PERSPECTIVE / PERSPECTIVE

Fish community change in Lake Superior, 1970–2000[1]

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Abstract: Changes in Lake Superior's fish community are reviewed from 1970 to 2000. Lake trout (*Salvelinus namaycush*) and lake whitefish (*Coregonus clupeaformis*) stocks have increased substantially and may be approaching ancestral states. Lake herring (*Coregonus artedi*) have also recovered, but under sporadic recruitment. Contaminant levels have declined and are in equilibrium with inputs, but toxaphene levels are higher than in all other Great Lakes. Sea lamprey (*Petromyzon marinus*) control, harvest limits, and stocking fostered recoveries of lake trout and allowed establishment of small nonnative salmonine populations. Natural reproduction supports most salmonine populations, therefore further stocking is not required. Nonnative salmonines will likely remain minor components of the fish community. Forage biomass has shifted from exotic rainbow smelt (*Osmerus mordax*) to native species, and high predation may prevent their recovery. Introductions of exotics have increased and threaten the recovering fish community. Agencies have little influence on the abundance of forage fish or the major predator, siscowet lake trout, and must now focus on habitat protection and enhancement in nearshore areas and prevent additional species introductions to further restoration. Persistence of Lake Superior's native deepwater species is in contrast to other Great Lakes where restoration will be difficult in the absence of these ecologically important fishes.

Résumé : On trouvera ici une revue des changements survenus dans la communauté des poissons du lac Supérieur de 1970 à 2000. Les stocks de touladis (*Salvelinus namaycush*) et de grands corégones (*Coregonus clupeaformis*) se sont considérablement accrus et sont peut-être en train d'atteindre leurs densités d'antan. Les stocks de ciscos de lac (*Coregonus artedi*) ont aussi récupéré, mais le recrutement est sporadique. Les concentrations de contaminants ont diminué et sont maintenant en équilibre avec les influx; les concentrations de toxaphène sont, cependant, plus élevées que dans les autres Grands Lacs. Le contrôle de la grande lamproie marine (*Petromyzon marinus*), l'établissement de limites de récolte et l'empoissonnement ont favorisé la récupération des stocks de touladis et permis l'établissement de petites populations de salmoninés non indigènes. Comme la reproduction naturelle assure le maintien de la plupart des populations de salmoninés, il n'est plus nécessaire de procéder à des empoissonnements additionnels. Les salmoninés non indigènes demeureront vraisemblablement une composante mineure de la communauté de poissons. Les biomasses des poissons fourrage ne sont plus dominées par l'éperlan arc-en-ciel (*Osmerus mordax*), une espèce introduite, mais plutôt par des espèces indigènes et il est possible que la forte prédation empêche leur récupération. L'introduction d'espèces non indigènes s'est accrue et menace la récupération de la communauté de poissons. Les agences de gestion ont peu d'influence sur l'abondance des poissons fourrage ou sur le prédateur principal, le touladi siscowet; afin de promouvoir

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la récupération, les agences doivent se concentrer sur la protection des habitats et l'amélioration des zones littorales et elles doivent prévenir l'introduction de nouvelles espèces non indigènes. Le maintien des poissons indigènes d'eau profonde distingue le lac Supérieur des autres Grands Lacs dans lesquels la récupération sera difficile en l'absence de ces poissons de grande importance écologique.

[Traduit par la Rédaction]

Introduction

The objective of the first International Symposium on Salmonid Communities in Oligotrophic Lakes (SCOL-1) in 1971 was to assess the effects of cultural eutrophication, exploitation, and species introductions on the native fish communities of the Laurentian Great Lakes and other large lakes from European settlement to the late 1960s. The Lake Superior account (Lawrie and Rahrer 1972) detailed the physical description of the basin, lake, and land use, the invasion of sea lamprey (*Petromyzon marinus*), the expansion and decline of commercial fisheries, and their combined effects on native fish communities. Early degradation was attributed to depreciation of fluvial, estuarine, and shallow water environments, which affected local stocks of selected species (i.e., lake sturgeon (*Acipenser fulvescens*), brook trout (*Salvelinus fontinalis*)), but habitat degradation did not account for any lakewide declines in nearshore or offshore fish populations. Overfishing and sea lamprey predation were clearly the major causes of the decline of commercially important fishes (lake trout (*Salvelinus namaycush*), lake herring (*Coregonus artedi*)). Failure of fisheries managers to control exploitation and recognize the stock structure of these species led to the sequential exploitation of discrete stocks. Sea lamprey predation and its indirect effects would likely have completed the demise of lake trout and other species if not for the timely arrival of chemical control in the late 1950s (Smith and Tibbles 1980), which allowed for the possibility of restoration and recovery of the fish community.

Before 1970, knowledge of the biological and ecological processes of Lake Superior was limited. Physical and chemical limnology of Lake Superior was detailed in comparison to the limited study of primary and secondary production. Status of fish populations was measured mostly from analysis of commercial fishery catch and effort statistics, as no independent stock assessments, other than for lake trout, were in place. Biological study was limited to life history descriptions of commercial species and the performance of hatchery-reared lake trout for the newly implemented restoration program. Exotic fishes, other than sea lamprey, were limited to alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*), and newly introduced Pacific salmon (*Onchorynchus* sp.), the former two implicated in the demise of native coregonines (Smith 1970) and the latter, intentionally introduced to create additional fishing opportunities. Sea lamprey control was limited to electrical weirs and chemical control. Contamination of sediments and bioaccumulation of toxic chemicals were of little concern or were unknown. The emphasis was clearly on the most obvious stressors, commercial fishing and sea lamprey predation, with minimal consideration of potential threats of less conspicuous factors.

The second International Symposium on Salmonid Communities in Oligotrophic Lakes (SCOL-2) concentrated on biological and anthropomorphic stressors that have resulted in changes to the Great Lakes since 1970. Fish community changes in Lake Superior since 1970 have been substantive and include the continued establishment of nonnative species along with the recovery of native species. Here we document the changes to Lake Superior's aquatic community from 1970 to 2000 in the face of the following potential stressors: habitat degradation, contaminants, changes in phosphorus loading, potential impacts from global warming, impacts of sea lamprey and other unintentional exotic species, impacts of intentional introductions of Pacific salmon and other nonnative salmonines, and fishery exploitation. We compare the expected outcome of the stressors to the observed changes to the fish community and offer expectations for the future of Lake Superior's fish community.

Habitat degradation

As was the case before 1970, the majority of habitat degradation in Lake Superior is limited to shoreline areas, embayments, and tributaries. These shallow-water habitats are most readily impacted by sediment and nutrient inputs from physical alterations of the watershed accompanying urban development, farming, mining, and logging. This results in sedimentation and loss of spawning habitat and local eutrophication, especially in areas draining surficial clay deposits, which predominate in western Lake Superior (Robertson 1997). Less than 5% of Lake Superior's shoreline is developed, but urban and recreational expansion will likely increase in future years. Fish species with early life histories in nearshore (<80 m; only 24% of lake surface area) and offshore (>80 m) waters do not appear to be limited by habitat loss. These include lean and siscowet lake trout (*Salvelinus namaycush*), lake herring, lake whitefish (*Coregonus clupeaformis*), deepwater ciscoes (*Coregonus* spp.), and round whitefish (*Prosopium cylindraceum*). In contrast, inshore species that have been impacted by habitat loss include brook and brown trout (*Salmo trutta*), walleye (*Stizostedion vitreum vitreum*), lake sturgeon, yellow perch (*Perca flavescens*), northern pike (*Esox lucius*), and smallmouth bass (*Micropterus dolomieui*), as well as other species that have not been monitored.

Physical and chemical degradation of spawning habitat was hypothesized to limit lake trout restoration in the Great Lakes, but there is little evidence of any significant biological impact to offshore areas in Lake Superior (Edsall and Kennedy 1995). All native species in Lake Superior proper have persisted and are reproducing, and in some cases, populations are expanding (i.e., lean and siscowet lake trout); hence, there is little evidence for habitat limitation and (or) degradation in nearshore and offshore areas. Future habitat restoration will involve attempts to reduce erosion to curb stream and embayment sedimentation and physical improvements to streams to increase spawning habitat and cover.

Contaminants

Because of its remote location, limited industrial activity, and the large lake surface area to watershed ratio, Lake Superior receives the majority of its chemical loading via atmospheric deposition, which is the dominant source of polychlorinated biphenyls, polychlorinated dibenzodioxins, polychlorinated dibenzofurans, toxaphene, and mercury (Eisenreich and Strachan 1992). It was thought that body burdens and background contamination would persist at high levels for many years given the chemical stability of many of the pollutants. The resulting impairment to the aquatic ecosystem would include reproductive failure of fish and birds and high mortality of young fishes and adults. Over the last 30 years, concentrations of nearly all measured contaminants in fish and the water column, with the exception of toxaphene, have declined in Lake Superior and remain at low levels. Where habitat is not limiting, natural reproduction appears to be evident in all native and nonnative fishes lakewide, which may suggest that biological impacts are minimal, although undetected effects may still be present.

Since the early 1980s, toxaphene concentrations have dramatically declined in lake trout across all Great Lakes except Lake Superior (Glassmeyer et al. 2000). Unlike other hydrophobic organic contaminants, atmospheric input of toxaphene is dominated by gas exchange across the air–water interface, therefore lower water temperature, larger surface area, and water volume may have led to higher historical concentrations in Lake Superior than in the other Great Lakes. The low primary productivity in Lake Superior results in very low sedimentation rates, which reduces toxaphene transport to sediments, while lower water temperatures reduce toxaphene loss through volatilization (Swackhamer et al. 1999). High concentrations of toxaphene and polychlorinated biphenyls and mercury in large lake trout are the primary reason for fish consumption advisories in Lake Superior and are of concern and will likely persist for some time.

Effect of climate warming

A growing amount of scientific evidence suggests that global warming is occurring and will result in significant changes in some ecosystems. Global climate models have been used to quantify effects of climate warming on annual temperature and precipitation in the Great Lakes region under twice the current CO_2 loadings. Summer and winter air temperatures in the Great Lakes increased during the 1900s (Magnuson et al. 1997), but significant change to the Lake Superior fish community has not yet been attributed to this warming. It is predicted that summer precipitation would be reduced by about 5% in western Lake Superior and winter precipitation would increase by up to 20% (especially in western Lake Superior). Summer temperatures would increase by 5 °C, and winter temperatures by 7 °C (Magnuson et al. 1997). An extrapolation of mean annual air temperature projections to water temperatures for Thunder Bay, Lake Superior (Hill and Magnuson 1990), indicated an increase in epilimnion and neritic waters of 1.8 °C to 5.7 °C during July–September. The 5 °C December isotherm would encompass most of Lake Superior by 2030 (Johnson and Evans 1990). These changes from climate warming would result in decreased ice cover (Hengeveld 1990), reduced lake levels (0.23–0.47 m) and outflow volumes (–8%) (Magnuson et al. 1997), and an increase in thermal habitat volume (Christie and Regier 1988). Lotic thermal habitat would also be affected. Stream temperatures in Minnesota are projected to increase 2.4 °C to 4.7 °C (Magnuson et al. 1997) and beyond the 15.5 °C for many cool-water streams. The downstream cooling effect of cold water from Minnesota streams could be shortened by 25–50% (Sinokrot et al. 1995), and the cooling ability of groundwater is expected to decrease (Meisner et al. 1987).

Climate warming would increase thermal habitat volume for lake trout, lake whitefish, coho salmon (*Onchorynchus kisutch*), yellow perch, smallmouth bass, walleye, and northern pike (Hill and Magnuson 1990; Shuter and Post 1990; Magnuson et al. 1997). In Lake Superior, smallmouth bass and yellow perch are currently restricted to warmer bays, and yellow perch are at the margins of their preferred thermal habitat (Hokansen 1977; Bronte et al. 1993); therefore, the distribution of these species should expand in Lake Superior (Shuter and Post 1990).

Nonindigenous species would benefit from climate warming (Magnuson et al. 1990). White perch (*Morone americana*; Johnson and Evans 1990) and alewife (Henderson and Brown 1985; Bronte et al. 1991) are rare in Lake Superior because of the duration of low water temperatures. White perch distribution should expand with the 5 °C December isotherm, which is correlated with white perch distribution (Johnson and Evans 1990). Alewife populations may expand beyond trace levels if water temperatures increase to allow successful egg incubation and osmoregulation (see Bronte et al. 1991). Increased temperatures of many cold-water streams would support additional sea lamprey populations (Christie and Kolenofsky 1980). Rainbow smelt would experience increased recruitment through earlier hatching promoted by warmer spring water temperatures (Nyberg et al. 2001), hence their populations may increase. Most potential invaders that are now thermally restricted to the lower Great Lakes would quickly colonize the upper Lakes under climate warming (Mandrak 1989).

A reduction in precipitation and an increase in temperature for western Lake Superior would affect fish populations, particularly those inhabiting streams, wetlands, and estuaries. The projected increase in stream temperatures would favor rainbow trout (*Oncorhynchus mykiss*) and Pacific salmon over brook trout (Fausch and White 1986; Rose 1986). In the embayments, lower lake levels could result in an increase in aquatic vegetation and thermal habitat for warm- and cool-water species, favoring centrarchids and percids. Habitat for smallmouth bass and yellow perch, which is currently marginal in Lake Superior (Hokansen 1977; Magnuson et al. 1990; Shuter and Post 1990), would increase.

Although the rate of primary production is not expected to increase, species composition would change, annual production would increase, and diversity and biomass might also increase (Magnuson et al. 1997). Primary production could increase by 1.6 to 2.7 times, zooplankton 1.4 to 2.1 times, and fish yield 1.4 to 2.1 times (Regier et al. 1990). Blue-green algae would be favored in warmer epilimnion water over chrysophytes and diatoms; these climate-altered communities will have different trophic efficiencies and potentially large ecosystem effects (Magnuson et al. 1997). Because most benthic production in Lake Superior occurs in the profundal zone, an increase in benthic invertebrate production would be minor.

Changes in phosphorus loading

Cultural eutrophication, primarily from increased phosphorus inputs, has caused changes in water quality and plankton and fish communities in the Great Lakes (Beeton 1965). Phosphorus is the major nutrient that limits phytoplankton growth and, hence, primary production. Lake Superior was the only Great Lake that historically did not experience measurable increases in phosphorus. Lakewide spring concentrations of total phosphorus are consistently below the International Joint Commissions' recommended maximum of 5 $mg \cdot L^{-1}$ with no temporal trend over the last 30 years. Elevated total phosphorus concentrations still occur in the western arm of the lake and in localized areas close to shore, particularly adjacent to tributaries transporting most of the phosphorus to U.S. waters of Lake Superior (Robertson 1997). Given the apparent long-term stability of phosphorus in Lake Superior and the decline of phosphorus in the other Great Lakes (Madenjian et al. 2002), we predict that the future potential for cultural eutrophication via phosphorus loading is minimal.

Intentional species introductions

Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon, rainbow trout (steelhead), Atlantic salmon (*Salmo salar*), and brown trout all have been intentionally introduced into Lake Superior by state and provincial management agencies to diversify and enhance sportfishing. Small populations developed and provided seasonal nearshore fisheries. Natural reproduction has been documented for all species, except Atlantic salmon, and wild fish represent the majority of recruitment (Peck et al. 1999).

Water temperature and life history characteristics are probably the major limiting factors for nonnative salmonine production in Lake Superior. Native predators (lean lake trout, siscowet lake trout, burbot (*Lota lota*)) are physiologically tolerant of extended periods of low water temperatures, consume large prey while expending minimal energy for predation and metabolism, grow slowly, are long-lived, and can reproduce many times throughout their lives. Most nonnative salmonines lack these life history characteristics (Kitchell et al. 2000), which puts them at a disadvantage in Lake Superior. Because of metabolic thermal requirements (Coutant 1977), most nonnative salmonines are generally restricted to the nearshore zone of Lake Superior, less than 80 m, or the top 20 m of the water column during much of the year (Wismer and Christie 1987). Only during July–October are water temperatures adequate for growth of Pacific salmon and brown trout. Rarely does any significant portion of Lake Superior reach temperatures for optimal growth for these species, therefore streams and bays are the only available warm-water refugia. Year-class strength and survival of stocked nonnative fish are highly dependent on these dynamics; hence stocking programs are of limited value. Wild stocks tend to fluctuate based on climatic conditions and appear to utilize the optimal thermal refuge when it becomes available. Though some areas may benefit from continued stocking, most agencies have realized that supplemental stocking of nonnative salmonines in Lake Superior is not cost effective and are re-examining their programs (Peck 1992).

Concern over competition between recovering lake trout and introduced salmonines arose in the early 1980s when growth of lake trout appeared to be declining (Busiahn 1985). During the 1980s, diet similarity was highest between lean lake trout and chinook salmon and lower between lake trout and coho salmon (Conner et al. 1993; Table 1). However, stable isotope analysis suggested that Pacific salmon occupy a lower trophic level than native predators (Harvey and Kitchell 2000); therefore, direct interactions are less likely. Bioenergetics modeling has been applied to determine if forage availability limits lake trout restoration in the presence of nonnative salmonines. Estimated prey consumption by lean lake trout and introduced salmonines in Minnesota waters exceeded prey standing stock and production (Negus 1995). Model simulations were limited by the assumption that predation and growth occurred in Minnesota waters only, which is unlikely given the lakewide movements of chinook salmon (Peck et al. 1999) and likely that of other predators. Ebener (1995) obtained similar results on a larger spatial scale and with the inclusion of siscowet lake trout in the simulations. Most of the predatory inertia was from the large standing stock of siscowet lake trout, which consumed more prey fish than all other predators combined (Fig 1). Because recruitment and natural mortality (as opposed to sea lamprey predation and fishing) control siscowet biomass, which accounts for most of the forage consumption, it is unlikely that the absence of nonnative salmonines would improve lean lake trout growth and survival significantly. Simulations at smaller spatial scales are needed to confirm this. Lean and siscowet lake trout life histories typified by slow growth, low natural mortality, and more diverse diet (Table 1) and habitat utilization make these species more resilient to changes in forage abundance and species composition (Kitchell et al. 2000), as previously suggested for Lake Michigan lake trout (Stewart and Ibarra 1991). The disparity between modeled consumption and available forage is likely due to errors in estimating predator and forage biomass. The general results of these simulations agree well with the perceptions of Lake Superior biologists: that introduced salmonines pose little risk to lake trout recovery, which has advanced lakewide (Hansen 1999; Wilberg et al. 2003).

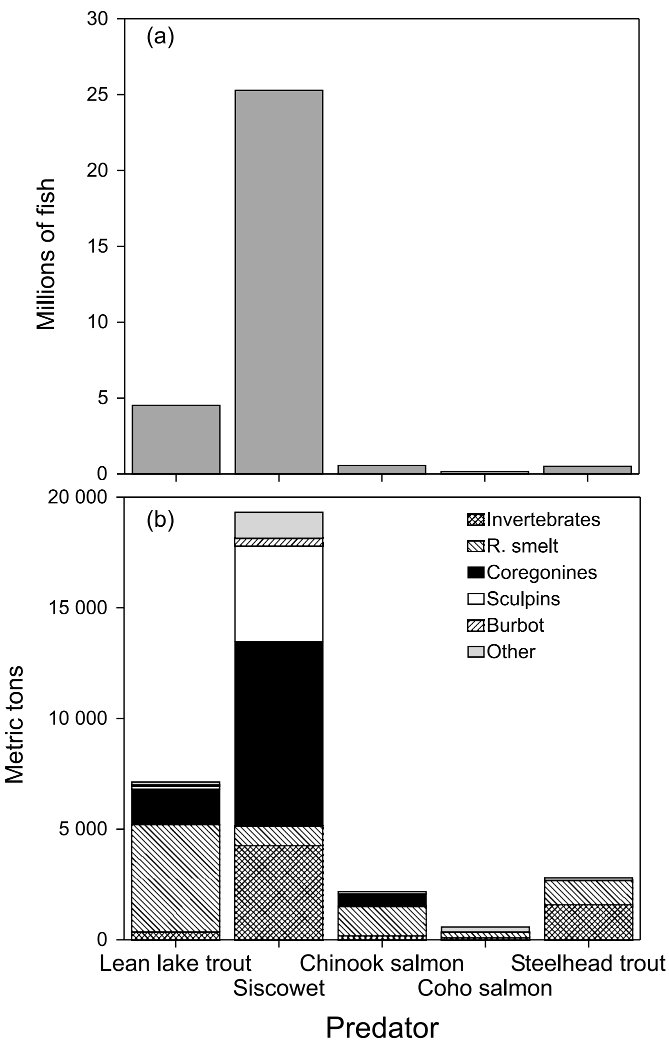
Unintentional species introductions

At least 39 new nonindigenous aquatic species have entered Lake Superior since 1970 (Table 2). Of these, nine (22%) are fish, seven (17%) are aquatic invertebrates, eight (19%) are fish diseases and parasites, and 17 (41%) are wetland, submerged, or emergent aquatic plants or shoreline woody plants. Additional species likely have been intro-

Table 1. Proportional diet similarity and Shannon–Wiener (H) diet diversity among principal predators in Lake Superior, based on diet data from multiple sources and summarized in Kitchell et al. (2000).

Predator	Lake trout	Siscowet	Burbot	Chinook salmon	Coho salmon	Rainbow trout
Lake trout	1.00	0.36	0.59	0.69	0.49	0.36
Siscowet		1.00	0.53	0.29	0.24	0.17
Burbot			1.00	0.50	0.49	0.44
Chinook salmon				1.00	0.65	0.36
Coho salmon					1.00	0.66
Rainbow trout						1.00
Diet diversity	1.35	1.62	1.61	1.18	1.14	0.62

Fig. 1. (*a*) Estimated standing stocks of major salmonine predators in western Lake Superior and (*b*) estimated consumption of major prey items (from Ebener 1995).



duced but failed to become conspicuous or established. Over 66% of all documented introductions have occurred since 1970, which represents an average introduction rate of 1.4 per year. Compared with other Great Lakes, Lake Superior has the least number of nonindigenous species (Mills et al. 1993).

Since 1970, transport mechanisms for most introduced species were human-mediated (Table 2). Major pathways are via ballast water (24% of introductions), cultivation of wetland and terrestrial plants (24%), release of parasites or pathogens carried by hatchery-reared fish (19%), railroads and highways, canals, and stocked fish (all at 2%), and a combination of mechanisms (multiple mechanisms, 15%). This latter category includes release by angler's bait buckets, release from aquaria, and overland transport by recreational boaters. For 10% of the nonindigenous species, methods of introduction are unknown.

The accelerated rate of unintentional introductions of nonindigenous species into Lake Superior has caused concern. Although no native aquatic species have been extirpated, the establishment of each new species has the potential to disrupt the food web and ecosystem function. Primary effects result from negative interactions with native species and secondary effects from interactions with other nonindigenous species; however, the scope and magnitude of these interactions are not well understood and such impacts to a large degree remain threats. Since 1970, many species arriving have remained localized in embayments and tributaries and are not widely distributed. Given that Lake Superior is the least species rich of all the Great Lakes, it may be the most prone to ecological and economic damage from species introductions. Interrupting the transport mechanisms is critical to preventing new infestations. The accelerated rate of new infestations combined with the increased potential of invasion from global warming is a wake-up call that the natural biodiversity of Lake Superior needs greater protection.

Sea lamprey

Sea lamprey continue to be the most detrimental exotic species in Lake Superior. Sea lamprey kill more lake trout than are harvested (Technical Fisheries Committee, Modeling Sub-Committee, unpublished data). Recent stable isotope analysis revealed that sea lamprey might have the greatest impact on nearshore coregonines (i.e., lake whitefish, lake herring) (Harvey 2001), which may be more available spatially and numerically, and continued control is required.

Lake trout that die from a sea lamprey attack have not been directly observed in Lake Superior, as in Lake Ontario (Bergstedt and Schneider 1988); therefore, attack mortality has been inferred from marking rates. Sea lamprey wounding (type-A, stages 1–3 marks; King 1980) of lean lake trout in U.S. waters of Lake Superior was stable throughout the 1970s, rose in the late 1980s and early 1990s, and has generally declined or remained stable since then (Fig. 2). Sea lamprey wounding averaged 1.2 marks·100 fish^{-1} for 432- to

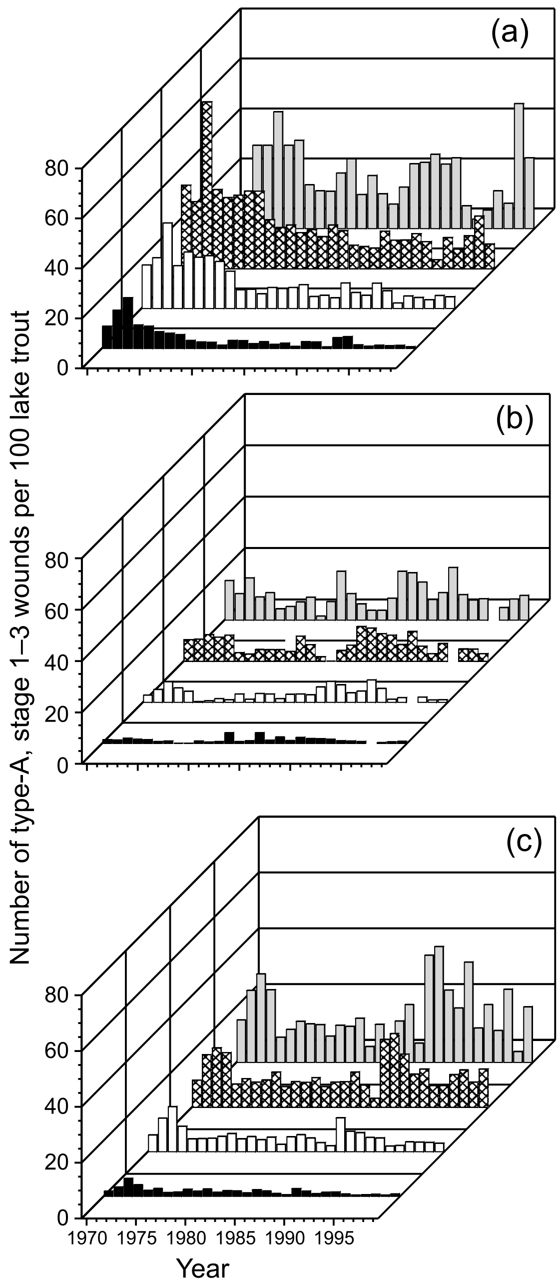
Table 2. Nonindigenous species introductions, year and earliest locations detected, and method of transport or release into Lake Superior since 1970.

Common name	Scientific name	Earliest record	Earliest location	Transport or release mechanism(s)
American eel	*Anguilla rostrata*	1970	Brule River, WI	Canals
Atlantic salmon	*Salmo salar*	1972	Lake Superior, WI	Stocked fish
Eurasian ruffe	*Gymnocephalus cernuus*	1986	St. Louis River, MN	Ballast water
European flounder	*Platichthys flesus*	1981	Keweenaw Peninsula, MI	Ballast water
Fourspine stickleback	*Apeltes quadracus*	1986	Thunder Bay, ON	Ballast water or live bait
Goldfish	*Carassius auratus*	1975	St. Louis River, MN	live bait or from aquaria
Round goby	*Neogobius melanostomus*	1995	St. Louis River, MN	Ballast water
Threespine Stickleback	*Gasterosteus aculeatus*	1987	Thunder Bay, ON	Ballast water or canals
White perch	*Morone americana*	1986	St. Louis River, MN	Ballast water
Aquatic oligochaete	*Ripistes parasita*	1987	Not Available	Ballast water
Asiatic clam	*Corbicula fluminea*	1999	St. Louis River, MN	Ballast water
Bosmonid waterflea	*Eubosmina coregoni*	1970s	Unknown	Ballast water
Calanoid copepod	*Eurytemora affinis*	1960s	Unknown	Ballast water
Rusty crayfish	*Orconectes rusticus*	1985	Thunder Bay, ON	Ballast water, live bait, or from aquaria
Spiny waterflea	*Bythotrephes cederstroemi*	1987	E. Lake Superior, ON	Ballast water
Zebra mussel	*Dreissena polymorpha*	1989	St. Louis River, MN	Ballast water
Bacterial kidney disease	*Corynebacterium* ssp.	pre-1975	Unknown	Fish parasite or pathogen fish
Furunculosis	*Aeromonas salmonicida*	Unknown	Unknown	Fish parasite or pathogen fish
Whirling disease	*Myxobolus cerebralis*	Unknown	Unknown	Fish parasite or pathogen fish
Round goby parasite	*Sphaeromyxa sevastopoli*	1995	St. Louis River, MN	Fish parasite or pathogen fish
Round goby disease	*Ichthyocotylurus pileatus*	1995	St. Louis River, MN	Fish parasite or pathogen fish
Ruffe parasite	*Tryponasoma acerinae*	1986	St. Louis River, MN	Fish parasite or pathogen fish
Ruffe parasite	*Dactylogirus amphibothrium*	1986	St. Louis River, MN	Fish parasite or pathogen fish
Ruffe parasite	*Dactylogirus hemiamphibothrium*	1986	St. Louis River, MN	Fish parasite or pathogen fish
Birdsfoot trefoil	*Lotus corniculatus*	1975	Kadunce River, MN	Cultivation
Common mullein	*Verbascum thapsus*		Unknown	Unknown
Creeping yellow cress	*Rorippa sylvestris*	<1985	E. Lake Superior, MI	Unknown
Curlyleaf pondweed	*Potamogeton crispus*	1988, 1996	Knife River Marina, MN; Washburn Harbor, WI	With fish or recreational boats
Eurasian watermilfoil	*Myriophyllum spicatum*	1996	Chequamegon Bay, WI	Aquaria or recreational boats
Flowering rush	*Butomus umbellatus*	Unknown	Unknown	Cultivation
Glossy buckthorn	*Rhamnus frangula*	<1985	E. Lake Superior, MI	Cultivation
Indian balsam	*Impatiens glandulifera*	1984	Grand Marais, MN	Cultivation
		1998	Lake Superior, ON	
Hairy willow herb	*Epilobium hirstutum*	<1998	Knife River mouth, Knife River, MN	Cultivation
	Epilobium parviflorum	<1998		Cultivation
Hawkweed	*Hieracium scabriscullum*	<1996	Sugar Loaf, MN	Cultivation
	Hieracium scabrum			Cultivation
King-devil	*Hieracium piloselloides*	<1996	Sugar Loaf, MN	Cultivation
Lady's thumb	*Polygonum caespitosum*	<1985	E. Lake Superior, MI	Unknown
Lupine	*Lupinus polyphyllus*	1982	Beaver Bay, MN	Cultivation
Oak-leaved goosefoot	*Chenopodium glaucum*	<1985	E. Lake Superior, MI	Railroads and highways
Spotted knapweed	*Centaurea maculosa* (*biebersteinii*)	<1996	Sugar Loaf, MN	Unknown

532-mm fish, 5.0 marks·100 fish^{-1} for 533- to 634-mm fish, 11.3 marks·100 fish^{-1} for 635- to 736-mm fish, and 17.9 marks·100 fish^{-1} for >736 mm fish.

The sea lamprey control program has been effective at reducing mortality on smaller lean lake trout, but not on adult fish. In U.S. jurisdictions, sea lamprey marking on 432- to

Fig. 2. Spring (May–June) sea lamprey (*Petromyzon marinus*) wounding (number of type-A, stages 1–3 wounds·100 fish^{-1}) for lean lake trout (*Salvelinus namaycush*) in (*a*) Minnesota, (*b*) Wisconsin, and (*c*) Michigan waters of Lake Superior by size class and year, 1970–1999. Length classes: solid bars, 432–532 mm; open bars, 533–634 mm; cross-hatched bars, 635–736 mm; shaded bars, >736 mm.



532-mm lake trout has declined to nearly zero and marking on 533- to 634-mm fish was lower during the 1990s in U.S. jurisdictions than in any other time since 1959 (Fig. 2). Unfortunately, the proportion of lake trout >634 mm with sea lamprey marks has not declined in any jurisdiction since the mid- to late 1970s. Sea lamprey marking rates on all sizes of lean lake trout were greater during 1959–1979 than after 1979, but roughly 15% of lean lake trout >634 mm still exhibited fresh wounds (type-A, stages 1–3 marks) in 1999. These trends indicate that large, adult lean lake trout may be buffering smaller fish from sea lamprey attacks, as sea lamprey prefer larger hosts (Swink 1991; Schneider et al. 1996).

The scope of the sea lamprey control program on Lake Superior has expanded to include both control and assessment activities (Heinrich et al. 2003) as initial chemical treatments dramatically reduced abundance of sea lamprey in the early 1960s (Smith and Tibbles 1980). The concept of integrated pest management has been applied to sea lamprey control to develop and use alternative techniques, which would result in a 50% reduction in lampricide used before 1990 (Great Lakes Fishery Commission (GLFC) 1992). Besides lampricides, sea lamprey control now involves releasing sterilized male sea lampreys into tributaries, placing barrier dams on tributaries, trapping and removing adult sea lampreys in tributaries (Heinrich et al. 2003), and conducting research to develop new control strategies. Stock assessments include mark–recapture studies on adult and metamorphosed sea lampreys to determine their relative abundance and to evaluate the effectiveness of control options.

Control has gradually suppressed sea lamprey adult abundance in Lake Superior from 800 000 in 1960 to less than 200 000 in 1999 (Heinrich et al. 2003). This contemporary population is greater than expectations previously established in fish community objectives for Lake Superior (Busiahn 1990). Those objectives called for a 50% reduction in parasitic sea lamprey abundance by 2000 and a 90% reduction by 2010. New objectives require that suppression continue until annual sea lamprey induced mortality is below 5% but with the realization that this will require new control methods to be implemented (Horns et al. 2003).

Further reductions in sea lamprey in Lake Superior will require increased frequency of chemical treatments, stream selection based on cost–benefit–risk analysis, and construction of low head barrier dams on streams with good habitat (Heinrich et al. 2003). Additional control options must be developed, such as use of pheromone attractants to increase trapping efficiency or disrupt spawning (see Bjerselius et al. 2000; Li et al. 2002), to further reduce sea lamprey populations.

Ruffe

The unintentional introduction of ruffe (*Gymnocephalus cernuus*) into the St. Louis River estuary has drawn considerable attention to the threat of exotic species in Lake Superior and elsewhere. These fish originated from the Elbe River drainage in northwestern Europe (C. Stepien, Cleveland State University, Cleveland, OH 44115, personal communication) and were likely transported in the ballast water of transoceanic cargo ships. Ruffe were first collected in the St. Louis River estuary in the mid-1980s but likely entered earlier and remained undetected (Bronte et al. 1998). By 1992, ruffe became the most abundant fish in the lower St. Louis River, based on bottom trawl stock assessments. An effort to control ruffe through increased predation failed (Mayo et al. 1998), and the population grew to about 6 million by 1996. Concurrent decreases in resident native fishes raised concerns over the ruffes' impact on the fish community; however, many of these declines were not correlated with increasing ruffe abundance, and natural population dynamics could have explained some of these changes (Bronte et al. 1998). Even though ruffe have dominated the fish community numerically for many years, no species losses have occurred. Brazner et al. (1998) contends that ruffe have not been as successful in colonizing some shallow, well-vegetated areas of the Duluth–Superior harbor and that protection of nearshore vegetated habitat from degradation may help confine range expansions. Ruffe have also become abundant in several south-shore streams in Wisconsin (Czypinski et al. 2001). Although lampricides antimycin and rotenone are effective in killing ruffe (Dawson et al. 1998), field applications that target ruffe concentrations are logistically difficult and unlikely to succeed (Horns et al. 2000). Other control measures (i.e., mechanical removal) are not practical, and therefore ruffe populations will likely continue to grow and spread along the coastlines and invade other Lake Superior tributaries.

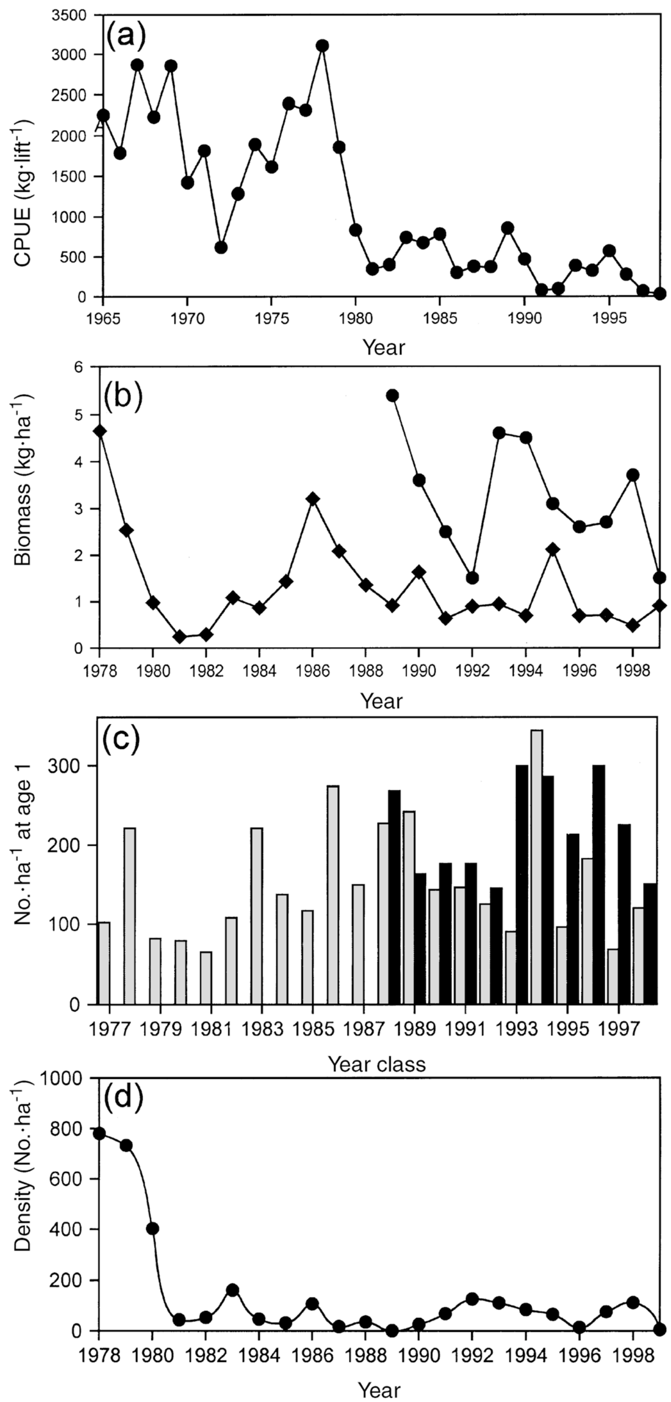
Changes in forage fishes

Rainbow smelt

Since the mid-1950s, rainbow smelt have played a major role as forage for salmonine predators in Lake Superior (Conner et al. 1993). Lakewide survey data are nonexistent before 1978, but catch-per-unit-effort data from the Minnesota commercial trap-net fishery indicate that rainbow smelt biomass averaged three times higher during 1965–1977 than during 1978–1999 (Fig. 3*a*). Peak abundance appeared to occur in 1978 followed by a steep decline into the early 1980s. This mirrors the trend observed in lakewide bottom trawl surveys (see Bronte et al. (1993) and Bronte and Hoff (1996) for survey details) in which rainbow smelt biomass significantly declined (F = 4.63, df = 21,1092, P < 0.0001) in U.S. waters by more than 90% (Fig. 2*b*). In 1982–1986, biomass recovered somewhat but declined gradually afterward. Biomass was significantly (F = 28.06, df = 1,10, P < 0.0001) higher in Canadian waters than in U.S. waters in 1989–1999, but changes in biomass have not been significant (F = 0.97, df = 10,357, P = 0.47) since 1989 (Fig. 3*b*).

Trends in rainbow smelt biomass in Lake Superior were driven by recruitment patterns and changes in total mortality. In U.S. waters, recruitment was low in 1977, 1979, 1980, and 1981 (Fig. 3*c*) and likely accounted for much of the lakewide decline in biomass during the early 1980s. The strong 1983, 1986, and 1994 year classes increased biomass of age-1 and age-2 fish and did not sustain any increase thereafter. This suggests that mortality, presumably from predation, was intense enough to preclude any recovery even with good recruitment. Fishery exploitation was not a factor as harvest has averaged less than 350 000 kg (<0.02 kg·ha^{-1}) annually in U.S. waters during the same years. Recruitment was generally higher and more stable in Canadian waters, especially for the 1993–1997 year classes, which supported higher biomass. Densities of large rainbow smelt >200 mm total length (ages 4+) declined in U.S. waters during the early 1980s (Fig. 3*d*) concurrent with biomass declines, which suggests an increase in mortality. Larger rainbow smelt (>120 mm total length), which are consumed by salmonines (Conner et al. 1993), are now scarce; hence, we concluded that predation from lean and siscowet lake trout is responsible for the high mortality and sustained low biomass. We anticipate no significant broadening of the size structure or increase in biomass future years if predation remains high.

Fig. 3. (*a*) Catch-per-unit-effort (CPUE) of rainbow smelt (*Osmerus mordax*) in commercial trap-net fishery in Minnesota waters in spring 1965–1998, (*b*) 1978–1999 biomass estimates of rainbow smelt in U.S. (■) and Canadian (●) waters, (*c*) estimated strength of the 1977–1998 year classes of rainbow smelt in U.S. (shaded bars) and Canadian waters (solid bars), and (*d*) density of rainbow smelt >200 mm total length in U.S. waters of Lake Superior, 1978–1999.



The scatter plot of recruitment versus parental stock size as measured from lakewide trawl surveys (Fig. 4*a*) appears to be linear (survival is density independent), with most observations close to the origin as would be expected at lower parental stock sizes, and supports our contention for reduced rainbow smelt biomass. A lack of contrast in parental stock sizes precludes any conclusions on recruitment regulation; however, any increases in parental stock size from reduced predation could cause a potential rebound of rainbow smelt stocks.

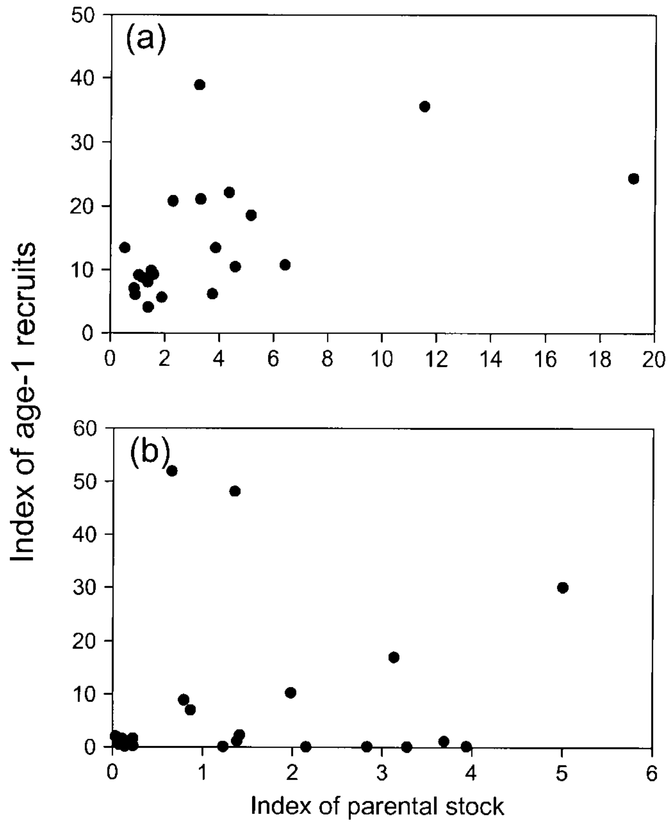
Lake herring

Before the population collapse in the 1960s, lake herring were the major component of the forage base and contributed to most of the commercial production in Lake Superior (Dryer and Beil 1964). Lake herring collapses were first attributed to interspecific competition with bloater (*Coregonus hoyi*) and introduced rainbow smelt and predation by rainbow smelt on lake herring larvae (Anderson and Smith 1971); however, more recent findings challenge these hypotheses. Selgeby et al. (1994) suggested that there was no competition for food between lake herring and rainbow smelt by virtue of spatial and temporal separation of the larvae of each species. Although predation by rainbow smelt on lake herring larvae has been documented in Black Bay, Ontario (Selgeby et al. 1978), lake herring stocks there appeared to be able to support high historical harvests (MacCallum and Selgeby 1987) up until 1990 and under higher densities of rainbow smelt than in U.S. waters (see preceding section); therefore, the effect of rainbow smelt on lake herring recruitment is unclear. Furthermore, if rainbow smelt were depressing lake herring abundance, the reductions in rainbow smelt density during 1978–1981 may have released lake herring from any predation–competition bottleneck. Rainbow smelt biomass has remained low since the late 1980s, yet lake herring recruitment failure has occurred since then, suggesting little interaction between these two species. Analysis of the lake herring fishery in Wisconsin waters strongly suggested that sequential overfishing of discrete stocks caused the collapse there (Selgeby 1982), and this likely occurred elsewhere. Recognition of this stock structure, which is apparent lakewide (Bronte et al. 1996), might have prevented collapse of the lake herring populations (Selgeby 1982).

Lake herring recruitment during the last 22 years has been sporadic. Measured as the density of age-1 fish in lakewide trawl surveys, recruitment has varied significantly from 1978 to 1999 (Fig. 5*a*), with only five significant year classes produced. Large multi-aged parental stocks have been present since the late 1980s but have produced few large year classes. Some of the weakest year classes were produced under the highest stock sizes (as measured in lakewide bottom trawl surveys) (Fig. 4*b*), which may suggest some density-dependent compensation; however, spatial correlation across U.S. and Canadian waters (Fig. 5*a*) and the contrast among levels of recruitment at any stock size also suggests that some lakewide, density-independent factor(s) (i.e., weather, water temperature) may also be important.

Inconsistent recruitment has regulated lake herring biomass over the past 22 years. Total biomass was low in U.S. waters during 1978–1984 but increased significantly (F = 11.86, df = 21,1092, P < 0.0001) thereafter as the large 1984

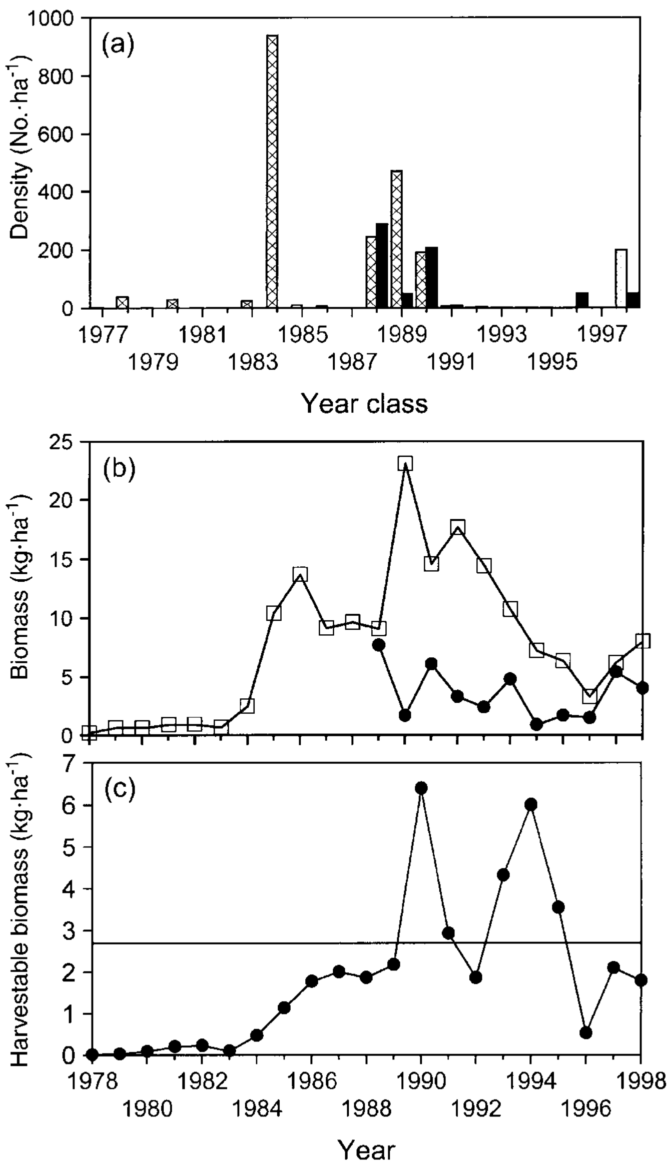
Fig. 4. Scatter plots of age-1 recruits versus adults for (*a*) rainbow smelt (*Osmerus mordax*) and (*b*) lake herring (*Coregonus artedi*) in U.S. waters of Lake Superior, 1978–1999. Data indexed from fish captured in lakewide bottom trawl surveys by the U.S. Geological Survey.



year class entered the catch (Fig. 5*b*). Biomass declined during 1987–1988, as the abundance of the 1984 year class declined and then increased in 1990 to a peak (23 kg·ha^{-1}) as the strong 1988 and 1989 year classes dominated the catch. Poor recruitment since the early 1990s has reduced lakewide biomass to below 10 kg·ha^{-1}. Lake herring biomass in Canadian waters during 1989–1999 was not statistically different (F = 0.38, df = 1,10, P = 0.54) than in U.S. waters, although means appeared lower. Similar to U.S. waters, biomass generally declined (F = 3.13, df = 10,357, P = 0.0006) during 1989–1999 because of limited recruitment, but lower total biomass may also be related to spawner-interception fisheries in Thunder and Black bays up until the mid-1990s.

Recruitment since 1978 may have increased lake herring populations to levels close to historical abundance at the time of maximum fishery removals. Maximum fishery removals were about 2.7 kg·ha^{-1} during 1941–1950 and likely exceeded maximum sustainable yield (Selgeby 1982) and were certainly lower than the level of the unfished stock. Biomass of the harvestable stock (historically fish 230–350 mm total length) (Dryer and Beil 1964) observed in contemporary populations ranged from near zero to 6.4 kg·ha^{-1} from 1978 to 1998 (Fig. 5*c*) and averaged around 3.0 kg·ha^{-1} during 1987–1998 after strong year classes became harvestable. Therefore, harvestable biomass in 1989–1995 approximated or exceeded historical levels of removal during 1941–1950, even with sporadic recruitment, but re-

Fig. 5. (*a*) Estimated strength of the 1977–1998 year classes of lake herring (*Coregonus artedi*) in U.S. (cross-hatched bars) and Canadian (solid bars) waters, (*b*) 1978–1999 biomass estimates of lake herring in U.S. (□) and Canadian (●) waters, and (*c*) biomass of harvestable lake herring (>230 mm) in U.S. waters of Lake Superior in 1978–1999 compared with average removals by the commercial fishery (vertical line) during 1941–1950. Data points near the vertical line indicate that harvestable stock sizes approximated or exceeded historical levels during the height of the fishery.



cent abundance has fallen to well below the 1941–1950 levels. Full recovery is likely impossible without more frequent recruitment events. Harvestable stock sizes are declining (Fig. 5*c*) in response to weaker recruitment, and the uncertainty in the causes of these recruitment dynamics will require diligent management to prevent overharvest.

Deepwater ciscoes

Bloater, kiyi (*Coregonus kiyi*), and shortjaw ciscoe (*Coregonus zenithicus*) became important to the commercial fisheries in all jurisdictions except Minnesota. Species delineation has and continues to be difficult because of morphological variability within and across populations and species (Todd et al. 1981), lack of readily apparent distinguishing features (Peck 1977), and lack of clear genetic differentiation (Todd 1981; Turgeon et al. 1999). Morphological differences have environmental as well as genetic origins (Todd et al. 1981). Given these problems, classifications tend to be subjective; therefore, population trends from the available data are unreliable. Species composition of the harvest in Michigan waters during the 1970s, based on morphological features, was mostly bloater (51–87%), followed by kiyi (38–40%), and shortjaw ciscoe (6–11%) (Peck 1977).

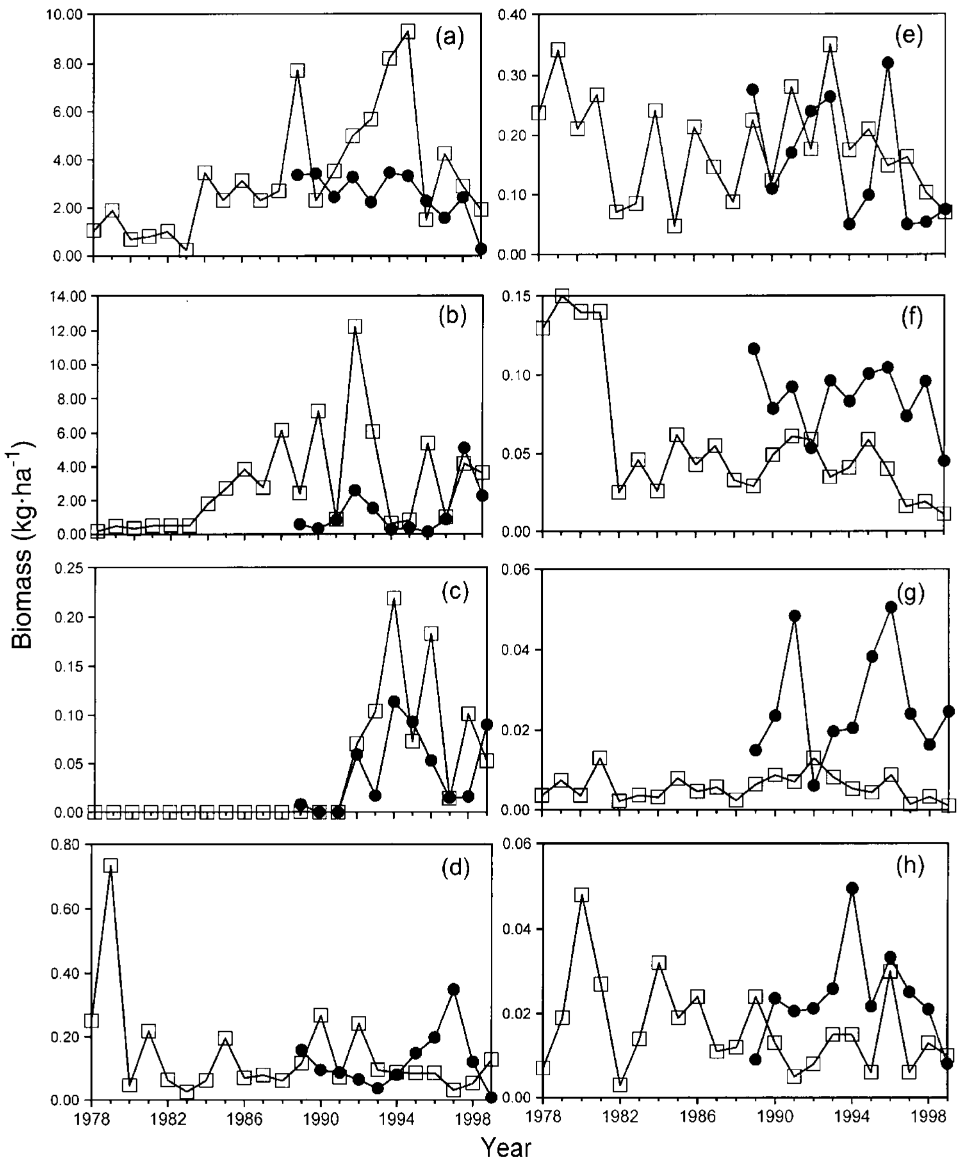
Survey data from bottom trawls indicate that bloater biomass increased (F = 3.96. df = 21,1097, P < 0.0001) in U.S. waters (Fig. 6*b*) at the same time as that of lake herring and could be an artifact of misidentification or that the same unknown factors are responsible for recruitment patterns in these closely related species. Biomass has ranged from 0.2 $kg \cdot ha^{-1}$ in 1978 to 12.2 $kg \cdot ha^{-1}$ in 1992. The lack of kiyi in trawl catches before 1989 (Fig. 6*c*) is also an artifact of identification problems, and because the nearshore trawl surveys generally do not extend into the deeper waters (>80 m) where kiyi are found, any quantifiable changes in biomass are uncertain. Shortjaw ciscoes are rarely encountered and are now being considered for listing as a threatened species. Comparisons of recent survey with historic data suggest that the decline of this species occurred before 1960 and stabilized at lower levels in the 1970s (T. Todd, U.S. Geological Survey, Great Lakes Science Center, Ann Arbor, MI 48105, personal communication).

Other forage species

Sculpins and other species that also play some role in the energy demand of predators and their dynamics may be important. In U.S. waters, ninespine stickleback (*Pungitius pungitius*) have averaged about 0.14 $kg \cdot ha^{-1}$ (Fig. 6*g*), but biomass was the highest in 1979, declining significantly thereafter (F = 2.12, df = 21,1092, P = 0.002) and remaining below 0.2 $kg \cdot ha^{-1}$ in most years. Biomass in Canadian waters averaged about 0.13 $kg \cdot ha^{-1}$ for 1989–1999 but has generally declined since 1996 (F = 5.09, df = 10,357, P < 0.0001). Biomass in Canadian waters has been generally higher (F = 48.54; df = 1, 10; P < 0.0001) than in U.S. waters since 1995. As with rainbow smelt, fewer large ninespine stickleback have been captured since the late 1970s, which could suggest a predation effect (Fig. 7*a*).

Total sculpin biomass in the nearshore waters is generally less than 0.10 $kg \cdot ha^{-1}$ and is composed mostly of slimy sculpin (*Cottus cognatus*) and to a far lesser extent of spoonhead (*Cottus ricei*) and deepwater sculpin (*Myoxocephalus thompsoni*) (Figs. 6*d*, 6*f*, 6*h*). In U. S. waters, slimy sculpin biomass was at its highest level during 1978–1981 (about 0.14 $kg \cdot ha^{-1}$) but declined significantly (F = 7.00, df = 21,1092, P < 0.0001) in 1982 and has remained at less than 0.06 $kg \cdot ha^{-1}$ since then. Sculpin densities in Canadian waters during 1989–1998 were twice as high as in U.S. waters during the same time period. Slimy sculpin biomass was generally stable at just under 0.1 $kg \cdot ha^{-1}$ but in 1999 declined significantly (F = 2.70, df = 10,357, P = 0.003) to below 0.005 $kg \cdot ha^{-1}$. As with rainbow smelt and ninespine stickle-

Fig. 6. Biomass of (*a*) lake whitefish (*Coregonus clupeaformis*), (*b*) burbot (*Lota lota*), (*c*) bloater (*Coregonus hoyi*), (*d*) slimy sculpin (*Cottus cognatus*), (*e*) kiyi (*Coregonus kiyi*), (*f*) spoonhead sculpin (*Cottus ricei*), (*g*) ninespine stickleback (*Pungitius pungitius*), and (*h*) deepwater sculpin (*Myoxocephalus thompsoni*) in U.S. (□) and Canadian (●) waters determined by lakewide bottom trawl surveys in nearshore waters (15–100 m), 1978–1999, conducted by the U.S. Geological Survey.



back, the maximum length range of slimy sculpins became reduced as biomass declined after 1982 (Fig. 7*b*), and this may also suggest increased predation.

Spoonhead and deepwater sculpin biomass is much lower than that of slimy sculpin in the nearshore zone and has generally declined (all $P < 0.003$) over time in both U.S. and Canadian waters (Fig. 6). Estimated deepwater sculpin density is likely not indicative of actual densities and trends as depths covered by the sampling program only reached the shallowest portions of their depth distribution.

Principal salmonine predators

Lean lake trout

The decline of lean lake trout stocks in Lake Superior in the 1950s and the success of the ensuring restoration effort have been adequately addressed elsewhere (Hansen 1999). Early efforts focused on sea lamprey control, harvest control, and stocking of lake trout. A coordinated multi-agency lake trout restoration plan was implemented, with specified stocking priorities, coordinated stock assessments, and standards of reporting and evaluating restoration progress. The recovery of wild, naturally reproducing populations of lean lake trout lakewide (Hansen 1999) has negated the need for intensive stocking since 1993 except in selected areas. The restoration program now focuses on the protection and management of wild fish through implementation of total allowable catches to limit fishing mortality.

Extremely high densities (compared with historical measures) of stocked fish and remnant, wild lake trout spurred recruitment in the 1960s and 1970s. Hansen (1999) suggested that hatchery-reared lake trout contributed to most of

Fig. 7. Total length frequency of (*a*) ninespine stickleback (*Pungitius pungitius*) and (*b*) slimy sculpin (*Cottus cognatus*) during selected years from 1979 to 1998. Smaller numbers of larger fish over time suggest a predation effect from increasing numbers of salmonine predators.

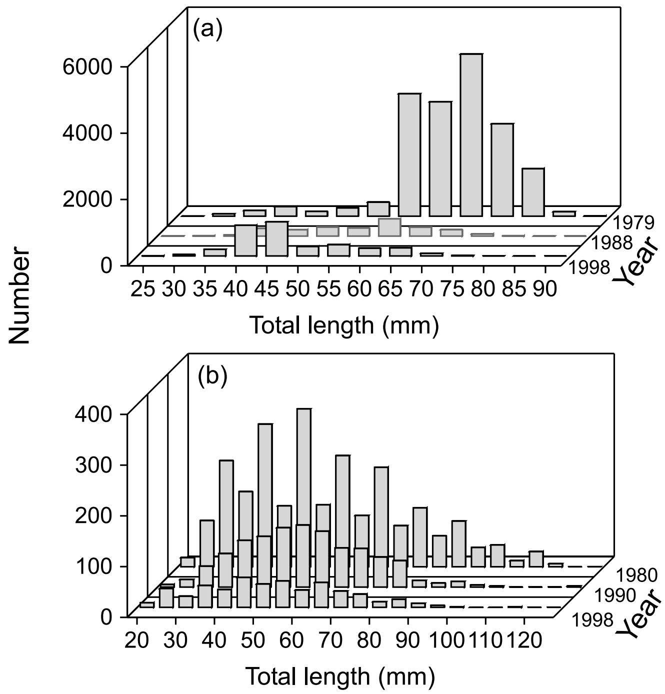
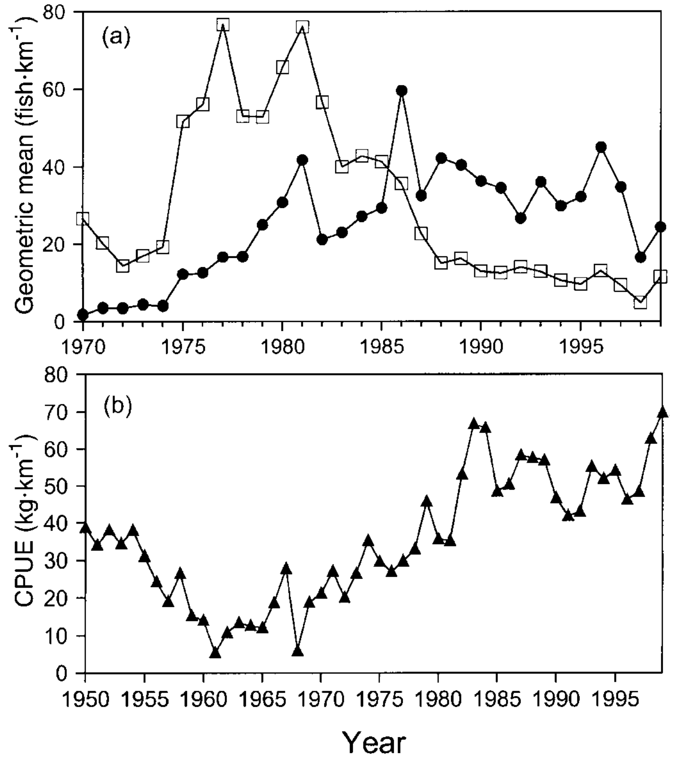


Fig. 8. (*a*) Relative abundance (geometric mean) of wild (●) and hatchery-reared (□) lean lake trout (*Salvelinus namaycush*) in 114-mm stretch measure gill nets in spring stock assessments in U.S. waters, 1970–1999, and (*b*) CPUE of an unknown mixture of lean and siscowet (▲) lake trout in nearshore commercial fisheries in Canadian waters, 1950–1999.



the recruitment, especially in Minnesota and Michigan waters. This is in contrast to earlier findings in which wild adult lake trout explained most of the wild recruitment at Gull Island Shoal (Schram et al. 1995); although at that location, wild fish made up most of the parental stock. A more detailed, age-structured stock–recruit analysis suggests that hatchery-reared fish may be as reproductively efficient as wild counterparts and likely played a significant role in the recovery of lake trout in Michigan waters (Richards et al. 2004).

Spring gill-net surveys indicate that densities of hatchery-reared lake trout have declined in U.S. waters (Fig. 8*a*), mostly as a result of declining survival (Hansen 1999) and reductions in stocking (Fig. 9), whereas wild fish have increased. In Ontario waters, directed stock assessments were only begun in 1997; therefore, historical trends (1950–1999) in lake trout biomass densities (kg·km^{-1} net) are only available from the commercial fishery, and these data strongly indicate that lake trout populations (an unknown combination of hatchery-reared and wild lean lake trout and siscowet lake trout) have increased significantly in Ontario waters over the last 50 years (Fig. 8*b*).

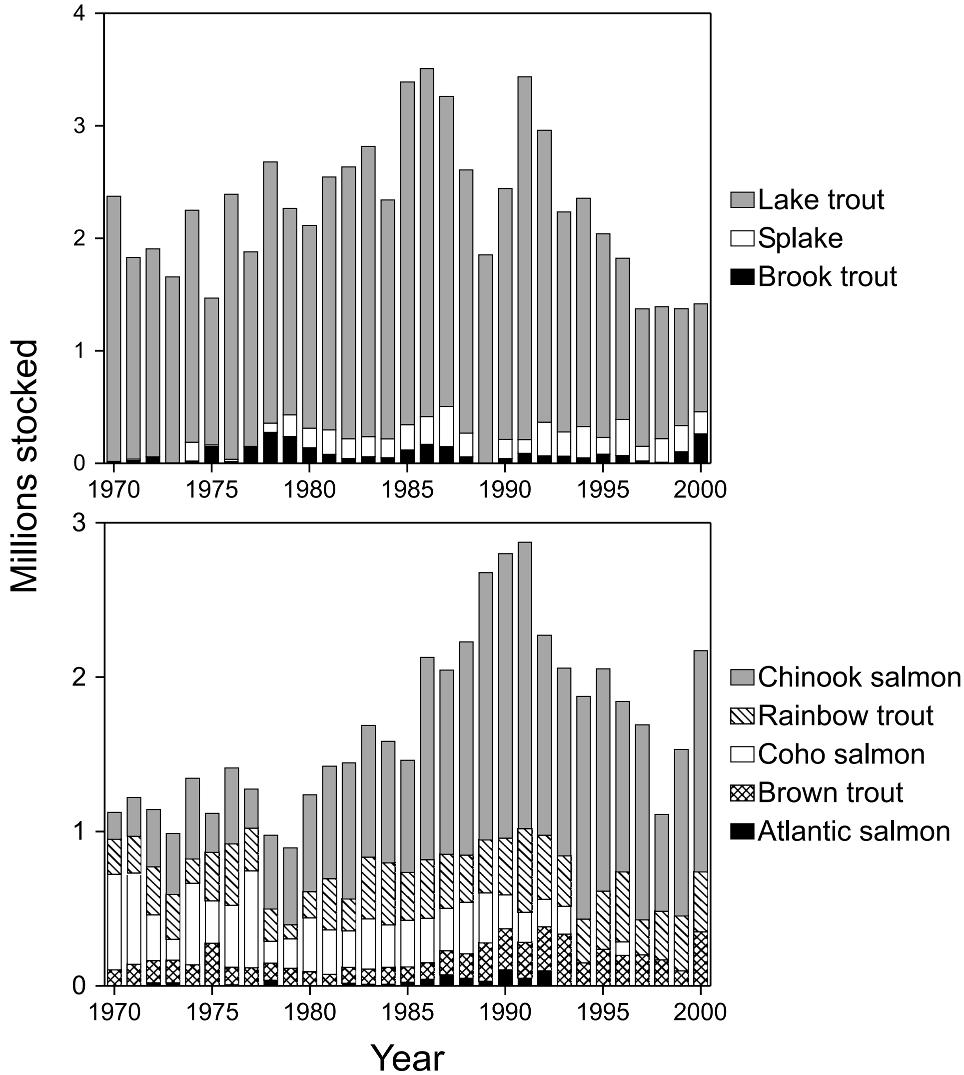
Lake trout are the principal salmonine taken by the sport fishery in Lake Superior and accounted for about 55% of the salmonine harvest in U.S. waters during 1970–1999 (Fig. 10). Landings gradually rose in the 1980s, declined throughout the 1990s, and have increased slightly in the last 5 years. Average harvest in U.S. waters from 1984 to 1999 is about 54 000 fish annually. Catch rates have gradually increased from the late 1970s and are at some of highest rates ever recorded in the last 30 years.

Recovery of lean lake trout is a milestone in the restoration of the Lake Superior ecosystem and would not have occurred without diligent sea lamprey control, limitations on fisheries, and protection of wild, remnant populations. Because of the loss of genetic diversity (Krueger and Ihssen 1995), changes in the forage and predator base, and continued sea lamprey predation, the biological potential of lake trout to reach historical stock sizes was thought to be limited (Bronte et al. 1995; Kitchell et al. 2000). Recruitment dynamics or, more specifically, the onset of density-dependent declines in survival at larger stock sizes may be an indicator of stock restoration (Bronte et al. 1995) at these new biological potentials. Richards et al. (2004) demonstrated that most wild lake trout stocks in Michigan waters underwent density-dependant declines in survival, and Wilberg et al. (2003) showed that stocks are at or higher than historical levels in most areas in Michigan waters. Both findings suggest that lake trout in these areas maybe close to restoration. The population dynamics and biology of Lake Superior's wild lake trout stocks should be used as a model to evaluate progress toward lake trout restoration in the other Great Lakes.

Siscowet lake trout

Historically, Lake Superior contained many morphotypes of lake trout occupying different depths and spawning locations (Khan and Qadri 1970; Goodier 1981; Moore and Bronte 2001). Of these, the siscowet is the most abundant morphotype in Lake Superior and is distinguished by the

Fig. 9. Total salmonine stocking in all jurisdictions of Lake Superior, 1970–2000.



presence of excessive fat in the flesh and viscera (Eschmeyer and Phillips 1965) and its preference for waters deeper than 80 m. Of the 82 000 km^2 of surface area of Lake Superior, 76% is greater than 80 m deep, and this defines the principal habitat for siscowet, as well as suggests the potential importance of this top predator in the Lake Superior ecosystem.

Little is known about the life history of siscowets. Recent surveys indicated that densities were much higher for siscowet than for lean lake trout from the same management unit in U.S waters (Figs. 11*a*, 11*b*; see Wilberg et al. 2003 for map of management units), and siscowet outnumbered lean lake trout by about 10 to 1 in gill-net catches. Siscowet densities increased with depth, whereas lean lake trout densities decreased (Figs. 11*c*, 11*d*). Most siscowets were captured at depths greater than 150 m in June but had a shallower distribution in late August – September, with more fish captured between 70 and 150 m, suggesting seasonal nearshore movement. Unknown differences in catchability between siscowet and lean lake trout in gill nets makes it difficult to assess the ratio estimates; however, all indications suggest that siscowet lake trout significantly outnumber lean lake trout lakewide. Sagittal otoliths revealed a broad age distribution comprised of 16–30 age groups depending on area. Siscowet harvest has remained low in recent years (Fig. 12); therefore, these advanced age compositions may reflect fully restored populations in some areas. It was thought that the expanding siscowet populations would affect recovery of lean lake trout stocks but there is little trophic overlap between these two morphotypes (Harvey et al. 2003) and siscowet expansion has been concurrent with lean lake trout recovery.

Sea lamprey predation may be a significant source of mortality, as fresh wounding (type-A, stages 1–3 marks; King 1980) and scaring (healed wounds: type-A, stage 4; type-B, stages 1–4) are high, especially on large fish >736 mm long. Sea lamprey wounds averaged 5.5 marks·100 fish^{-1} and ranged from 1.3 marks·100 fish^{-1} on 432- to 532-mm fish to 167 marks·100 fish^{-1} >736 mm long during June 1996. Sea lamprey attacks on the largest fish (>736 mm) were almost 17 times higher than on lean lake trout during the same time period (Ebener 1998), which suggests that siscowets may serve as a buffer for sea lamprey predation on recovering lean lake trout stocks. Extremely high scarring rates also suggest that siscowet may be able to survive sea lamprey at-

Fig. 10. Estimated numbers of salmonines harvested in U.S. waters of Lake Superior, 1970–1999.

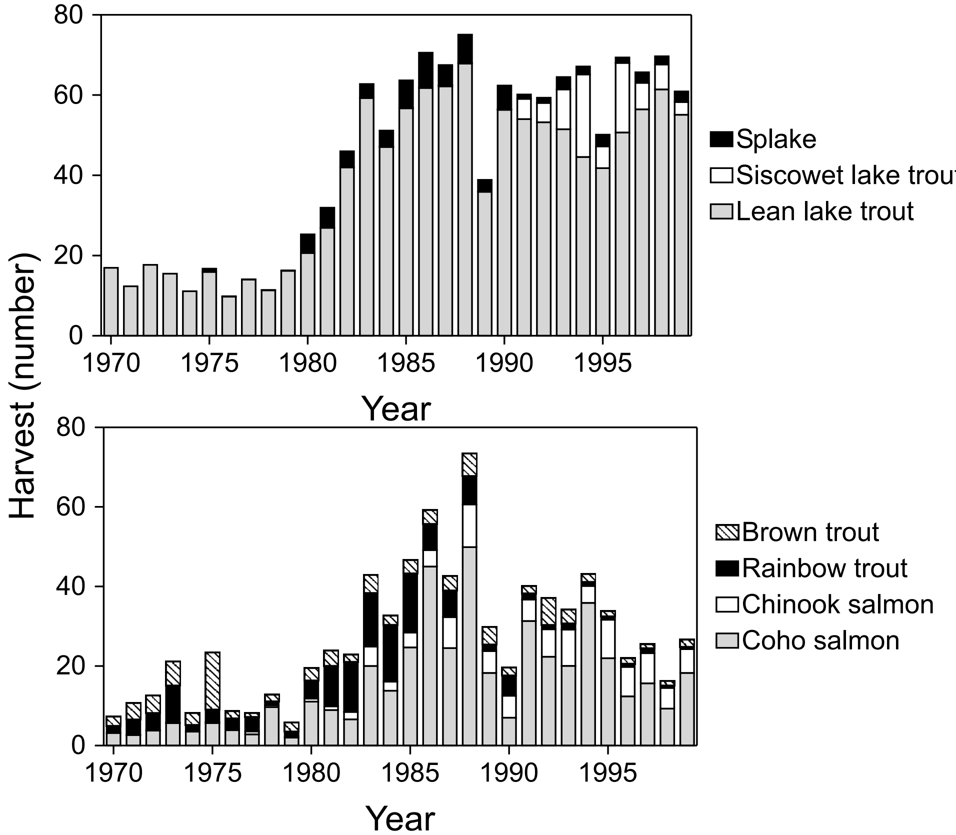
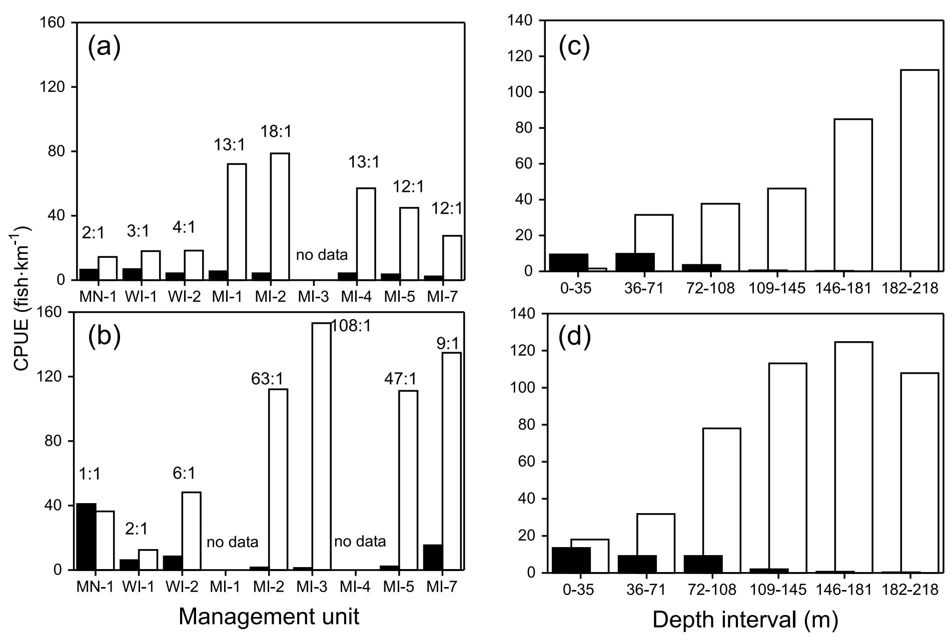


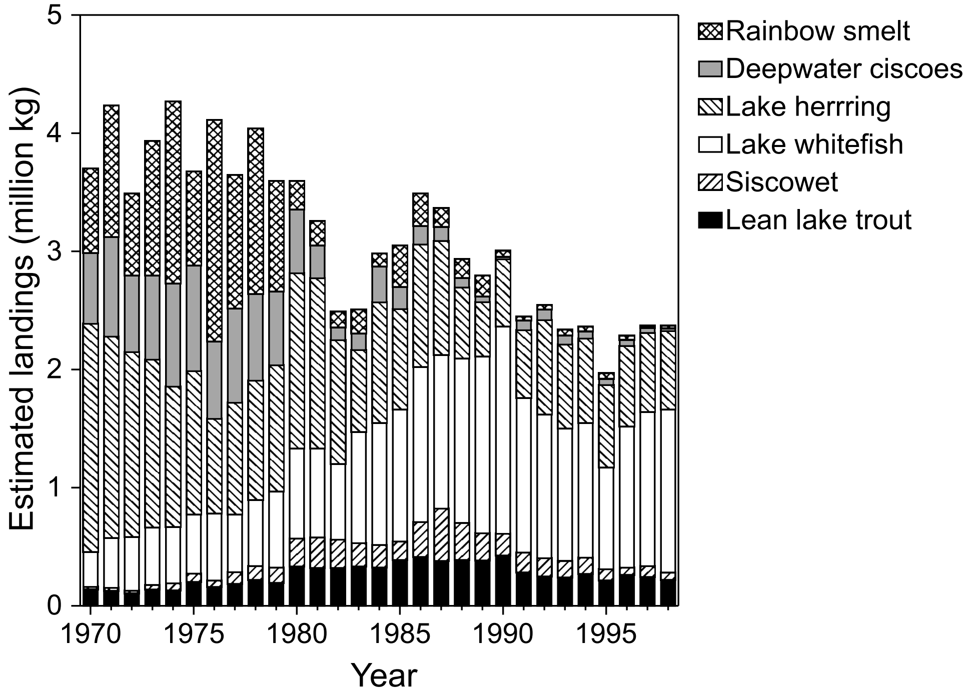
Fig. 11. Relative abundance (CPUE) and ratios of lean (solid bars) and siscowet (open bars) lake trout (*Salvelinus namaycush*) captured in graded-mesh gill-net assessments in U.S. waters of Lake Superior by (*a*, *b*) management unit and (*c*, *d*) depth during (*a*, *c*) June, 1996–1997, and (*b*, *d*) August–September, 1996–1997. See Wilberg et al. (2003) for a map of management units.



tacks better than lean lake trout. This may be related to the lower temperatures of the water that siscowets inhabit, which slows metabolic and physiologic processes associated with sea lamprey attack and feeding behavior (Schneider et al. 1996).

Siscowet abundance has increased lakewide in the past 30 years. Commercial gill-net catch and effort data from U.S. and Canadian waters indicate that densities increased steadily from >20 kg·km^{-1} net in the early 1950s to about 250 kg·km^{-1} net in the late 1990s (Fig. 13). Stock sizes have

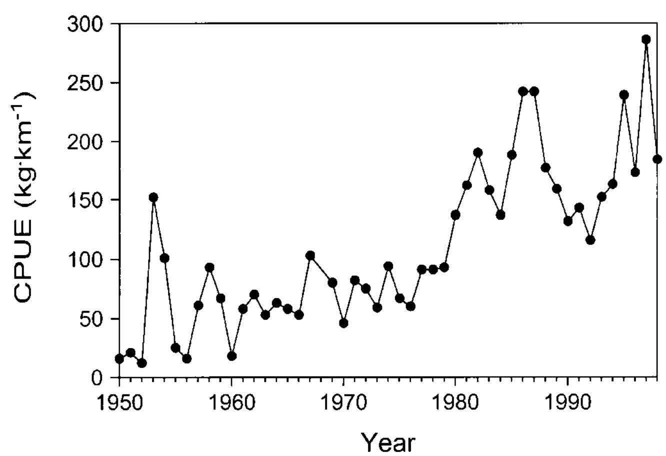
Fig. 12. Estimated commercial landings by species and year from Lake Superior, 1970–1998.



been estimated at 25 million fish of ages 1–21 years for U.S. waters west of the Keweenaw Peninsula compared with about 4.5 million for lean lake trout (Fig. 1; Ebener 1995), and this ratio (6:1) is close to that estimated from gill-net catch rates (10:1). Siscowet by-catch has increased in U.S. sport fisheries targeting lean lake trout since the early 1990s (Fig. 10), which further demonstrates the recovery and expansion of these offshore stocks.

Siscowet are the dominant predator lakewide (Harvey and Kitchell 2000) and consume mostly coregonines (lake herring, bloater, kiyi), sculpins, and burbot (Conner et al. 1993; Ebener 1998; Kitchell et al. 2000). Rainbow smelt, *Mysis*, and terrestrial insects are also consumed, as are miscellaneous items (i.e., pine needles, wood, grain, net twine, fish guts, bats, birds), suggesting extensive vertical movements to the surface and horizontal movements to nearshore areas. Nearshore species such as bullheads (*Ictalurus* sp.), unidentified shiners, and longnose dace (*Rhinichthys cataractae*) were also found in stomachs, further indicating that feeding is taking place in shallow, nearshore areas. Siscowet consume more coregonines, sculpins, and burbot and less rainbow smelt than lean lake trout (Fig. 1), which may partly explain the significant declines of bloater and burbot (F = 1.62, df = 21,1092, P = 0.04; Figs. 6*b*, 6*c*) in Lake Superior concurrent with the expansion of siscowet populations. More study of the deepwater zone of Lake Superior is needed to understand the dynamics of siscowet and their impact on the forage base.

Fig. 13. Relative abundance (CPUE) of siscowet lake trout (*Salvelinus namaycush*) in the commercial gill-net fishery, Lake Superior, 1950–1998.



Brook trout

Over the last 10 years, interest has increased in rehabilitating native migratory brook trout in Lake Superior. These fish, also as known as “coasters”, live in nearshore coastal areas, where they can attain larger sizes than stream-dwelling counterparts, but ascend rivers to spawn in the fall. Major stressors to brook trout historically were overfishing and habitat loss; currently, competition with nonnative salmonines is seen as a possible impediment to restoration. Attempts are underway to restore migratory brook trout (Newman et al. 1999); however, this may not be biologically possible for many historically important streams that have lost habitat or have stocks of nonnative salmonines. Strategies to achieve the goal include habitat protection and restoration, restrictive angling regulations, and stocking appropriate strains from remnant populations. Further research is also required on genetic profiling, general life history, and identification of remnant stocks, especially at remote sites such as those at Isle Royale.

Remnant populations of coaster brook trout still exist in a few isolated areas of Lake Superior. These include the Nipigon River system in Ontario, streams and bays around Isle Royale, and the Salmon-Trout River in Michigan (Peck et al. 1994). Adequate genetic variability still exists among remnant brook trout stocks; hence, stocking should proceed cautiously (Burnham-Curtis 2001). Additional genetic evidence suggests that migratory brook trout in Nipigon Bay are a life history variant and are progeny of stream stocks (D'Amelio 2002).

Brook trout stocking has been continuous by most agencies since 1970 (Fig. 9), but harvest in the sport fishery has usually been less than 100 fish·year^{-1} since 1970. Only scattered harvest information on brook trout exists for Ontario waters. Most agencies have, or are in the process of implementing, restrictive harvest regulations for brook trout in Lake Superior and its tributaries. Experimental stocking of genetic strains from Lake Superior is underway in selected areas.

Splake

Splake (lake trout × brook trout) were first introduced in Michigan in 1971 and then in Wisconsin in 1973 (Fig. 9). No natural reproduction by splake has been documented, but sexually mature splake have been found in spawning lake trout aggregations (Peck et al. 1994). Harvest occurs primarily near stocking sites; hence these fish are valued for developing local and nearshore fisheries. Wisconsin has a major splake fishery during winter in Chequamegon Bay, which accounts for most of the harvest in Lake Superior (Fig. 10). Catch rates for splake have been declining since the mid-1980s in response to reduced stocking.

Rainbow trout (steelhead)

Migratory rainbow trout or steelhead became naturalized soon after initial introductions in 1895. Since about 1970, several strains have been introduced to supplement naturalized stocks in areas with intense fisheries or limited spawning habitat. In 1972, Minnesota experimented with the Kamloops, Madison, and Donaldson strains and in 1976 chose the Kamloops strain to supplement naturalized populations. Michigan has used the summer-run Siletz strain since 1984 to provide increased angling opportunities. All three U.S. states have stocked with the Skamania strain of summer steelhead (Peck et al. 1994), but returns were poor and have been discontinued lakewide. Annual stocking has ranged from 90 000 to 540 000 fish (Fig. 9), but return rates have generally averaged 1% or less and have varied widely across streams; hence steelhead populations are composed of mostly wild fish. Lakewide, naturalized rainbow trout comprise 80–90% of fish caught (Peck 1992). Continued stocking on top of wild populations may be wasteful and can also pose genetic risks (Krueger et al. 1994).

Harvest has ranged from 600 fish in 1999 to about 15 000 in 1984 in U.S waters (Fig. 10), with most of these fish taken in Wisconsin waters. Rainbow trout populations were high during the 1950s, but as lake trout recovered and - Pacific salmon became established, abundance declined during the 1980s. Starting in the early 1990s, harvest restrictions have reduced exploitation and increased rainbow trout abundance as indicated by angler catch rates during the spring spawning run (Schreiner 2003; Ken Cullis, Ontario Ministry of Natural Resources, 435 James St. South, Thunder Bay, Ont., Canada, personal communication). In addition, unusually warm lake temperatures in 1998 increased both survival and growth rates of rainbow trout, which has been reflected by increasing returns to the Brule River in Wisconsin (Dennis Pratt, Wisconsin Department of Natural Resources, 1401 Tower Ave., Superior, WI 54880, personal communication). Although stocking supports a viable sport fishery for rainbow trout in a small number of Minnesota streams, it is clear that protection of naturalized spawning stocks is the best way for agencies to insure the long-term success of the rainbow trout fishery in Lake Superior.

Coho salmon

Coho salmon were first stocked by Michigan in 1966, followed by Minnesota and Ontario from 1969–1972 (Fig. 9), and quickly became naturalized throughout Lake Superior (Peck et al. 1994). These fish reproduce successfully in many tributaries that are accessible during the spawning period, have suitable substrate, and adequate winter groundwater flows. Michigan was the last agency to discontinue stocking in 1994 as stocked fish contributed less than 10% to the fishery (Peck 1992).

Coho salmon in Lake Superior have a 3-year life history, spending from 16 to 18 months in streams and the remaining 18–20 months in the lake before spawning and death. Anglers mostly exploit age-2+ fish, which results in wide harvest fluctuations, predicated by year-class strength. In most years, coho salmon are the second most harvested salmonine in the U.S. sport fishery after lake trout (Fig. 10). Total harvest in U.S. waters has ranged from 2700 fish in 1971 to 50 000 fish in 1988, with most fish taken in Michigan waters. Catch rates in the sport fishery have been slowly increasing since the early 1980s. Sport harvest regulations have become more restrictive in most jurisdictions to protect adequate numbers of parental stock, as all stocks are now supported by natural reproduction.

Chinook salmon

Chinook salmon were first introduced into Lake Superior by Michigan in 1967, followed by Minnesota in 1974, Wisconsin in 1977, and Ontario in 1988 (Peck et al. 1994). Annual stocking has ranged from 175 000 to 1.8 million fish (Fig. 9); however, the utility of continued stocking is being questioned. Lakewide, wild chinook salmon make up over 75% of all chinook salmon harvested (Peck et al. 1999). Stocked chinook salmon made up 57% of the angler harvest in Minnesota, 32% in Wisconsin, 25% in Michigan, and 9% in Ontario during the 1990–1994 fishery. Chinook salmon stocked in each jurisdiction contributed to the fisheries in all other jurisdictions, which indicates that these fish are free-ranging in Lake Superior and have little site affinity. Harvest in U.S. waters has ranged from a few fish in the early 1970s to about 11 000 fish in 1980 (Fig. 10), with most fish taken from Minnesota waters. Harvests have generally declined since then, even though catch rates in the fishery have steadily increased in the last 20 years.

Pink Salmon

In 1956, approximately 21 000 odd-year spawning pink salmon (*Oncorhynchus gorbuscha*) fry were accidentally introduced into the Current River in Ontario (Nunan 1967), became established, and are now naturalized in Lake Superior. Since 1970, abundance has fluctuated greatly but has never approached that of other Pacific salmon. In general, pink salmon abundance increased from the 1960s through the 1970s and then declined to extremely low levels during the late 1980s (Peck et al. 1994) and may have been affected by declines in rainbow smelt (MacCullum and Selgeby 1987). However, during the mid- to late 1990s, pink salmon abundance has again started to increase as indicated by harvest (Fig. 10), angler catch rates, and number of spawning adults in tributaries. Even-year spawning stocks have also developed and it is not unusual to capture 3-year-old spawners in many streams. Harvest during 1985–1999 has averaged <250 fish·year^{-1} in U.S. waters. In Ontario, the angler catch is unknown, but a dip-net fishery in the Michipicoten River took an average of 4200 pink salmon from 1979 to 1983 (Peck et al. 1994). Minor fisheries that target strong year classes develop periodically in the tributaries during the September–October spawning period.

Brown trout

Brown trout were introduced into Lake Superior in the 1890s and established naturalized populations in some tributary streams, especially in Wisconsin. Brown trout are still stocked in Wisconsin and Michigan tributaries (Fig. 9) where they support a few localized anadromous populations. Hatchery-reared brown trout make up 50% of the angler harvest of this species in Wisconsin and 40% in Michigan (Peck et al. 1994), indicating significant natural reproduction. Sport harvest is highest in Wisconsin waters, ranging from 534 fish in 1996 to about 14 000 fish in 1975 (Fig. 10). In most years, an active winter fishery develops on Chequamegon Bay, Wisconsin, largely supported by hatchery-reared fish. Lakewide angler catch rates declined from the 1970s to the 1980s but have remained fairly consistent over the last 15 years. The Brule River supports the largest known run of migratory brown trout in Lake Superior, averaging about 3600 fish during 1987–1999 and suggesting a relatively stable population since 1987. Significant genetic variation exists among naturalized brown trout populations in Wisconsin from different drainages and between migratory and resident fish in the Brule and Sioux rivers (Krueger and May 1987).

Atlantic salmon

At present, there is no active management program for Atlantic salmon in Lake Superior. From 1972 to 1992, each state in U.S. waters experimented with stocking Atlantic salmon (Fig. 9), but naturalized populations and significant returns never developed. Minnesota had the most extensive program, but it was discontinued in 1992 because of low returns, high cost, and limited angler interest. In U.S. waters, harvest has been generally 400 fish or less each year since the early 1980s, and no fish have been detected in any creel surveys since 1997.

The commercial fishery

The effects of overexploitation by the commercial fishery were a major factor in the degradation of the fish community of Lake Superior before 1970. During the late 1960s and 1970s, state agencies began to manage primarily for recreational-based fisheries (Brown et al. 1999), which reduced the number of commercial fishing licenses, limited fishing grounds and seasons, and restricted fishing gear types (Brown et al. 1999). Further change to the commercial fishery was expedited by the re-affirmation of treaty-protected fishing rights by Native Americans in the U.S. and Canada. Re-affirmation of treaty rights in Canada came later in the 1990s through “The Sparrow Decision”. No tribal fisheries were present in 1970, but in the last 10 years, tribal harvest accounted for 62% of the lake whitefish and 67% of the lake trout harvest. In 1965, there were 542 state-licensed commercial fishermen in U.S. waters of Lake Superior, but the size, scope, and effect of the fishery has declined significantly. In 1999, state, provincial, and tribal fishery agencies issued about 350 commercial licenses but very few licensees fished full-time. Total commercial harvest declined from about 4.0 million kg in 1970 to 2.4 million kg in 1996–1998 (Fig. 12). Fewer fishermen and low markets prices have reduced the fishery, and mainly those operators that control their own wholesale and retail markets fair well economically.

Lake whitefish fishery

Lake whitefish have been the primary target of the commercial fishery lakewide since the late 1980s (Fig. 12), mainly because of fishing restrictions on lake trout and lake herring, changing market conditions, and availability of large standing stocks for harvest. Lake whitefish made up only 6% of the total commercial harvest in 1970 but this increased to 40% in the 1990s. Since 1983, the annual harvest of lake whitefish has exceeded 1 million kg and has been greater than at any other time during the 20th century. Densities of young lake whitefish in bottom trawls increased lakewide during 1990–1995 (Fig. 6*a*) and recruitment of these fish to the fishery helped fuel the increased landings.

Management of lake whitefish populations is based mainly on protecting individual stocks as recommended by Lawrie and Rahrer (1972). Nine lake whitefish management units are recognized in Michigan waters (Technical Fisheries Review Committee 1992), and Ontario has about 21 units (Upper Great Lakes Management Unit 2001) where lake whitefish are managed as biological stocks. Each management unit likely contains smaller reproductively isolated stocks, but little information exists to delineate stock boundaries or structure. Rakoczy (1983) recognized six stocks of lake whitefish in Michigan waters based simply on the wide geographic distance between sampling locations and the spatial segregation of the fisheries. Large concentrations of spawning lake whitefish spatially segregated by 20–30 km have been identified along the Keweenaw Peninsula and may represent reproductively isolated stocks (Ebener 1990). Whitefish Bay has at least four discrete spawning aggregations separated by 8–40 km, but stocks intermingle during the year. At least two stocks exhibit unique growth and size differences. The Apostle Islands presumably contain many reproductively isolated populations of lake whitefish but are managed as a single stock. Lake whitefish fisheries are managed by total allowable catches in Michigan and Ontario waters and through effort limitations for gill-net fishers in Wisconsin waters, where the intent is to reduce the by-catch of nontarget lake trout. Conversion to trap nets in Michigan (Schorfhaar and Peck 1993) and Wisconsin has also reduced by-catch mortality significantly.

Age composition of the commercial harvest is similar among management areas. Except for very lightly exploited stocks, ages 5–9 make up over 80% of the commercial harvest. Lake whitefish begin recruiting to the trap-net fishery at age 4 and to the gill-net fishery at age 5, and the oldest whitefish observed in the harvest are 17–20 years old (Schorfhaar and Schneeberger 1997; Petzold 1999).

Lake whitefish stocks in Lake Superior experienced a substantial density-dependent growth response to the increase in biomass and abundance observed after 1970. In the late 1970s and early 1980s, L_∞ values from various stocks ranged from 700 to 800 mm total length and K values ranged from 0.15 to 0.25. By the mid- to late 1990s, L_∞ values had declined to 500–700 mm and K values ranged from 0.22 to 0.44 (Table 3). Declines in mean weight at age also occurred across the lake. The declines in growth affected age structure of lake whitefish caught by the commercial fishery. In Whitefish Bay, age structure of lake whitefish in the commercial gill-net fishery shifted from ages 4–7 in 1983 to ages 5–17 in 1998. Modal age of whitefish in the trap-net fishery at Munising increased from age 5 in 1983 to age 7 in 1998. In Thunder Bay, Ont., fish of ages 5–7 dominated the harvest during 1975–1982, whereas ages 8–15 made up most of the harvest in 1996–1997 and ages 5–7 barely contributed to the fishery (Petzold 1999).

Lake trout fishery

Commercial harvest is regulated by various methods, but mainly through biologically based catch quotas. Total allowable catches (TACs) are used to accommodate incidental catches of lake trout in large-mesh gill-net lake whitefish fisheries, while simultaneously permitting recovery of lean lake trout populations, except in Minnesota where lean lake trout harvest is prohibited. In Wisconsin and Michigan waters, TACs are estimated using population models based on commercial fishery and biological statistics, although more sophisticated statistical catch-at-age models are now being adopted in U.S. waters (Bence and Ebener 2002). In Ontario, individual transferable quotas are assigned to each licensee, and the quotas are calibrated to surface area ($kg \cdot ha^{-1}$) of water <136 m. Lakewide catch quotas totaled about 400 000 kg in 1998.

Contemporary commercial harvests of lean lake trout (Fig. 12) represent only a fraction of precollapse levels before 1950. The average harvest of lean lake trout was 262 000 kg during 1970–1998 and represents only 13% of the historic average harvest. The majority of the lean lake trout commercial harvest is taken with large-mesh gill nets in Ontario and Michigan. Few lake trout are killed as part of commercial trap-net fisheries (Schorfhaar and Peck 1993) in comparison to gill-net fisheries. Gill-net fisheries were implicated for declining survival of hatchery-reared lake trout (Hansen 1999), but this is unlikely given the sustained increase in wild fish subjected to the same gill-net fishery during the same period.

Although siscowets are more abundant than lean lake trout in Lake Superior, commercial harvests of this morphotype are generally less because of the high fat content of siscowets, which results in lower market demand and value. Annual harvests of siscowets ranged from a low of 23 200 kg in 1970 to a peak of 441 000 kg in 1987 and averaged 148 000 kg during 1970 through 1998 (Fig. 13). Peak catches occurred when Michigan state licensed commercial fisheries were allowed to target siscowet in water >110 m deep. In 1990, the Michigan siscowet fishery was closed because chlordane concentrations were greater than permitted by guidelines for fish consumption. Populations of siscowets increased substantially during the 1980s and, given the slow growth of siscowets, was likely the result of good reproduction and survival during the late 1960s and early 1970s.

Lake herring fishery

Since 1970, lake herring has made up most of the commercial landings from Lake Superior, but this represents only a fraction of historical removals (Fig. 12). Lake herring made up about 25% of the total lakewide commercial harvest from Lake Superior in the 1990s compared with 75% in the 1960s. Annual commercial harvests declined over the last three decades from 1.45 million kg in the 1970s, to 1.16 million kg in the 1980s, and to only 0.7 million kg in the 1990s. The peak harvest during 1970–1998 was 1.9 million kg in 1970 but represented only 22% of the peak historical harvest in 1941.

Based on commercial fishery catches, lake herring appear to be about one-half as abundant since 1980 compared with before the collapse of the fishery in the mid-1960s, although comparisons with bottom trawl survey estimates suggest higher abundance (Fig. 5*c*). Lakewide catch per unit effort (CPUE) of lake herring in the commercial small-mesh gill-net fishery declined to a low of 84 $kg \cdot km^{-1}$ in 1976, then increased rapidly thereafter, and has averaged 365 $kg \cdot ha^{-1}$ since 1981. Since 1993, lakewide CPUE of lake herring has ranged from 397 to 478 $kg \cdot km^{-1}$ compared with 719 $kg \cdot km^{-1}$ during 1953–1964, at the height of the historical fishery. These direct comparisons may not actually represent a state of recovery since the historical fishery was prosecuted with bottom-set gill nets; most of the contemporary fishery uses floating gill nets, especially in fall to target gravid females for the egg market. The increase in commercial harvest and CPUE correspond well with the increase in lakewide biomass from sporadic recruitment detected in lakewide trawl surveys.

Deepwater ciscoe fishery

Deepwater ciscoes currently make up less than 10% of the total commercial harvest from Lake Superior, and this fishery has been declining over the last two decades (Fig. 12). Deepwater ciscoes have never made up more than 25% of the total commercial harvest from Lake Superior and from 1970 to 1980 made up 12 to 25% of the lakewide commercial harvest.

Relative abundance of deepwater ciscoes in the small-mesh gill-net fishery was stable during 1973–1980 (90–100 kg per km of net) but declined thereafter to only 18 kg per km of net by 1998. The continual decline in abundance of deepwater ciscoes since 1980 corresponds to the lakewide increase in abundance of siscowets and their predation pressure. Recovery of deepwater ciscoe populations is unlikely unless siscowet populations decline substantially.

Table 3. Von Bertalanffy growth parameters for Lake Superior lake whitefish stocks estimated from length-at-age data collected from commercially harvested fish during 1978–1998.

Stock	Years	Gear	L_∞ (mm)	K	Source
Apostle Islands	1981	Gill net	704	0.170	Red Cliff Fisheries Department
	1990	Gill net	569	0.250	Red Cliff Fisheries Department
	1999	Gill net	537	0.311	Red Cliff Fisheries Department
West Keweenaw Peninsula	1983	Trap net	696	0.197	Peck (1994)
	1985	Trap net	658	0.214	Peck (1994)
	1988	Trap net	610	0.206	Peck (1994)
	1994–1995	Trap net	507	0.496	Schorfhaar and Schneeberger (1997)
East Keweenaw Peninsula	1983–1985	Trap net	783	0.156	Schorfhaar and Schneeberger (1997)
	1993–1994	Trap net	800	0.200	Schorfhaar and Schneeberger (1997)
Marquette	1983–1985	Trap net	804	0.176	Schorfhaar and Schneeberger (1997)
	1993–1995	Trap net	786	0.183	Schorfhaar and Schneeberger (1997)
	1996–1998	Trap net	719	0.219	Michigan Department of Natural Resources
Munising	1983–1985	Trap net	774	0.186	Schorfhaar and Schneeberger (1997)
	1993–1995	Trap net	733	0.219	Schorfhaar and Schneeberger (1997)
	1986–1998	Trap net	706	0.234	Michigan Department of Natural Resources
Whitefish Bay, U.S. waters	1978	Trap net	748	0.251	Chippewa-Ottawa Resource Authority
	1984	Trap net	780	0.180	Chippewa-Ottawa Resource Authority
	1992	Trap net	671	0.232	Chippewa-Ottawa Resource Authority
	1997	Trap net	629	0.237	Chippewa-Ottawa Resource Authority

Note: In general, estimates of L_∞ decreased and K increased from the late 1970s to the early 1980s to the 1990s in response to increasing densities of lake whitefish.

Overview

Since 1970, much more is known about the Lake Superior fish community than was available at the time of SCOL-1. Contaminant loadings, sources, and burdens have been identified and monitored, with promising indications of declining levels in lake trout and their prey. Independent fish stock assessments have been implemented on larger temporal and spatial scales necessary to measure fish community changes and the range of population dynamics. Attention has also turned toward native species other than salmonines (lake sturgeon, brook trout, and walleye) to further fish community restoration. Given the degree of lotic habitat alteration, the recovery of some of these species may never approach historical levels but may be confined to a few areas with good habitat.

Commercial fishery production, a major factor in the initial decline of lake trout and lake herring, is limited by the need for conservation and for allocation of resources among diverse user groups and market conditions. Harvest is only a fraction of that historically and has shifted from state-licensed fishers to Native American users under court-reaffirmed treaty rights. The initial controversy over the exercising of these rights has led to increased cooperation among tribal, state, and federal fishery agencies and has resulted in a better understanding of the biology and management of the exploited populations.

Continued introductions of plants and animals have increased, potentially threatening the recovering fish community in unknown ways, and are likely one of the most significant threats to the ecosystem. Although many new invaders have been documented and the potential for greater colonization is rising with the onset of global warming, sea lamprey still appear to be the most deleterious as their impact was and can still be lakewide if control efforts falter. Predation by sea lamprey continues to be a problem and will require continued control with an integrated combination of methods and biological and economic evaluation of control options. Restoration of native species and naturalization of nonnative salmonines would not have been possible without sea lamprey control, which should be credited as the most significant management action to affect fish community recovery in Lake Superior. Although Pacific salmon have become naturalized and support small but popular fisheries, the need for additional stocking is being questioned given the levels of wild recruitment. Their impact on the ecosystem appears relatively small on a lakewide perspective but may have some consequences at finer spatial scales.

Lean lake trout, lake herring, and siscowet lake trout have recovered and are approaching precollapse levels of abundance. The latter two species have recovered without direct intensive intervention, which may demonstrate natural ecosystem resiliency, although the effects of sea lamprey control and lower fishing mortality cannot be overlooked. Current abundance of siscowets may be approaching an ancestral state unrecognized by most whose experience with Lake Superior follows years of prolonged overharvest and high levels of sea lamprey predation. Lake whitefish stocks have also recovered to higher levels mostly without directed management and under continued exploitation and may illustrate a biological potential in the absence of severe sea lamprey predation.

The fish community of Lake Superior has remained relatively intact and may also be responsible for the progress toward restoration. Other than paddlefish (*Polyodon spathula*) and arctic grayling (*Thymallus arcticus*), which were extirpated in the early 1800s and early 1900s, respectively, from Lake Superior tributaries (G. Smith, University of Michigan, Ann Arbor, Mich., personal communication), there have been no native species losses from Lake Superior proper. Originally, the blackfin cisco (*Coregonus nigripinnis*) and shortnose cisco (*Coregonus reighardi*; Koelz 1929) were thought to be overfished to extinction; however, these fish never existed in Lake Superior and were likely shortjaw cisco (Todd and Smith 1980). Shortjaw ciscoe predominated historical commercial and assessment landings before 1950 but now make up only <5% of the deepwater ciscoes (T. Todd, U.S. Geological Survey, Great Lakes Science Center, Ann Arbor, MI 48105, personal communication); their decline may be related to targeted overfishing but this is our speculation. The apparent persistence of the deepwater fish community of Lake Superior is in stark contrast to that in the other Great Lakes where the deepwater piscivore (siscowet lake trout), planktivore (deepwater ciscoes), and benthivore (deepwater sculpins) assemblages were lost or disrupted from overfishing, exotic introductions, and cultural eutrophication (Eshenroder and Burnham-Curtis 1999). The deepwater fish community in Lake Superior, as was the case historically in the other Great Lakes, is highly evolved structurally and composed of species across all trophic levels (*Mysis* to siscowet) that are adapted for vertical migration (Eshenroder and Burnham-Curtis 1999). Vertical migration links production in benthic and pelagic communities through predation, thereby allowing these species to successfully use the vast hypolimnetic habitat present in Lake Superior and the other Great Lakes. This historical fish community is more sustainable than the exotic counterparts that dominate the other Great Lakes (Eshenroder and Burnham-Curtis 1999). Restoration in the other Great Lakes will likely be more difficult because of the absence of these ecologically important native species. Additionally, political and economic pressures that support less stable and sustainable fish communities composed of nonnative predator–prey complexes will also hamper restoration in the other Great Lakes.

The forage base of Lake Superior is now about 50% of its peak biomass in the early 1990s and the result of the combined effects of predation (principally from large standing stocks of lean and siscowet lake trout) and irregular recruitment of lake herring. Predation pressure appears to be high, as suggested by declining prey biomass coupled with the low occurrence of large rainbow smelt, ninespine stickleback, and slimy sculpin in bottom trawl surveys. Under the current predation pressure, rainbow smelt populations would likely not recover to pre-1978 levels. Future recruitment of lake herring is uncertain; therefore prey profiles will likely continue to consist of small rainbow smelt (<180 mm) and large adult lake herring and bloater (>200 mm). Lake trout growth and production may be highest using this prey profile (Mason et al. 1998) and suggests that the current forage situation may be desirable for this principal predator. Concern over forage demand by predators will resolve itself through density-dependent reductions in growth and survival and will remain largely out of the control of fishery managers, who have little influence on recruitment dynamics of forage fish and, to some extent, the major predator, siscowet lake trout.

Lawrie and Rahrar's (1972) prognosis for the future of Lake Superior focused on the recognition of hatcheries being critical to restoration of salmonine populations. Lean lake trout rehabilitation and establishment of Pacific salmon clearly would have been impossible without hatcheries. What probably was not envisioned was the relatively short time (30 years) that hatcheries contributed to the restoration effort, as the abundance of most salmonines in Lake Superior is no longer dependent on stocking. Hatcheries, however, will still continue to play a role in restoration of brook trout and lake sturgeon and hybrids such as splake. The recoveries of lake herring, siscowet, and lake whitefish are more noteworthy and in sharp contrast to the declining populations reported by Lawrie and Rahrar (1972). This suggests that past perturbations did not completely eliminate the reproductive and genetic potential for population increase. For siscowet and lake whitefish, reductions in sea lamprey predation and excessive fishing for prolonged periods were enough to result in restoration, whereas the case for lake herring is more complex given the intermittent recruitment over the last 20 years.

The future for Lake Superior appears to be brighter when compared with the other Great Lakes as the past 30 years is highlighted by recovery rather than by continued ecological disruption. For example, although certain Lake Michigan native fishes recovered after declines in alewife densities, certain invertebrates have declined and may be linked to continued exotic species invasions (Madenjian et al. 2002). Agencies on Lake Superior must now concentrate more on habitat protection and enhancement in nearshore and lotic areas and prevention of additional species introductions to further restore the fish community of Lake Superior.

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