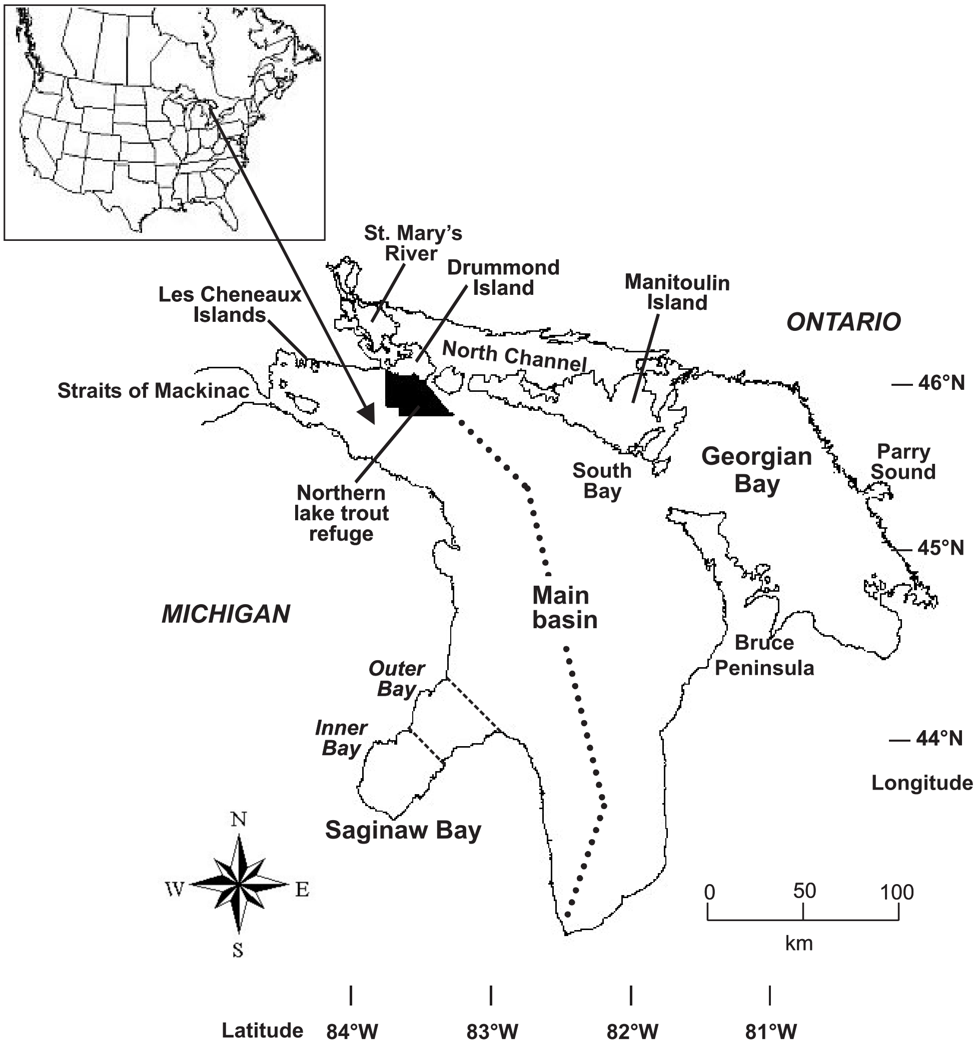
Although fishery declines were well underway by the time sea lamprey abundance reached high levels, their large numbers were viewed as a major impediment to recovery. This marine species selectively attacks and attaches to larger-bodied fishes, and its removal of bodily fluids frequently degrades blood quality so much that attacked fish die. The persistence of other larger-bodied fishes, such as burbot, suckers (Catostomidae), lake whitefish, and exotic rainbow trout (*Oncorhynchus mykiss*), was viewed as resulting from their life history strategy of reproducing at smaller sizes, before sea lamprey induced mortality became too severe (Berst and Spangler 1972). The selective removal of large-bodied fishes favored small-bodied exotic planktivores, alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*), which became extremely abundant (Berst and Spangler 1973). Berst and Spangler (1973) saw a recovery of the Lake Huron fish community as hinging on the successful control of sea lampreys and the reestablishment of climax predators. At the time of the SCOL-1 symposium, mass stocking of Pacific salmon and lake trout had just begun, and peak stocking levels (and recreational fishery harvests) were in the future. Although effective chemical methods for killing larval sea lampreys were available earlier, lake-wide treatment had only recently occurred and a response to the treatment had not been evaluated. Berst and Spangler (1972) viewed the effects of elevated nutrients and contaminants as relatively minor, although they expressed concerns that these effects could be understated owing to substantial time lags associated with the relationship between open-water concentrations and elevated loadings. They were hopeful that the forthcoming GLWQA would prevent further deterioration of the aquatic environment.

Much has changed in the Lake Huron ecosystem during the more than 30 years since the SCOL-1 symposium. The desired lake-wide recovery of self-sustaining lake trout populations has not occurred (Eshenroder et al. 1995), although massive stocking of Pacific salmon and lake trout led to a substantial increase in the abundance of top predators. In turn, populations of predator fish supported valuable recreational fisheries (Bence and Smith 1999). Recovery of lake whitefish populations led to increased commercial fishing effort and associated mortality of lake trout, which are often caught as bycatch in that fishery (Brown et al. 1999). Lake-wide chemical treatment of tributary streams initially led to a substantial decrease in the abundance of sea lampreys, but increased survival of juvenile sea lampreys originating from the untreated St. Mary's River followed this decline. As a consequence of the GLWQA, both nutrient and contaminant loadings to Lake Huron decreased. A number of additional exotic species invaded since 1971, but the full effects of these new species are still uncertain. We review these changes, focusing on the major species, and make a prognosis for the future.

Nutrient loading

Based on studies of total dissolved solids, transparency, and dissolved oxygen, the open waters of Lake Huron are

Fig. 1. Major basins and landmarks of Lake Huron. The boundary between US and Canadian waters (dotted line) and inner and outer Saginaw Bay (broken lines) are shown.



oligotrophic despite concerns in the early 1970s that the lake's water quality was deteriorating (Dobson et al. 1974). Declines in important recreational and commercial fishes in Saginaw Bay during the 1950s and 1960s led to concerns that human activities were altering productivity in nearshore mesotrophic areas (Beeton 1969). Cultural eutrophication and pollution were most severe in dense industrial and agricultural areas, and phosphorus loading was recognized as the major factor. First signed in 1972, the GLWQA brought commitments from the United States and Canada to restore and maintain the chemical, physical, and biological integrity of the Great Lakes ecosystem (International Joint Commission 1972) and, when revised in 1978, established the current Lake Huron phosphorus concentration and loading targets. Through programs that controlled nutrient inputs, phosphorus loading fell from 5.1 million kg·year^{-1} in 1978 to below the GLWQA target, 4.3 million kg·year^{-1}, by 1981 and has remained below the target in all but a few years (Beeton et al. 1999).

The feared increase in open-lake phosphorus concentrations did not materialize despite the higher loadings of the 1960s and 1970s, nor was a decrease in concentrations evident subsequent to decreases in loadings (Stevens et al. 1985). From 1978 to 1995, open-lake spring total phosphorus concentrations were stable and, with one minor exception, remained below the target level of 5.0 mg·m^{-3} (Fahnenstiel et al. 1998). During the period prior to and subsequent to the reduction in phosphorus loadings, a number of studies classified all three basins of Lake Huron as oligotrophic (Beeton and Saylor 1995).

Several nearshore areas, including Saginaw Bay and Georgian Bay, are characterized by higher phosphorus concentrations than are present in the main basin of Lake Huron (Nicholls et al. 2001). The largest is Saginaw Bay, where spring total phosphorus concentrations reached as high as 60.0 mg·m^{-3} by the early to mid-1970s (Smith et al. 1977). Phosphorus concentrations in the bay declined but remain substantially higher than in open waters of the lake. From 1991 through 1993, total phosphorus in the bay, averaged over April–October, decreased from 24.6 to 16.2 mg·m^{-3}, a change attributed to increased numbers of zebra mussels (*Dreissena polymorpha*) acting as a nutrient sink (Johengen et al. 1995). Clearly, the GLWQA target of 15 mg·m^{-3} remains a challenge in Saginaw Bay. Similarly, despite loading reductions in Georgian Bay, total phosphorus will have to be monitored because a 1 mg·m^{-3} increase could result in nuisance phytoplankton growths.

Nitrate is unlikely to be limiting in Lake Huron and the nutrient environment of the lake is favorable for diatoms and green algae. Increasing levels of nitrate plus nitrite have been reported across the Great Lakes for the past two decades. A significant increase in nitrate plus nitrite was observed in Lake Huron (Stevens et al. 1985), and the nitrogen to phosphorus ratio increased from an already high value of 53 in 1971 to 72 in 1991.

Phytoplankton

Phytoplankton community structure in Lake Huron changed very little from the late 1980s through the mid-1990s; all major groups were similarly abundant over the two periods (Makarewicz and Bertram 1991). Forty common species and varieties account for most of the abundance and biomass of phytoplankton in the lake (Makarewicz and Bertram 1991). Because of low phosphorus concentrations and high nitrogen to phosphorus ratios, Diatomeae predominate except in Saginaw Bay (Stevenson 1985; Makarewicz and Bertram 1991; Munawar et al. 1995). Species composition varies seasonally and between basins (Stevenson 1985).

Low and untrending phytoplankton biomasses are expected in offshore waters of the Great Lakes, and the limited time series data for the main basin of Lake Huron support this expectation. In 1971, phytoplankton biomass in the main basin was low, averaging 0.4–0.79 g·m^{-3} at most stations, but was moderately high at some inshore stations. Biomass varied seasonally with the highest values during spring diatom blooms (Munawar and Munawar 1982). From 1983 to 1985, biomass at offshore stations (measured by composite samples taken at 1, 5, 10, and 20 m) in the main basin remained low and ranged from 0.34 to 0.41 g·m^{-3}, with spring or early summer peaks. Phytoplankton biomass remained low, averaging less than 0.4 g·m^{-3} during 1998–1999.

Primary production has not increased appreciably from the time of the SCOL-1 symposium. Lake Huron ranks as the second lowest of the Great Lakes in terms of chlorophyll *a* and primary productivity (Beeton et al. 1999). With the exception of Saginaw Bay, chlorophyll *a* values in the main basin in the early 1970s rarely exceeded 3 mg·m^{-3} (Munawar and Munawar 1982). In 1974, chlorophyll concentrations ranged from 2.1 (main basin) to 0.91 (Georgian Bay) (International Joint Commission 1977) and were lower than or as low as in 1980 (Moll et al. 1985) and 1985 (Makarewicz et al. 1989).

Benthic invertebrates

Any change in total abundance of benthic invertebrates between the early 1970s and 1997–1998 is obscured by large variations among sampling locations and among years (Table 1). The composition of the benthic community, however, clearly did change during this period. The benthos of the main basin is typical of that found in offshore waters of the other upper lakes. At depths below the thermocline (>30 m), amphipods (*Diporeia* spp.) are the predominant form followed by oligochaetes, sphaeriids, and chironomids. *Diporeia* increased from 43%–72% in 1970–1972 to 77%–83% in 1997–1998, while oligochaetes declined from 18%–42% to only 12%–18% over the same years.

Peterson-grab surveys in the 1950s and in 1965 indicate that the recent community shift to *Diporeia* is a return to an earlier state (Teter 1960; Schuytema and Powers 1966). Although these early data cannot be quantitatively compared with the more recent Ponar-based estimates (the Peterson-grab is less efficient than the Ponar), they can be used to compare community composition across years. In the 1950s, *Diporeia* and oligochaetes accounted for 81% and 9%, respectively, of total numbers as compared with 48%–76% *Diporeia* (depending on sampling location) and 22%–30% oligochaetes in 1965. Abundance and community composition of the offshore benthos in Georgian Bay and the North Channel, surveyed extensively only in 1973 (Cook and Johnson 1976), indicate similar conditions as reported for the main basin during the same period.

The biggest change in the macroinvertebrate community of inner Saginaw Bay (Fig. 1) prior to the early 1970s was the decline in populations of the mayfly *Hexagenia*. In the mid-1950s, abundance of *Hexagenia* in soft sediments was 63 m^{-2}, but by the mid-1960s, the population fell to near zero (Schneider et al. 1969). The decline was attributed to increased eutrophication and oxygen depletion in the near-bottom waters. This organism is still rare in Saginaw Bay (Nalepa et al. 2003).

Abundances of the three major macroinvertebrate groups changed markedly in inner Saginaw Bay (Fig. 1) between the early 1970s and the 1990s (Table 2). Over this period, oligochaetes and chironomids declined in both hard and soft substrates, while amphipods (*Gammarus* spp.) increased. These changes most likely reflect phosphorus control and the introduction and rapid expansion of zebra mussels. First found in the bay in 1990, zebra mussels had densities of 2000 – 34 000 m^{-2} at inner bay sites with hard substrates during 1991–1996 (Nalepa et al. 1999). The increased density of *Gammarus* spp. at hard-substrate sites in the inner bay is similar to increases found in the other Great Lakes after mussels became established (Ricciardi et al. 1997). The decline in oligochaetes and chironomids in Saginaw Bay, however, contrasts with increases in the density of these taxa reported in the same studies for the other Great Lakes. The reason for the decline of these two groups at hard-substrate sites in Saginaw Bay is not clear.

Abundances of most major benthic taxa also declined in outer Saginaw Bay (Fig. 1) between the early 1970s and the 1990s (Table 2). The decline of *Diporeia* has the greatest implication for the bay's food web. Following the establishment of zebra mussels in Lake Michigan (Nalepa et al. 1998), *Diporeia* populations declined, and the condition of fish that fed on *Diporeia* declined subsequently (Pothoven et al. 2001; Madenjian et al. 2003). *Diporeia* relies on freshly settled material (e.g., diatoms) as a food source, and zebra mussels filter and remove this material. Although food limitation has been a suspected mechanism, a clear link between the *Diporeia* population declines and reduced detrital settling rates has not been established. *Diporeia* populations declined in abundance in outer Saginaw Bay but are still abundant in the main basin (Table 1).

Mysis is important in the food webs of the Great Lakes, but its dynamics and role in Lake Huron are poorly studied.

Table 1. Mean ± SE densities (m^{-2}) of major benthic macroinvertebrates and number of Ponar grabs (n) for the open waters of Lake Huron by depth.

	1970[a]	1971[b]	1972[c]	1997[d]	1998[d]
<30 m	n = 8	n = 20	n = 26		
Diporeia spp.	867±547	111±59	866±23	—	—
Oligochaeta	1495±1204	274±106	2679±590	—	—
Sphaeriidae	40±30	250±129	299±798	—	—
Chironomidae	124±79	60±15	407±81	—	—
Total	2564±1858	806±276	4427±828	—	—
30–50 m	n = 3	n = 10	n = 14	n = 2	n = 2
Diporeia spp.	2612±955	471±187	5418±714	2610±469	3429±414
Oligochaeta	674±307	502±149	2870±414	617±109	493±182
Sphaeriidae	394±151	194±56	1324±211	89±46	61±4
Chironomidae	26±23	31±10	334±116	73±16	124±3
Total	3764±1160	1209±360	9956±1244	3388±607	4107±239
50–90 m	n = 7	n = 18	n = 12	n = 5	n = 5
Diporeia spp.	2145±390	500±82	5393±648	3353±464	2274±696
Oligochaeta	683±200	289±51	1484±364	516±115	368±107
Sphaeriidae	112±40	346±224	538±84	231±85	185±63
Chironomidae	39±15	104±41	73±14	31±8	33±14
Total	3007±459	1167±256	7489±1023	4130±559	2860±853
>90 m		n = 16		n = 3	n = 3
Diporeia spp.	—	490±82	—	4266±738	2949±570
Oligochaeta	—	212±64	—	520±254	340±154
Sphaeriidae	—	33±16	—	33±8	25±4
Chironomidae	—	11±3	—	98±33	59±26
Total	—	745±109	—	4917±993	3373±584

[a] Schelske and Roth (1973).

[b] Shrivastava (1974).

[c] S. Mozley, Department of Zoology, North Carolina State University, 4105 North Gardner Hall, Raleigh, NC 27695, USA, unpublished data.

[d] Marc Tuchman, Great Lakes National Program Office, Environmental Protection Agency, 77 West Jackson Boulevard, Chicago, IL 60604, USA, unpublished data.

Carpenter et al. (1974) noted that abundance in 1971 increased with depth, that *Mysis* was scarce during summer except in the deeper waters of the northern main basin, and that their distribution was more uniform at other seasons. Sell (1982) analyzed these same data and reported an average biomass of 0.53 g dry mass·m^{-2} and production (dry) of 1.5 g·m^{-2}·$year^{-1}$. These numbers are lower than some (but not all) values that he calculated for Lake Michigan, but the deeper sampling depths in Lake Huron would result in a positive bias as compared with Lake Michigan. The production to biomass ratio of *Mysis* was similar (2.8) in both lakes.

Zooplankton

Zooplankton community composition in Lake Huron is different among the main basin, Georgian Bay, and the North Channel but similar to that in the other upper Great Lakes, particularly Lake Michigan (Barbiero et al. 2001). Lake Huron's zooplankton community has been dominated by calanoid and diaptomid copepods (Watson and Carpenter 1974; Sprules and Jin 1990; Barbiero and Tuchman 2000). Dominance varies by season, with naupli and rotifers dominating in April and diaptomids and cladocerans dominating in June and July (Evans 1986). The most abundant copepod throughout the lake is *Cyclops bicuspidatus thomasi* (Watson and Carpenter 1974).

Bythotrephes, an exotic predaceous zooplankter, which became established in Lake Huron in 1984, may be responsible for a shift to larger-bodied cladocerans during 1970–1999 (Lehman 1991; Laxson et al. 2003). The contribution of various groups of copepods differs between spring and summer, but their annual contribution to the planktonic–crustacean community composition was stable between 1970 and 2000 (Barbiero et al. 2001). In contrast, the cladoceran community during this period shifted from a predominance of bosminids to a predominance of daphnids. Daphnids accounted for less than 10% of the planktonic crustacean numbers during the 1970s and 1980s (Watson and Carpenter 1974; Evans 1986) but increased to 22% in 1988 (Sprules and Jin 1990) and to 25% in 1998 (Barbiero et al. 2001). Contributions by bosminids declined from 14% by numbers in 1988 (Sprules and Jin 1990) to 8% in 1998 (Barbiero et al. 2001).

Prey fish

In their review of Lake Huron, Berst and Spangler (1972) identified introduced rainbow smelt and alewives and native deepwater ciscoes as the dominant forage fishes. During

Table 2. Mean ± SE abundance (m^{-2}) of major benthic macroinvertebrate groups in the inner (sites with hard and soft substrate) and outer portions of Saginaw Bay.

	1971	1987–1990	1993–1996
Inner Saginaw Bay			
Substrate: sand	$n = 3^a$	$n = 3^b$	$n = 3$
Oligochaeta	1436±204	1197±498	668±101
Chironomidae	764±493	267±129	186±74
Gammarus sp.	143±72	49±29	346±60
Substrate: silt	$n = 4$	$n = 4$	$n = 3$
Oligochaeta	13 662±1123	17 394±1986	1976±924
Chironomidae	2499±602	1296±213	1130±601
Gammarus sp.	6±5	1±1	11±3
Outer Saginaw Bay	$n = 9^c$	$n = 1^b$	–1
Diporeia spp.	1158±536	819±189	254±98
Oligochaeta	4553±1299	388±88	607±162
Sphaeriidae	549±172	288±68	168±60
Chironomidae	t688±176	218±49	420±140

Note: *n* is the the number of sites; 1971, prephosphorus control; 1987–1990, postphosphorus control and pre-*Dreissena*; 1993–1996, postphosphorus control and post-*Dreissena*. For outer Saginaw Bay, variability in 1971 is between sites, while variability in 1987–1996 is between years.

[a] Batchelder (1973).

[b] Nalepa et al. (2003).

[c] S. Mozley, Department of Zoology, North Carolina State University, 4105 North Gardner Hall, Raleigh, NC 27695, USA, unpublished data.

1970–1999, the abundance of deepwater ciscoes diminished, while exotic prey fishes became ubiquitous. Since annual bottom-trawl prey assessments began in Lake Huron in the early 1970s, rainbow smelt and alewives have accounted for at least 60% of the catch by weight (Argyle 1982) and have become the major component in the diets of lake trout and other salmonines (Dobiesz 2003).

Following the buildup of top-predator populations in the main basin in the late 1970s to early 1980s, smaller, younger fish dominated the populations of rainbow smelt and alewives. Mean age of alewives age 1+ was 2.9 years from 1973 through 1981 but declined to 1.8 years in the mid- to late 1980s. Mean age continued declining after the late 1980s except in 1993–1995, when recruitment of several strong year-classes briefly shifted age and size structure back to older, larger fish (R.L. Argyle, unpublished data). Similarly, more than 80% of the adult rainbow smelt population is age 2 or younger, and in most years, less than 10% of the adults are older than age 3 (R.L. Argyle, unpublished data). The shift to smaller, younger alewives and rainbow smelt after the mid-1980s was accompanied by declines in adult biomass despite appearances of strong age-0 cohorts (Fig. 2). For example, age-0 alewives were abundant in 1995, but for some reason, age-3 alewives were scarce 3 years later when they should have boosted adult biomass. Age-0 cohorts of rainbow smelt were also abundant in the 1990s, but biomass of adults declined as the mean weight of adult rainbow smelt dwindled from 16 to 10 g during 1975–1999 (R.L. Argyle, unpublished data). Whether the level of predation on young alewives was sufficient to suppress recruitment is unclear. Alewives are also susceptible to overwinter mortality, particularly during harsh winters. Other climatic conditions such as fall cooling and spring warming rates can have a large impact on the success of individual year-classes (O'Gorman and Stewart 1999).

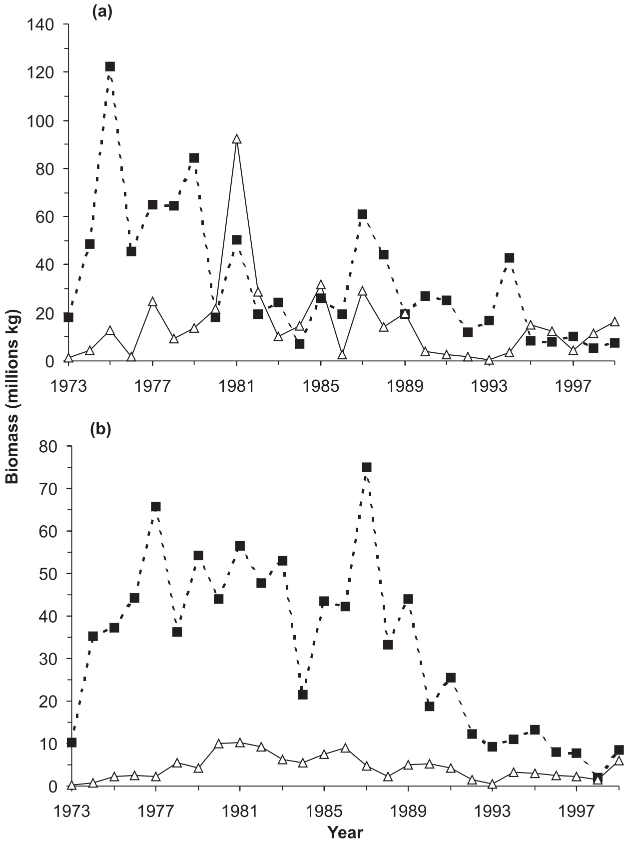
The remaining 40% of the bottom-trawl catches in the main basin comprised, in order of decreasing importance, deepwater sculpins (*Myoxocephalus thompsoni*), slimy sculpins (*Cottus cognatus*), ninespine sticklebacks (*Pungitius pungitius*), and trout-perch (*Percopsis omiscomaycus*). Of these species, only ninespine sticklebacks have been prominent in top-predator stomachs and then only in chinook salmon (*Oncorhynchus tshawytscha*) (Diana 1990). The ninespine stickleback is the only one of these four species that declined in abundance after the introduction of salmonines, whereas trout-perch abundance increased from 1973 through 1999.

Ciscoes

Lake herring

Lake herring, also known as shallow-water cisco, remained at a relatively low abundance in Lake Huron during 1970–1999, having changed little since Berst and Spangler (1973) implied that it was a victim of competition with introduced rainbow smelt. The lake herring fishery had been intensive historically only in Michigan's waters and there mostly in Saginaw Bay where the fishery intercepted a massive spawning run (Van Oosten 1929). Dramatic changes in lake herring abundance did not occur when rainbow smelt first proliferated, although Berst and Spangler (1973) noted that lake herring populations declined as rainbow smelt numbers increased. Rainbow smelt may have contributed to declines in lake herring numbers — lake herring were most persistent where rainbow smelt densities were lowest: in the North Channel (Spangler and Collins 1992) — but whether major

Fig. 2. Estimated biomass of adult (squares) and young-of-the-year (triangles) (*a*) alewife (*Alosa pseudoharengus*) and (*b*) rainbow smelt (*Osmerus mordax*) from 1973 to 1999 in US waters of Lake Huron. Annual systematic surveys of prey fish populations were conducted using a 12-m bottom trawl from 1973 to 1991 and a 21-m bottom trawl from 1992 to 1999. Locations, depths fished, and trawling gear are described in Argyle (1982).



interactions occurred remains obscure. Lake herring populations could no longer support major fisheries after the mid-1960s and persist now only in the northern waters of the main basin, the lower St. Mary's River, and the North Channel. These northern populations are of particular interest because they are the nearest source of colonists for depopulated areas farther south in Lake Huron. Assessment gillnetting along the south shore of Drummond Island suggests that year-class strength improved markedly in the mid-1990s. The 1993–1995 year-classes at ages 3–5 were 20 times larger than the 1988–1992 year-classes (M.P. Ebener, unpublished data). This improvement is encouraging assuming that range expansion would begin with increases in abundance of the source population.

Deepwater ciscoes

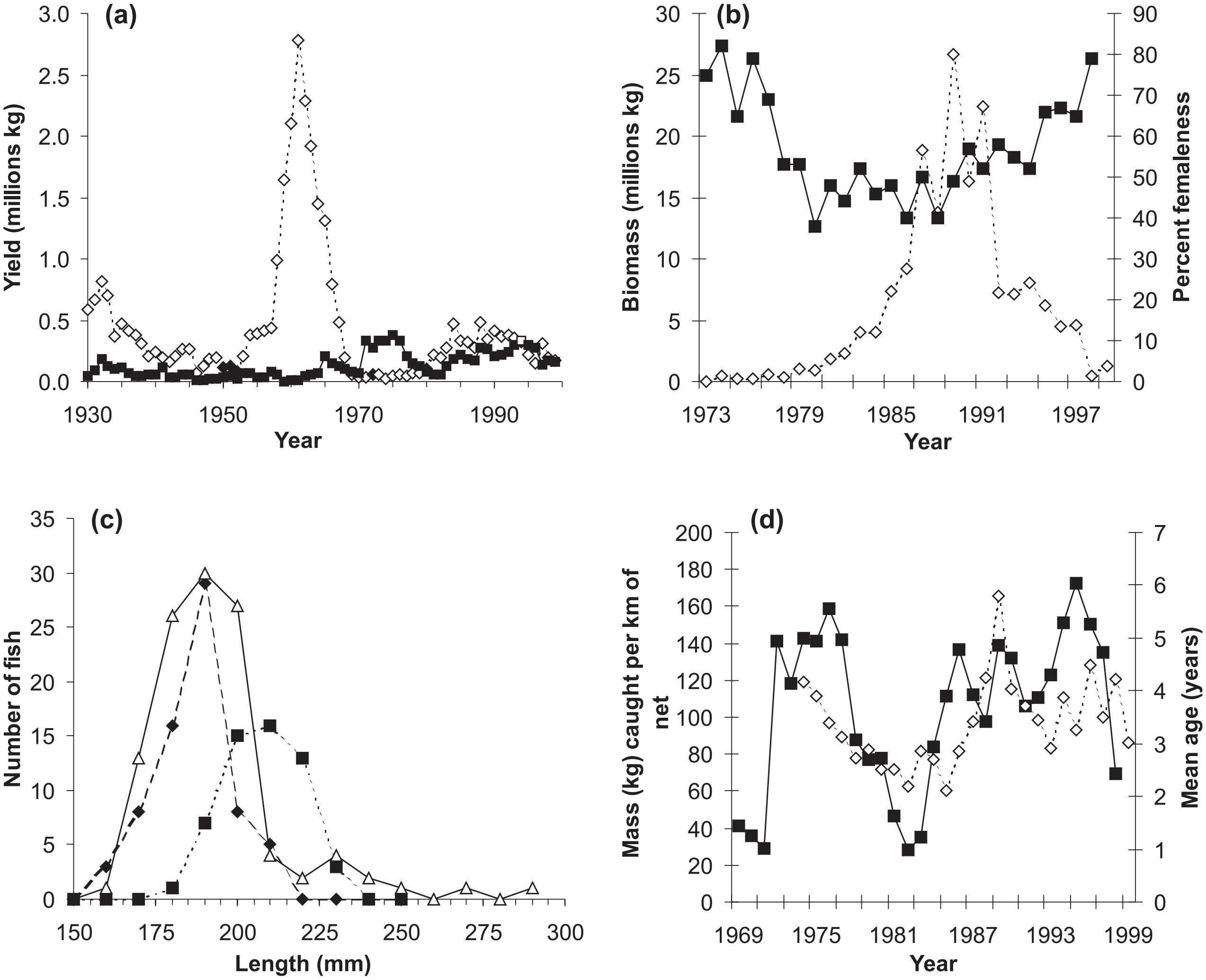
Deepwater ciscoes (commercially known as chubs) appear to have been very sensitive to pulses in fishing pressure for two reasons: (*i*) cyclic recruitment associated with female predominance made populations particularly vulnerable to collapse and (*ii*) depletion of one species did not result in a relaxation of fishing pressure as long as other deepwater ciscoe species were present to support the fishery (Smith 1968). Originally, there were six deepwater ciscoe species, but by the late 1990s, only the smallest of these species (bloater) persisted in Lake Huron. Berst and Spangler (1973) did not list deepwater ciscoes among the species whose demise they attributed solely to overfishing. At the time of their paper, a bout of intensified fishing that produced record but apparently unsustainable catches was coming to an end (Fig. 3*a*). They suggested that the record chub catches of the late 1950s and 1960s were supported by the smaller-bodied species of deepwater ciscoes, which prospered after being released from competition. Their competitors, larger-bodied fish such as lake whitefish, lake herring, and the larger-bodied species of deepwater ciscoes, had been greatly reduced in abundance by sea lamprey parasitism and fishing.

Cycles in the sex ratio and weak recruitment are well documented for Lake Michigan bloaters (TeWinkel et al. 2002). In the early part of a cycle, adult abundance is low, females predominate markedly, and recruitment is weak. In the middle of a cycle, recruitment is reestablished and the sex ratio becomes less biased as males are well represented among recruits. In the last part of a cycle, adult abundance declines, females predominate as males are winnowed by higher mortality, and recruitment nearly ceases. The bloater population in Lake Huron's main basin also appears to follow this type of cyclic behavior (Fig. 3*b*) with adult biomass increasing from low levels in the mid-1970s (Brown et al. 1987) and returning to low levels by 1998–1999.

We believe that two bouts of intensified chub fishing in Lake Huron, one that began in the late 1950s in the main basin and another that began in the 1970s in Georgian Bay, caused severe declines in population abundance, including extirpation, because both episodes coincided with the late part of a population cycle when recruitment was weak. We assume, based on Lake Michigan, that weak recruitment by itself or exaggerated female predominance can be used to mark where a population is in a cycle. In the main basin example, length frequencies of bloaters were significantly shifted towards larger fish in 1956 when intensified fishing started as compared with 1938 (before intensified fishing began) and with 1977 (when population recovery was well underway) (Fig. 3*c*). These admittedly sparse data from outer Saginaw Bay suggest that when the fishery was gearing up in the late 1950s, the chub population was in the latter half of a population cycle typified by high adult biomass and weak recruitment. This hypothesis explains how catches could decline so rapidly from record-high levels (Fig. 3*a*) — there was little replacement for the adult fish being removed by the fishery.

In the second example, which involves a period of intensified fishing on Georgian Bay chubs during the 1970s and early 1980s, growth of bloaters was faster and female predominance was high just before fishing started (Brown et al. 1987), suggesting that the population was in the early part of a cycle. Mean age of bloaters, which is positively related to female predominance (TeWinkel et al. 2002), was also high when fishing started but fell rapidly as catch per unit effort plunged in response to the fishing-up of adult chubs in the late 1970s (Fig. 3*d*). Younger fish supported the fishery into the early 1980s, indicating that by the mid-1980s, the population was still in the first half of a cycle, but apparently, recruits were too few and (or) small to stave off the plunge in catch per unit effort, which reached its nadir in the early

Fig. 3. Population and catch statistics for deepwater ciscoes (chubs; *Coregonus* spp.) in Lake Huron. (*a*) Commercial yield of chubs from the main basin (diamonds) of Lake Huron and Georgian Bay (squares), 1930–1999. (*b*) Estimated biomass (diamonds) and percent females (squares) for adult bloaters (*Coregonus hoyi*) (age 1+) taken in assessment bottom trawls in Lake Huron's main basin, 1973–1999 (R.L. Argyle, unpublished data). (*c*) Length–frequency distributions of bloater taken in 38-mm gill nets from outer Saginaw Bay in 1938 (diamonds), 1956 (squares), and 1979 (triangles) (R.L. Eshenroder, unpublished data). (*d*) Catch per unit effort (squares) for the commercial chub fishery and mean age of chubs (diamonds) taken in graded-mesh gill nets in Georgian Bay, 1969–1999 (L.C. Mohr, unpublished data).



1980s. These recruits, however, enabled a second bout of intensified fishing during the late 1980s and 1990s. Their presence also explains why the second bout of intensified fishing was more sustainable than the first (Fig. 3*d*) — fishery expansion coincided with the middle part of a population cycle when recruitment is stronger.

The role of rainbow smelt and alewives in the ciscoe population collapse in the Great Lakes is still debated. Berst and Spangler (1973) dismissed the alewife as an impediment to recruitment of deepwater ciscoes in the main basin of Lake Huron because they believed that alewives did not become abundant until the early 1960s, when deepwater cisco recruitment was already reduced. Carr (1962), however, reported that age-0 alewives were the predominant fish in Saginaw Bay in 1956, when intensified chub fishing in the main basin was just starting. If adult alewives were sufficiently abundant to produce a dominant year-class in 1956, we believe that they were abundant enough to interfere with a recovery of deepwater ciscoes following the bout of intensified chub fishing of the late 1950s and early 1960s. Insomuch as peak catches of chubs occurred in 1961, well after rainbow smelt became prominent, it is unlikely that rainbow smelt triggered recent (after 1956) extirpations of deepwater ciscoes in Lake Huron.

Lake whitefish

During the last two decades, lake whitefish populations were more abundant than during the Berst and Spangler (1972) review. Consistently strong reproduction occurred throughout most areas of Lake Huron beginning with the 1977 year-class and progressing through about the 1994 year-class (M.P. Ebener, unpublished data). In the Canadian waters of the main basin, the successful year-classes ended in

1991, and by 1994, three weak year-classes led to reductions in quotas in these waters (L.C. Mohr, unpublished data).

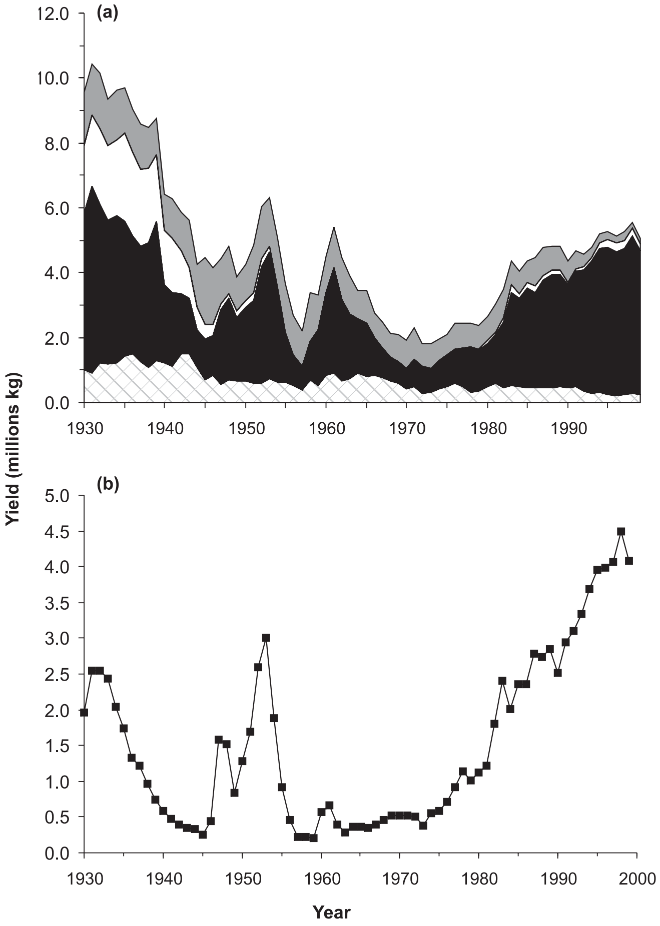
Survival of adult lake whitefish increased substantially, especially in the main basin and North Channel, after the first full round of chemical treatments of sea lamprey inhabited streams (Spangler and Collins 1980). At the same time, abundance of lake trout and chinook salmon in Lake Huron was increasing as was their predatory effects on rainbow smelt and alewives. This predation pressure likely increased the survival of lake whitefish juveniles by reducing predation, and potentially competition, between them and alewives and rainbow smelt (Ebener 1997). Favorable environmental conditions also promoted high lake whitefish egg and fry survival resulting in consistently strong year-classes that were spatially segregated and subjected to different levels of fishing and sea lamprey predation (Brown et al. 1993).

The prolonged surge in lake whitefish abundance appears to be ending. Commercial catches have peaked in the main basin (Fig. 4*a*) and lake whitefish growth is declining. In the southern main basin, where the decline in growth was most pronounced, mean weight of age-3 lake whitefish decreased from 1.10 kg in 1979 to 0.25 kg in 1998. The decline in growth was less pronounced outside the main basin. During 1976–1998, the average decrease in weight-at-age was approximately 20% in Georgian Bay and 23% in the North Channel (L.C. Mohr, unpublished data). Declines in growth were accompanied by delayed maturation. In northern US waters during 1976–1982, 50% of female lake whitefish were sexually mature by age 4 and all females age 6 and older were sexually mature, but by 1998, about 50% of females were not sexually mature until age 5 and 100% maturity did not occur until after age 10. Causes of the decline in lake whitefish growth in the main basin are not clear. In Lake Michigan, condition and growth of lake whitefish declined as dreissenid mussels proliferated and *Diporeia* populations crashed (Pothoven et al. 2001). As of 1999, declines in *Diporeia* populations in Lake Huron have only been detected in outer Saginaw Bay. Measurement of benthic production has been limited to very few locations outside the bay, most of which are in US waters, making it difficult to assess the effect of lakewide changes in *Diporeia* abundance on lake whitefish growth.

Piscivores

Ambitious salmonine stocking programs had already begun in the Great Lakes in the late 1960s when Berst and Spangler (1973) reviewed the status of Lake Huron's fish community. The initial intentions for introducing Pacific salmon were to control populations of alewife and rainbow smelt and to create a sport fishery (Tody and Tanner 1966). Since 1973, the numbers of planted Pacific salmon, brown trout (*Salmo trutta*), rainbow trout or steelhead, and lake trout expanded. A variety of life stages were planted, including eyed eggs, fry, fingerlings, and yearlings. Annual stocking of all species combined increased from 0.8 million in 1968 to 15.9 million in 1992. The latter figure includes walleye (*Sander vitreus*), which have been stocked since 1978. Management agencies capped predator stocking in 1992, and stocking of chinook salmon was reduced by 20% in 1992 and by another 20% in 1999.

Fig. 4. (*a*) Commercial yield of coregonids (solid area), salmonids (open), percids (cross-hatched), and other species (shaded) from Lake Huron between 1930 and 1999. (*b*) Commercial yield of lake whitefish only.



Lake trout

Berst and Spangler (1973) doubted that economically sound lake trout management could be achieved in Lake Huron even if sea lamprey abundance could be held to low levels. Their pessimistic assessment was based on a belief that lake trout were extremely vulnerable to sea lamprey predation. To resolve the problem of extreme vulnerability, the province of Ontario had already begun stocking splake as an alternative to the late-maturing lake trout.

During the 1990s, vigorous debate over the collapse of lake trout populations centered on the relative importance of sea lamprey predation and overfishing. Some researchers attributed the collapse principally to sea lamprey predation (Berst and Spangler 1973; Coble et al. 1990) and others to overfishing (Eshenroder et al. 1995; Spangler and Peters 1995), while some argued that both the sea lamprey and fishing were important (Hansen 1999). In Lake Huron, the debate focused on the lean form of the lake trout harvested in the main basin in the 1940s. Deepwater forms of lake trout were extirpated by 1925, well before sea lampreys entered the lake (see Sea lamprey section). The role of deepwater lake trout in Lake Huron continued to be overlooked when reintroduction of lake trout and splake stocking began in the early 1970s.

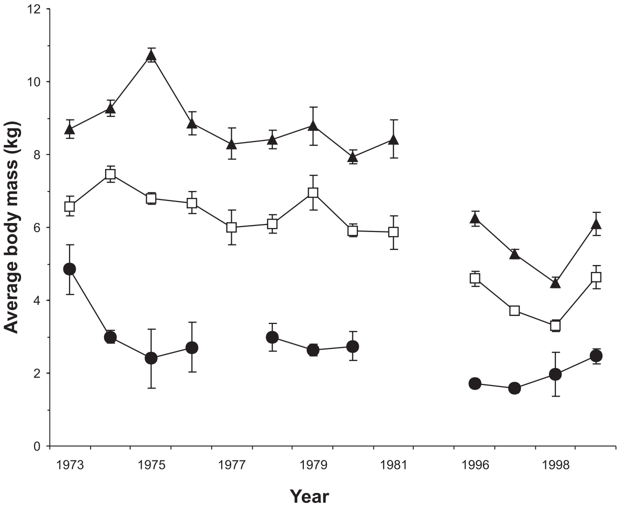
By 1974, lake trout were stocked only in the main basin, and there only in Michigan waters. The planting of approximately 1 million lake trout per year has not led to sustainable reproduction. Naturally reproduced lake trout in the main basin were as scarce at the end of the 1990s as they were at the start of that decade. Exactly what inhibits natural reproduction of lake trout is not clear (Eshenroder et al. 1999), but the problems identified by Eshenroder et al. (1995) for the main basin remain unresolved: low stocking levels aggravated by stocking an already inadequate allocation of fish in areas of sparse reproductive habitat, a net migration of fish from Michigan waters into unstocked areas on the Ontario side of the main basin, and excessive mortality from fishing and sea lampreys (also see Sitar et al. 1999). Sea lamprey predation and fishing mortality rates, however, are likely to be lower in the near future than in the 1990s, a result of sea lamprey control efforts on the St. Mary's River and fishery management efforts associated with the 2000 renegotiation of an agreement on Native American treaty rights in US waters. Treatment of the St. Mary's River has already led to a modest reallocation of lake trout stockings to the northern part of the main basin where lake trout spawning habitat is more concentrated (see Sea lamprey and Fisheries sections).

The prospects for rehabilitation of lake trout appear to be better in Georgian Bay where two small populations persisted (Berst and Spangler 1973), in part because sea lampreys were less abundant there (Eshenroder et al. 1995). The genotype stocked in Georgian Bay has changed from splake in the 1970s to a predominance of splake backcrossed to lake trout in the 1980s to a predominance of pure lake trout in the 1990s (Eshenroder et al. 1995). The stronger of two persisting populations in the Bay, the one in Parry Sound (Fig. 1), was augmented with stocked lake trout spawned from adults collected at the same locality. Reid et al. (2001) estimated that the spawning population in 1994–1997 ranged from 16 000 to 29 000 individuals. As the lake trout population increased, sea lamprey marking rates approached zero, reflecting a favorable sea lamprey to lake trout ratio and negligible mortality caused by sea lamprey. In comparison, during 1958, prior to effects of sea lamprey control in the bay that began that year, high marking rates in Parry Sound indicated that sea lamprey attacks were causing an increase in instantaneous mortality rates between 0.32 and 0.58·year^{-1} (Reid et al. 2001). The spawning stock that produced wild recruits was fortified by high stocking rates, but stocking in Parry Sound discontinued after 1997 because the large spawning population was composed mainly of wild fish. The Parry Sound lake trout population is the only Lake Huron population considered to be rehabilitated.

Trends in biomass and consumption by piscivores

Increases in predator stocking rates, rehabilitation of lake trout, and treatment of the St. Mary's River for sea lampreys prompted concerns that increased predator populations could exceed the productive capacity of the open-water prey fish community. Increases in salmon stocking during the 1980s were associated with declines in prey abundance and slower growth of chinook salmon (Fig. 5). The proportion of age-4 chinook salmon, the oldest age in the spawning run, increased from 0.4% from 1974 to 1981 to 15.2% from 1996 to 1999 (J.E. Johnson, unpublished data). Thus, as growth declined, possibly in response to declining alewife abundance, maturation of salmon was delayed. A similar scenario preceded a collapse of the chinook salmon fishery in Lake Michigan (Holey et al. 1998).

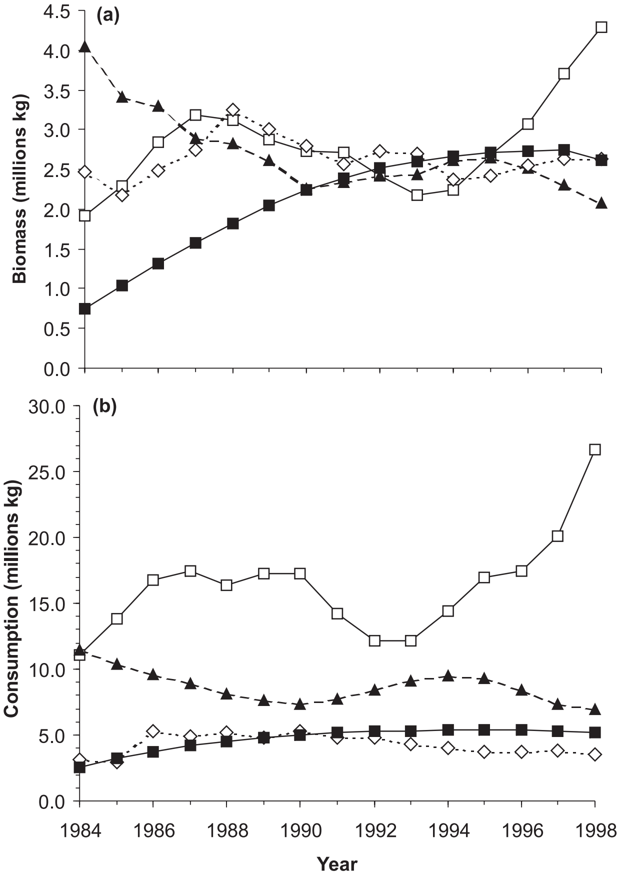
Fig. 5. Average mass and 95% confidence intervals for individual age-1 (circles), age-2 (squares), and age-3 (triangles) mature chinook salmon (*Oncorhynchus tshawytscha*) caught on the AuSable River, western Lake Huron, 1973–1999. Mean masses at each age were significantly different between 1973–1981 and 1996–1999. Two-tailed Mann–Kendall trends tests yielded $S = -29$ and $p = 0.0293$, $S = -54$ and $p = 0.0012$, and $S = -52$ and $p = 0.0019$ for ages 1–3, respectively. Significant Mann–Kendall trend tests indicate a nonrandom pattern generated by systematic trend or temporal correlation in the time series.



To explore whether top predators were overly abundant and to determine how the system has changed since Berst and Spangler's (1973) account, a time when planktivores dominated the fish community, mean predator biomass and consumption of prey in Lake Huron were estimated for the period 1984–1998 (Dobiesz 2003). This exercise was restricted to the main basin because of the availability of data and focuses on four key predators: chinook salmon, lake trout, walleye, and burbot. Other species, coho salmon (*Oncorhynchus kisutch*), brown trout, pink salmon (*Oncorhynchus gorbuscha*), and rainbow trout, have played a less significant role in fish community dynamics.

We used the Mann–Kendall trend test (Kendall 1975) to examine trends in biomass and consumption. The combined biomass of the key predators trended slightly upward ($S = 45$, $p = 0.0294$) during 1984–1998, but the composition of that biomass changed substantially (Fig. 6*a*). Total biomass averaged 10.3 million kg, with average species-specific contributions ranging from 2.1 million kg for burbot to 2.8 million kg for chinook salmon. Lake trout biomass was the only one that declined substantially. Most of this decline occurred in the southern main basin and was attributed primarily to declines in stocking in that region (Sitar et al. 1999). By contrast, chinook salmon biomass increased substantially

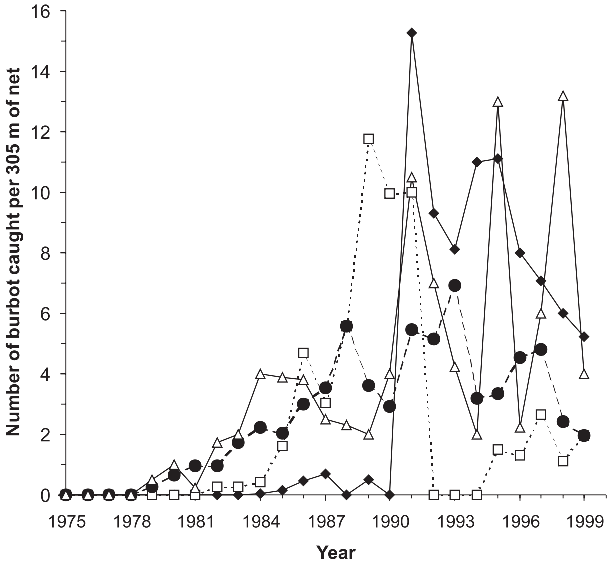
Fig. 6. Estimated (*a*) biomass and (*b*) consumption by the major piscivores chinook salmon (*Oncorhynchus tshawytscha*) (open squares), lake trout (*Salvelinus namaycush*) (triangles), walleye (*Sander vitreus*) (open diamonds), and burbot (*Lota lota*) (closed squares) in the main basin of Lake Huron during 1984–1998 estimated from stock assessment and bioenergetics models (Dobiesz 2003). Two-tailed Mann–Kendall trend tests of biomass yielded S = 21 and p = 0.3223, S = –63 and p = 0.0022, S = –3 and p = 0.9212, and S = 97 and p < 0.0001 for chinook salmon, lake trout, walleye, and burbot, respectively. Two-tailed Mann–Kendall trends tests of consumption yielded S = 39 and p = 0.0600, S = –43 and p = 0.0377, S = –41 and p = 0.0478, and S = 85 and p < 0.0001 for chinook salmon, lake trout, walleye, and burbot, respectively. Significant Mann–Kendall trend tests indicate a nonrandom pattern generated by systematic trend or temporal correlation in the time series. Trends for burbot are based on assumed constant recruitment at age 1 with constant natural and fishing mortality and decreasing sea lamprey induced mortality, so these patterns reflect an overall trend and not year-to-year variation.



(Fig. 6*a*). Almost all of this increase was in 1997–1998, which occurred despite declines in mean weight-at-age between 1974–1981 and 1996–1999 (Fig. 5).

Even though burbot mean biomass is relatively low (Fig. 6*a*), historically, burbot were likely an important predator in Lake Huron. Berst and Spangler (1973) noted that the burbot population declined concomitantly with the collapse of the lake trout population, but no data were presented. Until the early 1980s, burbot were rare in Lake Huron assessments but they were taken frequently in recent years (Fig. 7). Although there is no way to compare their current abundance with that of pre-sea lamprey days, this species was consuming a nonnegligible amount of prey biomass by the 1990s (Fig. 7) and is important in the lake's food web (Eshenroder and Burnham-Curtis 1999).

Fig. 7. Number of burbot (*Lota lota*) caught in 305 m of index gill nets set by the Michigan Department of Natural Resources at several sites throughout Lake Huron, 1975–1999, in Georgian Bay (triangles) and the northern (diamonds), central (squares), and southern (circles) regions of the main basin.



Overall, walleye biomass varied without trend, but the biomass of Saginaw Bay walleyes, which feed in the main basin proper, increased, while the biomass of walleyes in the southern main basin declined (Dobiesz 2003). Except for the recovery of walleye populations in Saginaw Bay (Mrozinski et al. 1991), walleye populations do not appear to have changed much since Berst and Spangler (1973) gave their account. Substantial numbers still migrate from Lake Erie into southern Lake Huron (McParland 1996) and support commercial and angling fisheries. Populations inhabiting the larger rivers along the east shore of the North Channel and Georgian Bay also persist, while those inhabiting the smaller rivers remain depleted (Reckahn and Thurston 1991; Eshenroder 2003).

Lake trout and chinook salmon accounted for 73% of the 34.2 million kg of prey fish consumed on average by all four key piscivores during 1984–1998. Chinook salmon increasingly dominated consumption, with a significant upwards trend during the 1990s (S = 20, p = 0.0476). Since the increase happened over just a few years, the trend over the entire modeled period was nonsignificant (S = 39, p = 0.06) (Fig. 6*b*). Most of the increase occurred in the latter years and was caused by increased stocking of chinook salmon during the first half of the 1990s and improved stocking methods (e.g., net pens) during the later half of the 1990s. Already the dominant predator in 1984, chinook salmon became even more abundant, partly at the expense of lake trout, during 1984–1998. In this period, estimated total consumption of prey fish by lake trout declined from a high of 12.2 million kg to 7.6 million kg. During 1984–1998, consumption by walleye and burbot was similar, accounting for 20% of the total annual consumption.

From 1996 to 1998, when consumption averaged 37.8 million kg, alewives were the predominant prey and comprised 54% of total consumption. Rainbow smelt were next in importance and comprised 28% of total consumption. Lake trout, chinook salmon, and walleyes fed heavily on alewives and rainbow smelt, which comprised 97%, 83%, and 60% of their diets, respectively. In contrast, burbot fed more on invertebrates and sculpins, which accounted for approximately 49% of their diet (Dobiesz 2003).

Cormorants

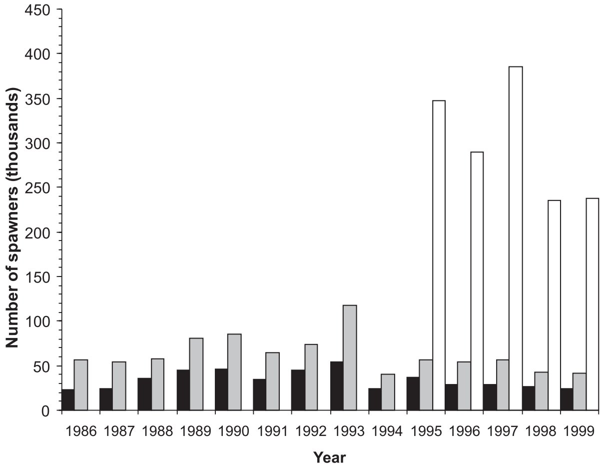
The double-crested cormorant (*Phalacrocorax auritus*), a piscivorous waterbird, has gained some importance as a fish consumer in Lake Huron (Weseloh et al. 1995). The first confirmed nesting occurred in 1932, and by the 1940s, as many as 3000 breeding pairs resided on Lake Huron (Ludwig and Summer 1997). Egg-shell thinning and other reproductive failures tied to dichlorodiphenyltrichloroethane (DDT) contamination caused populations to plummet by the 1970s. Consequently, Berst and Spangler (1973) did not identify this bird as an important piscivore. Following the DDT ban, cormorants exhibited a spectacular population increase on Lake Huron (Weseloh et al. 1995), from fewer than 1000 active nests in 1980 to about 27 000 nests in the mid-1990s (Ludwig and Summer 1997; Weseloh et al. 2002) and 40 000 nests in 2000 (Weseloh et al. 2002; C. Weseloh, Canadian Wildlife Service, 4905 Dufferin Street, Downsville, ON M3H 5T4, Canada, personal communication; D. Fielder, Michigan Department of Natural Resources, 106 East Fletcher, Alpena, MI 49707, USA, personal communication.). Although the highest density of nests is in the North Channel, cormorants have also expanded their nesting range (Weseloh et al. 2002). By 2000, 38% of nests were around the main basin and the remaining nests were equally divided between the North Channel, including the St. Mary's River, and Georgian Bay.

We estimated that in 2000, cormorants consumed approximately 13.9 million kg of fish, 5.3 million kg of which was consumed in the main basin. Consumption by cormorants in the main basin is equivalent to about 18% of the estimated consumption by key piscivores in the main basin during 1996–1998. These estimates assume that 346 kg were consumed annually by the birds associated with each nest (Madenjian and Gabrey 1995). Although we do not have an estimate of consumption for nonresident (migrant) birds in Lake Huron, migrant birds consumed 19% of the resident total in western Lake Erie. Because cormorant foraging is centered around shore and island colonies, shore-associated fishes such as smallmouth bass (*Micropterus dolomieu*), yellow perch (*Perca flavescens*), walleye, and recently stocked salmonines can figure prominently in diets. Cormorant predation has been a particular concern regarding anglers of yellow perch in the Les Cheneaux Islands region (Diana and Maruca 1997) and some populations of smallmouth bass.

Sea lamprey

Sea lampreys have been at pest levels of abundance in Lake Huron since the 1980s, despite intensive control efforts. Berst and Spangler (1973) implicated the sea lamprey as the principal cause of the impairment of Lake Huron fisheries and advocated a second round of lampricide applications in infested streams. As of 1999, eight rounds involving 620 applications have been made to Lake Huron tributaries (Morse et al. 2003).

Fig. 8. Numbers of spawning-phase sea lampreys (*Petromyzon marinus*) captured in assessment traps from an average of 13 Lake Huron streams (range 9–16, solid bars), their estimated populations in the Cheboygan, St. Mary's, and Thessalon Rivers from 1986 to 1999 (shaded bars), and the estimated lake population from 1995 to 1999 (open bars).



Juvenile sea lampreys were not abundant when reintroduction of lake trout began in earnest in the main basin in 1973. Although the parasitic (juvenile) population expanded after the first individuals were observed in 1937 (Applegate 1950), numbers declined by as much as 85% from 1949 to 1970 (Schleen et al. 2003). Thus, the juvenile (parasitic) population in the main basin was already reduced in number when the first round of lampricide treatments was completed, but low abundance of juveniles was largely attributable to a dearth of suitable hosts rather than just to reduced survival of stream-inhabiting larvae caused by lampricide treatments. The dynamics of this situation became clearer when sea lamprey numbers surged in the early 1980s (Fig. 8) in association with a modest recovery of bloater, a preferred prey of young juveniles (Eshenroder et al. 1995).

The only large population of untreated larvae known in Lake Huron was in the St. Mary's River, a wide connecting channel that drains Lake Superior. Although sea lamprey larvae infested the river as early as 1962 (Schleen et al. 2003), two factors weighed against a treatment: its great discharge (mean 2100 $m^3 \cdot s^{-1}$) made the efficacy of a conventional and potentially costly treatment problematical and the extent of the larval population was unknown. By 1996, this situation was rectified when the St. Mary's population of larvae was estimated at 5.2 million individuals based on a multiyear survey (Fodale et al. 2003).

Treatment of the St. Mary's River with the commonly used lampricide TFM was ruled out because maintaining a lethal dose at the bottom of the water column was problematic. Indeed, the amount of TFM needed for a conventional treatment of the river was estimated at 2.5–6.5 times the average annual use in all of the Great Lakes (Schleen et al. 2003). An alternative approach using Baylucide embedded in time-release granules was employed in 1998 and 1999 to treat 860 ha of the riverbed, estimated to harbor 45% of the larval population (Schleen et al. 2003). This treatment was intended to enhance sterile-male release and adult trapping control programs. Combined, these methods were projected to reduce the number of juvenile sea lampreys in Lake Huron by 85% (Morse et al. 2003). The high level of parasitism in the main basin before the Baylucide treatment was seen as so onerous that stocking of lake trout in northern waters was halted in 1993 — stocking resumed prior to the treatments in the St. Mary's River, in anticipation of reduced sea lamprey predation.

The outcome of the recent control efforts on the St. Mary's River remains to be determined. The success of lake trout rehabilitation in the main basin and the North Channel is assumed to be tied to successful sea lamprey control. In these areas, a mid-1990s population in excess of 0.5 million was believed to limit the reestablishment of a viable lake trout population (Eshenroder et al. 1995). By contrast, prospects for lake trout rehabilitation are much better in Georgian Bay. Sea lampreys were slower to colonize the bay and control has been more effective (Eshenroder et al. 1995), and wild lake trout are already abundant in some areas. Although sea lampreys may have the upper hand in most of Lake Huron, ongoing experimentation with pheromone-based control methods (Li et al. 2002) will hopefully improve suppression.

Fisheries

Berst and Spangler (1973) advocated a greater role for overfishing than for sea lampreys in restructuring the lake's fish community. Spangler and Peters (1995) held that overfishing was pervasive by the late 1800s and suggested that landings of lake trout held up for as long as they did because the populations were being fished-up sequentially. The fishing-up process accelerated with the introduction of the steam tug, first used in Michigan waters in 1860, which allowed the fishery to expand to offshore waters. Spangler and Peters (1995) were not clear whether offshore fishing in any of the basins before the twentieth century represented growth overfishing (harvesting below the optimum size) or recruitment overfishing. Lake trout landings held up for a remarkably long time, until the 1930s, considering how long the offshore populations were accessible to the fishery.

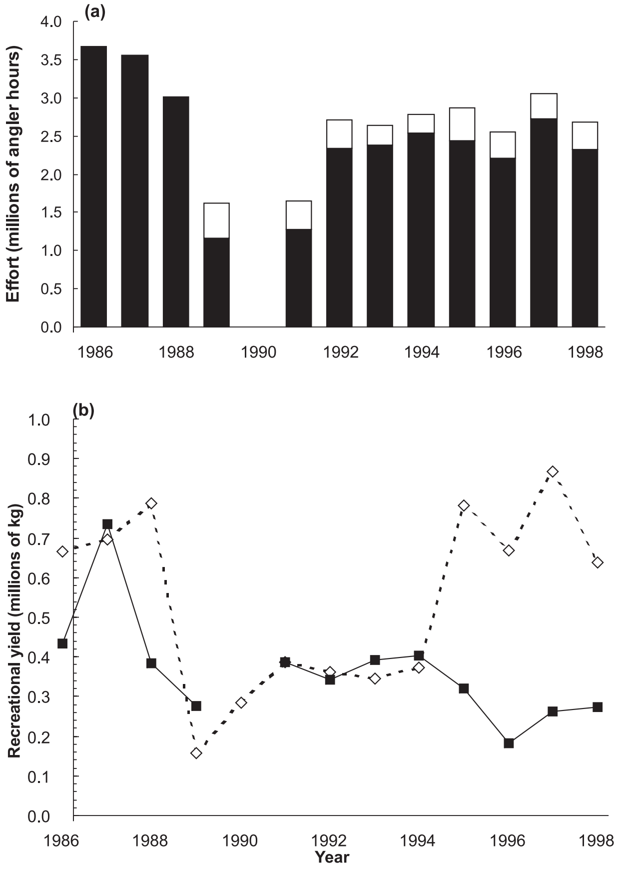
During 1970–1999, the regulatory framework and gears used in the commercial fisheries underwent profound changes, and a more sophisticated offshore recreational fishery targeting Pacific salmon and lake trout developed. The traditional regulatory framework (offshore fisheries were essentially commercial with open entry and equal access to fishing grounds) was still in place when Berst and Spangler (1973) wrote their overview. Shortly after introducing salmon in the late 1960s, the State of Michigan initiated major regulatory changes in its commercial fisheries that partly reflected their new emphasis on recreational fishing. The most important modifications were the closing of all waters except Saginaw Bay to large-mesh gill nets, typically used to take lake whitefish and lake trout, banning the catch of deepwater ciscoes and walleyes, and issuing licenses only to those who could demonstrate a livelihood from fishing (Brege and Kevern 1978). In 1984, the Province of Ontario also made major regulatory changes that entailed a system of transferable quotas (Brown et al. 1999).

The reduction in commercial fishing and associated decrease in fishing mortality on lake trout were short lived. Commercial fishing under treaty rights began first in Michigan waters and then in Ontario waters, and recreational fisheries began to take substantial numbers of lake trout. Treaty fishing led to increased commercial landings during the late 1970s and 1980s (Fig. 4*b*) as more gear was being fished, especially in Michigan, although these larger yields would not have been possible without the rebounding lake whitefish populations. During the 1960s, lake whitefish comprised 18% of the total landings and by 1999 this figure increased to 80% (Fig. 4*a*). The use of large-mesh gill nets (10.16–30.48 cm), which Michigan and Ontario wanted to minimize to reduce bycatch of lake trout, also increased during this period (Brown et al. 1999). Of all of the fishing gears employed, lake whitefish gill nets have undergone the most improvement. Monofilament twine of only 0.17-mm diameter has replaced multifilament twine of 0.27 mm, and nets have deepened by a factor of 3 (Brown et al. 1999).

Following two negotiated settlements (United States of America and four Native American bands v. State of Michigan et al. 1985; United States of America and eight Native American bands v. State of Michigan et al. 2000), commercial fishing in Michigan's northern waters became restricted to tribal members and was managed under tribal regulations. A state-managed recreational fishery shares the lake trout resource under agreed-upon mortality targets and allocations of yield. Under the 1985 agreement (United States of America and four Native American bands v. State of Michigan et al. 1985), target mortality rates for lake trout were not put in place for the northernmost Michigan waters of the main basin, except for a refuge where commercial fishing and recreational take of lake trout were not allowed (Fig. 1). Lake trout rehabilitation was deferred in these waters, which contained some of the historically most productive lake trout spawning grounds (Eshenroder et al. 1995). The 2000 agreement (United States of America and eight Native American bands v. State of Michigan et al. 2000) established target mortality rates for lake trout and an approach for encouraging a change from gill nets to trap nets. A similar management arrangement between Ontario First Nations and management agencies does not exist (Brown et al. 1999).

Assessment of recreational fishing effort and harvest began during the mid-1980s. Of the three main recreational fisheries, the offshore salmonine and nearshore warm- and cool-water fisheries have been at least partially assessed in most years, whereas the river fishery for salmonines has been essentially unmonitored in a number of years. An extended time series for the in-lake fisheries is available for the main basin but not for Georgian Bay or the North Channel. Recreational effort in the combined offshore and warm- and cool-water recreational fisheries (in-lake fishing) of the main basin was at a peak of over 4 million angler hours in 1986, the first year for which there is an overall estimate, and subsequently declined and stabilized during the 1990s at approximately 3 million angler hours per year (Fig. 9*a*). Michigan anglers accounted for most of this fishing activity. Main basin in-lake recreational fishing effort has been almost equally divided between salmonine and percid fisher-

Fig. 9. (*a*) Recreational fishing effort in Canadian waters (open bars) and US waters (solid). (*b*) Recreational yield of salmonines (diamonds) and nonsalmonines (squares). Data derived from creel surveys conducted by Michigan Department of Natural Resources and the Ontario Ministry of Natural Resources in the main basin of Lake Huron, 1986–1998.



ies, although during the 1990s, the emphasis in Ontario waters shifted from other species to salmonines (Mohr and Nichol 1998). In the main basin (excluding rivers), percids far exceed salmonines in the numbers harvested (but not in yield), reflecting the high catch rates of smaller-sized yellow perch (Bence and Smith 1999). However, in the late 1990s, the contribution of salmonines increased, reflecting a decrease in the yield of percids and an increase in the yield of salmonines (Fig. 9*b*). The recreational yield for Georgian Bay and the North Channel combined was roughly equal to the main basin yield in 1995 and consisted primarily of inshore fishes: yellow perch, walleye, and smallmouth bass.

Yield can only be compared between the angling and commercial fisheries for the whole lake for 1995, a year when anglers took just over 2 million kg of fish and the commercial fishery took just under 6 million kg. Angler yield that year was equally divided between the main basin and the North Channel and Georgian Bay combined. In the late 1990s, annual recreational yield in the main basin continued to average near the 1 million kg taken in 1995 (Fig. 9*b*).

Contaminants

Concentrations of contaminants in the waters and fishes of Lake Huron declined during 1970–1999. Berst and Spangler (1973) cautioned that chlorinated hydrocarbons and toxic metals under the right conditions might jeopardize the survival of lake whitefish, ciscoes, and lake trout. Since that time, bans on the use of major pollutants such as DDT and polychlorinated biphenyls contributed to declines in concentrations of both chemicals (Stevens and Neilson 1989). Ongoing monitoring and shorter term studies have shown that concentrations in Lake Huron fish from both US and Canadian waters are now lower than they were in the 1970s, although the decline has been slower than expected and may reflect food web changes (Frank et al. 1978; De Vault et al. 1996; Scheider et al. 1998). Lake trout are the most sensitive fish tested, but ambient levels of polychlorinated biphenyls (a toxin of particular concern) in lake trout from all of the Great Lakes are below levels associated with acute effects (Fitzsimons 1995). Consequently, recent research on toxic substances is shifting to chronic effects and to interactions between toxic chemicals and other maladies (Eshenroder et al. 1999). Despite reductions in contaminant loading, fish consumption advisories continue to be issued for certain fishes.

Exotics

Introductions with the potential to cause lake-wide impacts in the Great Lakes can be viewed as having arrived in two waves. The first wave arrived during the 1920s–1930s, well before SCOL-1 (Berst and Spangler 1973), and consisted of rainbow smelt, alewife, and sea lamprey. The second, more recent wave, entering via ballast water from ocean-going ships, was predominantly invertebrates: the spiny water flea (*Bythotrephes longimanas*), dreissenid mussels (*D. polymorpha* and *D. bugensis*), the fishhook water flea (*Cercopagis pengoi*), and the round goby (*Neogobius melanostomus*) (Shuter and Mason 2001).

Community effects of first-wave invaders are still not completely understood (Eshenroder and Burnham-Curtis 1999) even though the second wave is well established. Moreover, first-wave invaders typically exert effects at higher trophic levels, more readily analyzed with existing fishery models, whereas second-wave invertebrates are expected to impact lower levels, not readily evaluated by conventional fishery models (Shuter and Mason 2001). New invaders will likely also alter, mask, or confound the effects of earlier invaders, making catching up with system changes difficult. Thus, the issue of introductions, already complex at the time of SCOL-1, has become even less tractable because sampling of lower trophic levels, especially in Lake Huron, is sparser than it is for fish.

Aquaculture

The commercial culture of fish in cages or pens expanded substantially on Lake Huron in the 1990s. Since 1980, the number of cages increased from 0 to over 100 producing approximately 7.0 million kg of rainbow trout annually. Escapement of cultured fish in the North Channel may range from 7000 to 10 000 fish each year. Cage culture is an emerging concern because such fish can be vectors for disease and escapees could breed with wild rainbow trout.

Prognosis

Prospects for rehabilitation of the native salmonid communities of Lake Huron appear far brighter to us than they did to Berst and Spangler (1972, 1973). Our perceptions reflect the recovery of lake whitefish populations, reestablishment of substantial populations of top-level predators, and progress toward control of sea lamprey and limitation of fishing mortality. Nevertheless, maintaining what has heretofore been accomplished will require intensive management, and further progress in rehabilitating native species is uncertain.

We see two scenarios for Lake Huron's fish community — which one prevails depends on whether lake trout become self-sustaining. Assuming no surprises such as another inimical introduction, if lake trout recover and their population is allowed to expand, we anticipate that they would eventually replace hatcheries as drivers of the system, as in Lake Superior (Hansen et al. 1995). Under this scenario, we would expect a substantial recovery of yellow perch (beyond the large bays), walleye, lake herring, and deepwater ciscoes, whose fry, including those of two extirpated species, entrain regularly into Lake Huron via the St. Mary's River. Salmon fisheries would scale back but remain more prominent than they are in Lake Superior. In our second scenario, lake trout rehabilitation largely fails. Periodic dieoffs of alewives and salmon occur and major concerns become preventing loss of fitness in hatchery-origin populations and promoting naturalization of Pacific salmon. Room obviously exists between these scenarios, for instance, a full lake trout recovery in Georgian Bay, where it now has a head start, and no recovery in the main basin — an intriguing situation that would make vivid the differences between community types in the same lake.

Which of these scenarios will occur is unpredictable, in part because of our uncertain knowledge of how Lake Huron functions. We can make educated guesses on how fishery management actions, and other "forcing functions", will influence the relative likelihood of these alternatives. The forcing functions that seem to us most influential are related to top-down actions of fishery management. In particular, the outcome is likely to be influenced by the success of sea lamprey control, limitation of harvest (particularly of lake trout), and plantings of fish. In essence, we believe that rehabilitation of self-sustaining stocks of lake trout will require (*i*) development of a large, diverse population of lake trout spawners and (*ii*) maintaining sufficient numbers of predators so that alewife and rainbow smelt are maintained at low densities. In addition, an at least partial recovery of ciscoes will require limits on fishing them.

Development of a large population of spawning lake trout will require holding lake trout mortality rates to low levels. Control of fishing and sea lamprey is critical here. The need to suppress sea lampreys was identified long ago by Berst and Spangler (1973). In large part, we do not share their pessimism about lake trout restoration in the face of sea lampreys because self-sustaining populations of lake trout were reestablished in Lake Superior subsequent to successful sea lamprey control. Similar reductions in mortality caused by sea lamprey were not sustained in the main basin of Lake Huron because of the large number of parasitic-phase sea lamprey entering the lake from the previously uncontrolled St. Mary's River. Sea lamprey control on this river intensified in the late 1990s, and an 85% reduction in sea lamprey induced mortality on lake trout in the main basin was projected (Schleen et al. 2003). If this projection is met, sea lamprey induced mortality on lake trout in the main basin of Lake Huron will be comparable with levels in Lake Superior. If intensified control is unsuccessful, we doubt whether widespread rehabilitation of lake trout is possible, particularly in the main basin. Sea lampreys from the St. Mary's River play a lesser role in Georgian Bay; thus, some further expansion of the self-sustaining population of lake trout in the bay seems possible without successful control on the St. Mary's River.

Fishery management on Lake Huron currently limits harvest and restricts fishing mortality on most at-risk species, including lake trout. We emphasize that fishery removals reduce the spawning biomass that is potentially obtainable from each stocked lake trout (Sitar et al. 1999) — there is no harvestable surplus that can be removed without a cost to rehabilitation. On Lake Superior, where lake trout have recovered, fishing pressure has generally been lower than on Lake Huron. In that area of Georgian Bay where a population of lake trout is recovering, fishing is highly restricted (Reid et al. 2001). Thus, there will continue to be a trade-off between improved chances of rehabilitation and current fishery harvest.

Although we believe that fishery management is currently sustainable for most fishes except lake trout, we have concerns regarding current harvest policies for bloater. These same concerns would apply to other deepwater ciscoes (chubs) if they were to reestablish in Lake Huron. Bloater fishing is managed typically through quotas based on recent yields. Cycles in population size and sex ratio, not precipitated by overfishing, can create a situation where even seemingly low levels of fishing, in fact, become too high.

We believe that the prospects for our first scenario, which involves rehabilitation of lake trout, would be vastly improved were the plantings more diverse phenotypically, greater in number, and concentrated in regions where spawning habitat is most plentiful. Recovery of a self-sustaining population of lake trout in Georgian Bay followed a period of stocking that exceeded levels recommended by Ebener (1998). Stocking levels in the remainder of Lake Huron have generally been lower than recommended by Ebener (1998), and stocking often has not been targeted on the best spawning habitat, which is most plentiful in northern waters (Eshenroder et al. 1995). Recovery of self-sustaining populations of lake trout in Lake Superior, too, followed high levels of stocking. The resulting spawning populations were larger than those seen well before the collapse of historical populations (Wilberg et al. 2003). The diversity of lake trout in Lake Superior during rehabilitation was also much greater than it has been in Lake Huron, as deepwater forms of lake trout (siscowets and humpers) remained reasonably abundant in Lake Superior during rehabilitation (Hansen et al. 1995). The historical populations of lake trout in Lake Huron were also phenotypically diverse (Eshenroder et al. 1995), and the current attempt to replace them with only the lean (inshore) form may be self-defeating (Eshenroder et al. 1999). We urge inclusion of deepwater forms of lake trout as part of a stocking strategy aimed at recolonizing both inshore and offshore waters.

We suspect that suppression of exotic planktivores, particularly alewife, by chinook salmon primarily, will play an important role in determining whether lake trout restoration occurs. Alewife is a known predator of lake trout larvae (Krueger et al. 1995). Furthermore, lake trout that feed heavily on alewife suffer from thiamine deficiency, resulting in high mortality of their fry from early mortality syndrome (McDonald et al. 1998). Low abundances of alewife may promote restoration of other species. The evidence is compelling that alewife as well as rainbow smelt suppress the recruitment of important native species: ciscoes, lake trout, burbot, walleye, yellow perch, and deepwater sculpins (reviewed in Eshenroder and Burnham-Curtis 1999). Current and anticipated levels of lake trout stocking alone will not exert the predation pressure necessary to drive alewife and rainbow smelt populations to more tolerable densities. Chinook salmon clearly exert substantial predation pressure on exotic planktivores in Lake Huron as they have in other lakes. Recent reductions in the abundance and survival of alewives and rainbow smelt (J. Schaffer, USGS Great Lakes Science Center, 1451 Green Road, Ann Arbor, MI 48105, USA, personal communication; Dobiesz 2003) are likely a consequence, at least partly, of high predatory demand by piscivores.

Managing for recovery of lake trout as a dominant top predator, as called for in the lake's fish community objectives (DesJardine et al. 1995), is intertwined with the concern that densities of alewife will become too low to support a substantial recreational fishery for salmon. Recent observations of slower growth by chinook salmon combined with evidence they consume a substantial proportion of available alewife (Dobiesz 2003) led managers in 1999 to reduce chinook salmon stocking to avoid a collapse of the salmon fishery as occurred in Lake Michigan during the 1980s. These cuts may have been detrimental to lake trout rehabilitation. We suspect that no balance point exists where exotic planktivores are abundant enough to support a salmon fishery, like that of the 1990s, but not too abundant so as to interfere with a widespread recovery of lake trout populations. This conundrum presents a dilemma to fishery managers. While managers continue to wrestle with this thorny issue, the "stocking lever" may no longer function as in the past. Preliminary results from a marking study to assess wild production of chinook salmon suggest that most salmon in the lake are wild born rather than hatchery reared (J.E. Johnson, unpublished data). This observation may represent a transition in the system that can facilitate recovery of lake trout.

Other forcing functions, besides top-down actions, are less likely, in our opinion, to determine the overall trajectory of the lake's fish community. King et al. (1997) found a detectable warming signal at South Bay, indicating that Lake Huron's fish community is probably already affected by climate change. A reduction in the production of juvenile salmonines in streams in response to warming (Meisner et al. 1987) could play a role in shaping the fish community, if it were to occur prior to reestablishment of large self-sustaining populations of lake trout, which presumably would by themselves suppress alewife populations. Warming may also have strong affects on fish community dynamics in shallow nearshore areas and bays by reducing the growth and survival of cold-water fishes while improving them for warmwater fishes. Although alewife is near the lower end of its winter thermal tolerance in the Great Lakes (O'Gorman et al. 2004), warming may not enhance its productivity. Dieoffs may occur more often in association with cold springs and (or) winters because severe weather events are predicted to increase with changes in global climate. We suspect that Lake Huron, given its large size and extensive deep water, will remain a suitable habitat for cold-water fishes such as lake trout.

We doubt that changes in nutrient or contaminant inputs will greatly influence the future trajectory of the salmonid fish community and predict that, among the Great Lakes, Lake Huron will likely remain closest to Lake Superior in being least impacted by cultural eutrophication. Berst and Spangler (1972) reported that the limnology of the lake had changed little since the 1800s, except for areas near centers of human activity, particularly inner Saginaw Bay. We found that the offshore waters have changed little in terms of enrichment in the three decades since SCOL-1 except for an increase in nitrate plus nitrite and declining contaminant concentrations. Although some areas, primarily in Ontario waters, may see increases in eutrophication resulting from increased cage culture and hog farming, these influences should be localized and nearshore.

Our prognoses regarding the future direction of the Lake Huron fish community are contingent on the basic structure of the system remaining largely as it is now and on the supposition that our understanding of the current system is not fatally flawed. If fishery scientists had made predictions regarding the future of the lake's fish community prior to the invasion of the sea lamprey and alewife, their predictions would have considerably missed the mark. Both dreissenids and exotic predatory cladocerans (*Bythotrephes* and *Cercopagis*) may alter the future food web in ways that have important and unexpected consequences for fish community structure and fishery production. We suspect that a further proliferation of dreissenids will cause additional declines of *Diporeia* populations in Lake Huron. *Diporeia* populations declined in outer Saginaw Bay in association with mussel colonization, and dreissenids are suspected of causing widespread declines of *Diporeia* populations in Lakes Ontario (Mills et al. 2003) and Michigan (Madenjian et al. 2002). In these two lakes, diet shifts and reduced growth occurred in a variety of fishes: rainbow smelt, lake whitefish, young lake trout, and older alewife. We expect similar changes in fish production in Lake Huron, but we are not predicting that such changes will preclude or enhance the recovery of self-sustaining lake trout populations. The lake whitefish fishery, however, appears to be imperiled now by food web changes even though populations remain abundant. Wholesalers are rejecting or discounting the lean, slow-growing fish from the main basin. If the slow growth and poor condition turn out to be a permanent change related to an as yet unconfirmed decline in *Diporeia*, the decrease in useable yield and its value on the market could be ruinous for the fishery. Further, exotic predacious zooplankters may be responsible for a compositional shift of zooplankton, especially cladocerans, impacting larval fish survival (Lehman 1991; Laxson et al. 2003). We are not predicting that dreissenids and exotic predacious cladocerans will cause fish community succession, but the future impacts of these invertebrates are an area of great uncertainty. Likewise, the threat from new exotic species from the Ponto-Caspian region and elsewhere is difficult to overstate (Ricciardi and MacIsaac 2000). All of the progress that has gone into restoring the lake's fisheries and our understanding of the system is jeopardized by inadequate regulation of the shipping industry.

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