THE STATE OF LAKE SUPERIOR IN 2005

Great Lakes Fishery Commission

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August 2010

THE STATE OF LAKE SUPERIOR IN 2005

Editors

Owen T. Gorman
U.S. Geological Survey—Lake Superior Biological Station
2800 Lakeshore Drive East
Ashland, WI 54806, USA

Mark P. Ebener
Chippewa Ottawa Resource Authority
179 West Three Mile Road
Sault Sainte Marie, MI 49783, USA

Mark R. Vinson
U.S. Geological Survey—Lake Superior Biological Station
2800 Lakeshore Drive East
Ashland, WI 54806, USA

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ABSTRACT

With the exception of the objective for sea lamprey (*Petromyzon marinus*), all fish-community objectives for Lake Superior were met or exceeded during the 2001-2005 reporting period. Because of recent conservation initiatives, there was no net loss of habitat during 2001-2005, and some degraded inshore habitats were restored or scheduled to be restored. As of 2005, targets for achieving reduced levels of most contaminants in fish flesh were met or exceeded. Fish assemblages in the **inshore zone**, defined as waters <15-m deep including wetlands, and tributaries, remained dominated by stable populations of native (indigenous) species. While the abundance of non-native (non-indigenous) fishes, such as ruffe (*Gymnocephalus cernua*), round goby (*Neogobius melanostomus*), and white perch (*Morone americana*), declined or remained stable and low, the abundance of the non-native threespine stickleback (*Gasterosteus aculeatus*) increased. The small area of Lake Superior's inshore zone likely means that it plays a minor role in system-wide energetics. Recent studies suggest that inshore habitats, despite their small relative size, may be critical to maintaining lakewide fish diversity, especially by providing spawning and nursery habitat for fishes inhabiting other zones. In the **nearshore zone**, defined as waters within the 15-80-m depth contour, prey-fish abundance remained low during 2001-2005 following declines that began in the late 1990s. Almost all of the lean lake trout (*Salvelinus namaycush*) populations within this zone were self-sustaining and at or near historical abundance levels during 2001-2005; however, growth, size at age, and biomass of lake trout all declined. Sea lamprey marking rates on lake trout were above the objective for the lake. The harvest of lake whitefish (*Coregonus clupeaformis*), a prominent species in the nearshore zone, during 2001-2005 was close to the historical highs of the late 1800s. Non-native salmon and trout played a relatively minor role in the nearshore zone during 2001-2005. Most populations of salmon and trout in the nearshore zone were self-sustaining and of socioeconomic importance to the sport fishery. With a population estimated at 26 million in 2005, siscowet lake trout remains the dominant predator in the **offshore zone** (waters >80-m deep) and in the lake. The offshore zone has important benthic and pelagic food webs that also contribute energy and nutrients to the nearshore zone. Energy transfer between pelagic and benthic habitats and nearshore and offshore habitats were found to occur daily, seasonally, and annually.

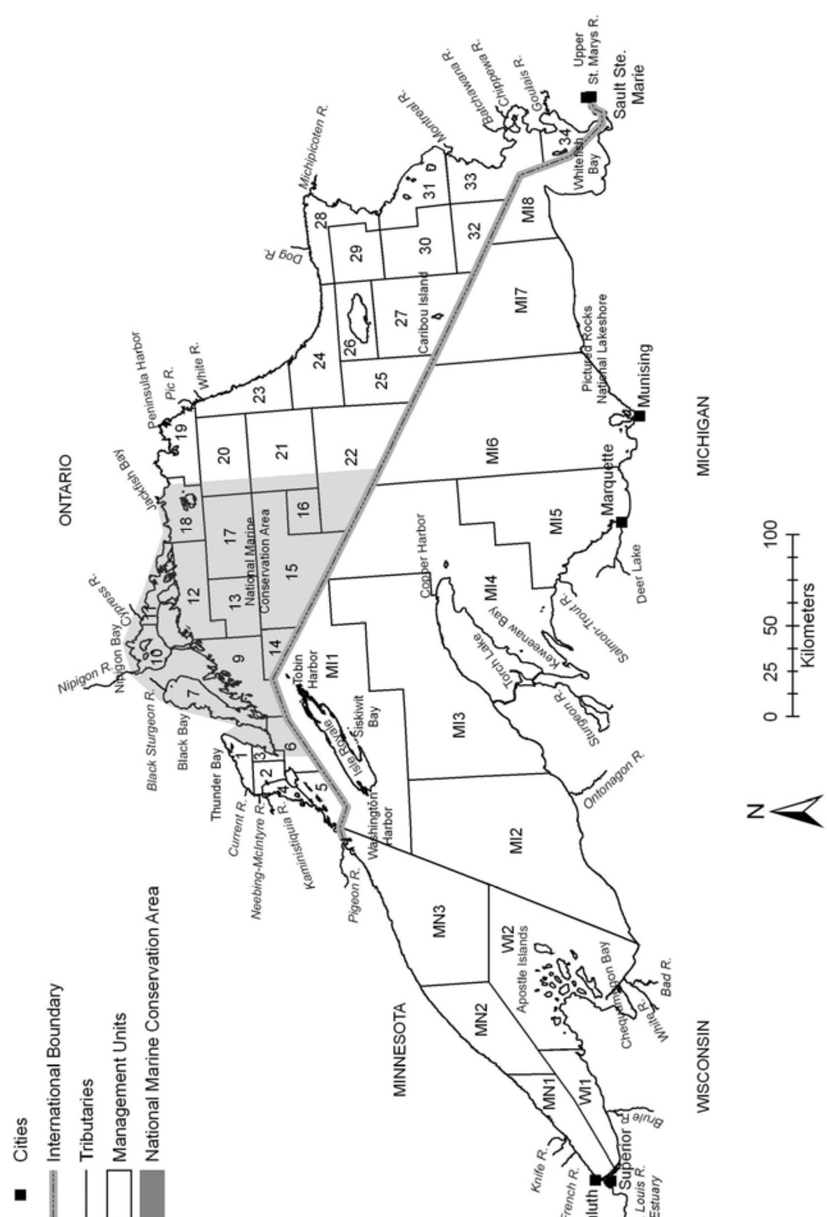
Our major recommendations are:

1. Increase lakewide assessment and development of models that estimate abundance of fish species by zone.
2. Standardize reporting with a goal of creating a shared database.
3. Focus research on the effects of global climate change, measurement of energy transfer among habitats, and interactions between native and non-native fishes.
4. Increase suppression of sea lamprey to achieve the target marking rate.

INTRODUCTION

This report assesses progress in achieving the fish-community objectives (FCOs) for Lake Superior (Horns et al. 2003) during 2001-2005 and the commitment of collaborating fishery-management agencies in achieving the goal “to rehabilitate and maintain a diverse, healthy, and self-regulating fish community, dominated by native species and supporting sustainable fisheries.” Pursuant to this goal, 11 FCOs were developed to guide protection and management of the following key resources: habitat, prey species, lake trout, lake whitefish, walleye, lake sturgeon, brook trout, non-native salmonines, sea lamprey, nuisance species, and species diversity (Horns et al. 2003). The Lake Superior basin, including agency management units and major tributaries, is presented in Fig. 1, and a list of common and scientific names of fishes mentioned in this report is presented in Table 1.

Fig. 1. The Lake Superior basin, including management units and major tributaries (italics).



Cities
International Boundary
Tributaries
Management Units
National Marine Conservation Area
ONTARIO
MINNESOTA
WISCONSIN
MICHIGAN
Duluth
Superior
Marquette
Munising
Sault Ste. Marie
Upper St. Marys R.
Thunder Bay
Black Bay
Nipigon Bay
Jackfish Bay
Peninsula Harbor
Whitefish Bay
Chequamegon Bay
Keweenaw Bay
Copper Harbor
Torch Lake
Deer Lake
Apostle Islands
Isle Royale
Tobin Harbor
Siskiwit Bay
Washington Harbor
Caribou Island
Pictured Rocks National Lakeshore
National Marine Conservation Area
St. Louis R. Estuary
French R.
Knife R.
Brule R.
Bad R.
White R.
Pigeon R.
Kaministiquia R.
Neebing-McIntyre R.
Current R.
Black Sturgeon R.
Nipigon R.
Cypress R.
Pic R.
White R.
Dog R.
Michipicoten R.
Montreal R.
Batchawana R.
Chippewa R.
Goulais R.
Sturgeon R.
Salmon-Trout R.
Ontonagon R.
MN1
MN2
MN3
WI1
WI2
MI1
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MI3
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MI5
MI6
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Table 1. Common and scientific names of fishes referenced in this report.

Common Name	Scientific Name
Native Species:	
bloater	*Coregonus hoyi*
brook stickleback	*Culaea inconstans*
brook trout	*Salvelinus fontinalis*
burbot	*Lota lota*
cisco (lake herring)	*Coregonus artedi*
deepwater cisco	*Coregonus* spp.
deepwater sculpin	*Myoxocephalus thompsoni*
kiyi	*Coregonus kiyi*
lake chub	*Couesius plumbeus*
lake sturgeon	*Acipenser fulvescens*
lake trout (lean, siscowet, humper)	*Salvelinus namaycush*
lake whitefish	*Coregonus clupeaformis*
longnose dace	*Rhinichthys cataractae*
longnose sucker	*Catostomus catostomus*
minnows	Cyprinidae
ninespine stickleback	*Pungitius pungitius*
northern pike	*Esox lucius*
pygmy whitefish	*Prosopium coulterii*
rock bass	*Ambloplites rupestris*
sculpins	Cottidae
shortjaw cisco	*Coregonus zenithicus*
slimy sculpin	*Cottus cognatus*
smallmouth bass	*Micropterus dolomieu*
spoonhead sculpin	*Cottus ricei*
spottail shiner	*Notropis hudsonius*

Table 1, continued.

Common Name	Scientific Name
suckers	Catostomidae
trout-perch	*Percopis omiscomaycus*
walleye	*Zander vitreus*
white sucker	*Catostomus commersoni*
yellow perch	*Perca flavescens*
Non-Native Species:	
alewife	*Alosa pseudoharengus*
brown trout	*Salmo trutta*
Chinook salmon	*Oncorhynchus tshawytscha*
coho salmon	*Oncorhynchus kisutch*
fourspine stickleback	*Apeltes quadracus*
Pacific salmon	*Oncorhynchus* spp.
pink salmon	*Oncorhynchus gorbuscha*
rainbow smelt	*Osmerus mordax*
rainbow/steelhead (trout)	*Oncorhynchus mykiss*
round goby	*Neogobius melanostomus*
ruffe	*Gymnocephalus cernua*
sea lamprey	*Petromyzon marinus*
splake	*Salvelinus fontinalis* x *S. namaycush*
threespine stickleback	*Gasterosteus aculeatus*
white perch	*Morone americana*

Previous state-of-the-lake reports (Hansen 1990; Hansen 1994; Ebener 2007) focused largely on important fish species and did not present status by depth zone. In this report, we distinguish inshore (0-15-m depth), nearshore (15-80-m depth), and offshore (>80-m depth) zones, describe the status of their resident fish communities, and address progress toward achieving the corresponding FCOs. Included in the inshore zone are coastal wetlands, embayments (natural bays, man-made harbors), and tributaries, including estuaries (subject to seiches) and reaches not subject to seiches. Approximately 7% of the surface area of Lake Superior is classified as inshore habitat, 16% as nearshore habitat, and 77% as offshore habitat. The rationale for this new organization was based on research since 2000 that confirmed the discreteness of trophic structure and fish communities within these zones. The research is summarized in this report and provides a framework for future research that will increase our understanding of the Lake Superior ecosystem.

HABITAT

Owen T. Gorman, John C. Brazner, Carri Lohse-Hanson, and Thomas C. Pratt

…achieve no net loss of the productive capacity of habitat supporting Lake Superior fishes; where feasible, restore habitats that have been degraded and have lost their capacity for fish production; reduce contaminants so that fish are safe to eat; and develop comprehensive and detailed inventories of fish habitats.

The above fish-community objective for habitat in Lake Superior (Horns et al. 2003) is based on the principle that healthy fish communities require abundant and diverse physical habitats and clean water. Resurgent interest in habitat identification, protection, and remediation, in combination with developing spatial-research tools, has provided an opportunity for substantial advances in understanding the function and importance of aquatic habitat basinwide.

O.T. Gorman.[1] U.S. Geological Survey—Lake Superior Biological Station, 2800 Lakeshore Drive East, Ashland, WI 54806, USA.

J.C. Brazner. U.S. Environmental Protection Agency, Mid-Continent Ecology Division, 6201 Congdon Boulevard, Duluth, MN 55804, USA.

C. Lohse-Hanson. Minnesota Pollution Control Agency, 520 Lafayette Road, St. Paul, MN 55155, USA.

T.C. Pratt. Fisheries and Oceans Canada, Great Lakes Laboratory for Fisheries and Aquatic Sciences, 1219 Queen Street East, Sault Sainte Marie, ON P6A 6W4, Canada.

[1]Corresponding author (e-mail: owen.gorman@usgs.gov).

Lake Superior is a deep, bathymetrically complex lake with an array of habitats ranging from coastal wetlands to a vast and perennially cold profundal zone. Horns et al. (2003) classified Lake Superior aquatic habitat into four zones: tributary reaches not subject to seiches, embayments (harbors, estuaries, and bays subject to seiches), nearshore (0-80-m deep), and offshore (>80-m deep). In this report, we utilize a slightly different zone classification that better reflects the structure of Lake Superior fish communities: inshore (<15-m deep), including tributaries, coastal wetlands, embayments (bays, harbors, and estuaries), as well as the open lakeshore within the 15-m depth contour; nearshore (15-80-m deep); and offshore (>80-m deep). Historically, most agency monitoring and research, as well as fishery harvest, has been focused on the nearshore zone. This zone encompasses ~16% of the surface area of Lake Superior, contains most of the known lean lake trout, cisco, and lake whitefish spawning grounds (Horns et al. 2003) and includes the depth range where lean lake trout is the dominant predator (Hansen 1999). The offshore zone encompasses ~77% of the lake's surface area and contains abundant populations of siscowet, deepwater ciscos, and deepwater sculpin and most of the lake's population of large adult cisco. Since 2000, exploratory surveys and research in this zone increased, providing a greater understanding of the Lake Superior ecosystem, including its fish community. Although the inshore zone represents only ~7% of the lake's surface area, it is the most diverse and contains important nursery and rearing habitat for most nearshore and some offshore fishes, including lean lake trout, burbot, cisco, lake whitefish, rainbow smelt, slimy sculpin, ninespine stickleback, and trout-perch (Wei et al. 2004; Gorman and Moore 2006). Moreover, many species remain in the inshore zone during all life stages (e.g., longnose dace, brook stickleback, rock bass, smallmouth bass, and brook trout) (Wei et al. 2004). The outer limit of the inshore zone (15 m) was established based on where the thermocline typically intersects the lake bed in late summer and represents lake habitat where the water column and the substrate are subject to substantial seasonal warming and cooling (Edsall and Charlton 1997).

The physical habitats of the Lake Superior ecosystem are less impacted by human activity than any of the other Great Lakes, but they are nevertheless subject to anthropogenic stressors that vary by habitat zone (Lake Superior Binational Program 2006b). The offshore zone is the least impacted habitat zone, and the number of stressors increases in a shoreward direction and with human population so that components of the inshore zone, particularly wetlands, embayments, and tributaries, in and adjacent to cities, are the most impacted. To address impacts of human activities in embayments, the U.S. and Canadian governments identified eight Areas of Concern (AOCs) and implemented Remedial Action Plans to restore these areas (Lake Superior Binational Program 2006b). The AOCs include Thunder Bay, Nipigon Bay, Jackfish Bay, Peninsula Harbour, St. Marys River, Deer Lake, Torch Lake, and the lower St. Louis River. In addition, environmental impairments affecting tributaries throughout the Lake Superior basin have been, or are being, identified by state and provincial natural-resource agencies as to the principal types of environmental impairment. Tributary remediation is being accomplished by implementing changes in land-use practices and by regular monitoring of stream habitat (Lake Superior Binational Program 2006b).

As in the other Great Lakes, Lake Superior has been subjected to long-term inputs of a broad array of contaminants. Discharge of major contaminants (mercury, polychlorinated biphenyls (PCBs), dioxin/hexachlorobenzene, carbonyl sulfide, and pesticides) have been reduced 60-80% from 1990 levels, and these reductions are on target for achieving zero discharge by 2020, as set by the Lake Superior Lakewide Management Program (Lake Superior LaMP Stage 2 1999). As a result, levels of most contaminants in fish have declined during 1999-2003, with the exception of the level of methyl mercury in lake trout (Hudson 2006). Given the substantial reduction in in-lake contaminant discharge and contaminant levels in fish, the rate of future reductions will likely slow as these chemicals reach equilibrium in the lake and in its aquatic life (Lake Superior Binational Program 2006b). Contaminants entering Lake Superior from outside the basin are problematic for implementing strategies to reduce future contaminant loadings as they are primarily atmospherically derived and cannot be controlled locally. Toxic chemicals with significant atmospheric input include mercury, toxaphene, and polybrominated diphenyl ethers (PBDEs). While levels of contaminants, such as mercury, PCBs, DDT, and dioxin, are declining in Lake Superior fish, trends are not as clear for toxaphene, and levels of PBDEs are increasing (Lake Superior Binational Program 2006a). Despite recent declines in contaminant levels in fish, the Canadian and U.S. governments continue to consider concentrations of mercury, dioxins/furans, PCBs, toxaphene, and chlordane in the flesh of certain Lake Superior fishes, particularly larger fish, high enough to warrant continuation of consumption advisories to protect human health.

Effects of global climate change appear to be already occurring in the Great Lakes (Kling et al. 2003). Particularly noticeable in Lake Superior is the trend toward shorter periods of ice cover and elevated summer water-surface temperatures since 1979 (Austin and Colman 2007). Climate change is predicted to have its greatest impact on the inshore zone through loss of wetland habitat and changes in lake temperature that are expected to negatively affect the fish community (Kling et al. 2003).

Efforts to protect and restore Lake Superior habitat since the last state-of-the-lake report in 2000 have occurred across the basin at many jurisdictional levels (Lake Superior Binational Program 2006b). Examples include establishment of the Lake Superior National Marine Conservation Area, protection of more than 5,000 acres of wetland habitat through the Lake Superior Coastal Wetland Initiative, development of a long-term coastal wetlands monitoring program by the Great Lakes Coastal Wetlands Consortium, and development of indicators that estimate both ecological condition and causes of degradation for Lake Superior coastal and wetland habitat via the Great Lakes Environmental Indicators research project (2001-2006). These restoration and protection initiatives have offset losses of inshore habitat due to anthropogenic impacts since 2000, and their continued implementation will ameliorate past and future losses. To aid in understanding relationships between fish communities, environmental variables, and anthropogenic stressors, spatially referenced data is being integrated into a basinwide Lake Superior Geographic Information System (Great Lakes Geographic Information System 2009).

Recommendations

1. Develop and implement lakewide monitoring and research programs that focus on the physical, chemical, and biological components of the inshore zone and associated wetlands, and determine their relationship to the nearshore and offshore zones.
2. Develop and implement research programs to address the effects of global warming on the Lake Superior ecosystem.
3. Continue to reduce within-basin sources of chemical contaminants. Locate the sources and explore the means to reduce input from atmosphere-borne contaminants.
4. Continue efforts to protect or restore aquatic habitats, particularly those in the inshore zone as they are most vulnerable to anthropogenic disturbance.

INSHORE FISH COMMUNITY: WALLEYE

Stephen T. Schram, Thomas C. Pratt, Michael J. Seider, and Patrick D. Furlong

Maintain, enhance, and rehabilitate self-sustaining populations of walleye and their habitat over their historical range.

One response to the above fish-community objective (FCO) for walleye (Horns et al. 2003) resulted in the making of a rehabilitation plan (Hoff 2002) outlining issues and strategies for achievement of the FCO. Although walleye is a top-level predator, due to habitat constraints, it is a small component of the overall Lake Superior fish community. Walleye is a cool-water species with an affinity for turbid water found only in the limited inshore waters of Lake Superior. Populations are primarily associated with those large bays and tributaries having suitable spawning and nursery habitat.

S.T. Schram. Wisconsin Department of Natural Resources, PO Box 589, 141 South Third Street, Bayfield, WI 54814, USA.

T.C. Pratt. Fisheries and Oceans Canada, Great Lakes Laboratory for Fisheries and Aquatic Sciences, 1219 Queen Street East, Sault Sainte Marie, ON P6A 6W4, Canada.

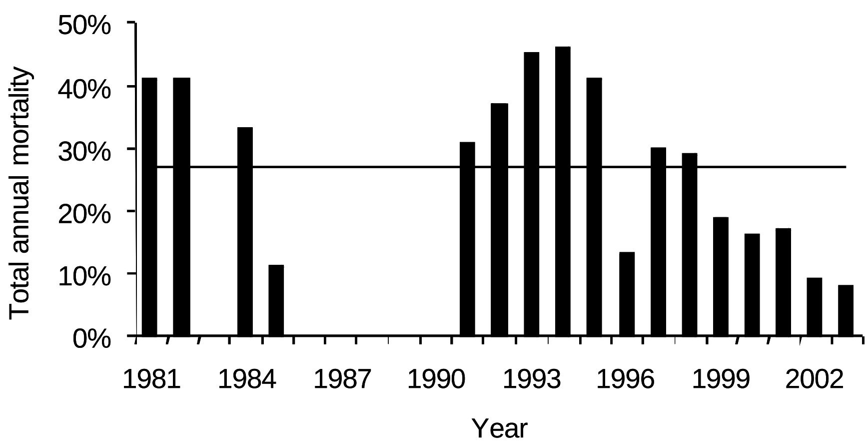
M.J. Seider.[2] Wisconsin Department of Natural Resources, PO Box 589, 141 South Third Street, Bayfield, WI 54814, USA.

P.D. Furlong. Ontario Ministry of Natural Resources. 435 James Street South, Suite 221e, Thunder Bay, ON P7E 6S8, Canada.

[2]Corresponding author (e-mail: stschram@charter.net).

During 2001-2005, most walleye populations were well below historical abundance levels. The St. Louis River walleye population is the only one at or near historical abundance mainly due to conservative regulations enacted following water-quality improvement (Schram et al. 1992). The St. Louis River population has been monitored for over two decades using stock-status indicators suggested by Colby et al. (1994). Highly variable recruitment, slow growth, and long-lived individuals characterize the St. Louis River walleye population. Mean length of age-10 fish (sexes combined) has remained relatively stable over the past 25 yr (MJS, unpublished data). Total annual mortality rates for the past 25 yr (Fig. 2) have generally been below the 45% rate recommended by the Lake Superior Technical Committee walleye subcommittee (Hoff 2002).

Fig. 2. Total annual mortality rates for the St. Louis River walleye population during 1981-2004. The horizontal line represents the mean annual mortality rate (27%) for the years sampled (1981-1982, 1984-1985, 1991-2004).



Other populations are found throughout the lake near spawning tributaries, bays, and estuaries and provide fishery harvest unless fishing closures are in effect. A number of these walleye populations are augmented by stocking and are highly regulated to restore the population and/or maintain a fishery. In Chequamegon Bay, Wisconsin, walleye is stocked sporadically, and harvest by the sport fishery is well regulated (5 fish•day^{-1} catch limit and 381-mm minimum length limit with only 1 fish >508 mm). As a consequence, the number of walleye >508 mm has increased, but stocking will be continued because recruitment appears to be limited (Schram et al. 2010). The increased abundance of larger walleye does not appear to be detrimental to the bay's fish community (Devine et al. 2005).

Within Canadian waters, Black Bay historically supported large commercial and sport walleye fisheries. Construction of the Black Sturgeon Dam in 1960 and a doubling of commercial walleye harvest following dam construction are believed to be the major factors responsible for the abrupt collapse of the walleye population in 1966. Since this collapse, few walleye have been reported in Black Bay, but a small population still exists in the river downstream from the dam. However, most of the suitable river spawning habitat was rendered inaccessible by the dam. Genetic comparison of samples collected in the bay prior to the collapse with samples collected from fish recently found in the Black Sturgeon River above and below the dam indicated a common origin (Wilson et al. 2007), suggesting the population has maintained its genetic identity despite the collapse. An assessment of these results suggests that the Black Sturgeon dam was a major factor in the collapse of the Black Bay population and especially in its failure to recover over the past 40 yr. However, having the original genetic diversity still present is a strong reason for developing a rehabilitation strategy for the Black Bay population, because spawning and nursery habitats are virtually unchanged—the problem is one of allowing spawning fish passage above the dam.

In fact, in 2005, the Ontario Ministry of Natural Resources developed a management plan for rehabilitation of the Black Bay population (Furlong et al. 2006). Removal of the dam on the Black Sturgeon River would allow spawning walleye to ascend to historical spawning grounds and potentially rehabilitate the population to historical levels without the need for additional management efforts. However, dam removal would also allow sea lamprey unrestricted access to the headwaters of the Black Sturgeon River. A 2006 telemetry study found that walleye and sea lamprey ascend the river at the same time during their spring spawning migrations (L. O'Connor, Fisheries and Oceans Canada, personal communication, 2006), thus complicating rehabilitation plans for walleye and control plans for sea lamprey. If a methodology could be developed that would allow walleye upstream access but stop sea lamprey, it would be beneficial for management of fish communities throughout the Great Lakes. To protect the remnant walleye stock, an angling closure has been implemented in Black Bay and the lower Black Sturgeon River. An assessment of walleye mortality in the Black Bay yellow perch gillnet fishery is also under way to determine commercial bycatch.

INSHORE FISH COMMUNITY: LAKE STURGEON

Henry R. Quinlan, Thomas C. Pratt, Michael J. Friday, Stephen T. Schram, Michael J. Seider, and William P. Mattes

Rehabilitate and maintain spawning populations of lake sturgeon that are self-sustaining throughout their native range.

The above fish-community objective (Horns et al. 2003) reflects efforts by fishery agencies since the 1980s to restore lake sturgeon populations (Auer 1996; Schram et al. 1999). These efforts have culminated in the consolidation of restoration goals and strategies into a restoration plan (Auer 2003). Specific criteria used to describe a self-sustaining population in the plan include: a minimum of 1,500 mature adults using a common tributary for spawning, a near-equal sex ratio in the nonspawning population, 20 or more year-classes of adult fish, annual reproduction evidenced by collection of viable eggs, and measurable recruitment of fish ages 0-5 (Auer 2003).

H.R. Quinlan.[3] U.S. Fish and Wildlife Service, Ashland Fish and Wildlife Conservation Office, 2800 Lake Shore Drive East, Ashland, WI 54806, USA.

T.C. Pratt. Fisheries and Oceans Canada, Great Lakes Laboratory for Fisheries and Aquatic Sciences, 1219 Queen Street East, Sault Sainte Marie, ON P6A 6W4, Canada.

M.J. Friday. Ontario Ministry of Natural Resources, Upper Great Lakes Management Unit, 435 James Street South, Suite 221e, Thunder Bay, ON P7E 6S8, Canada

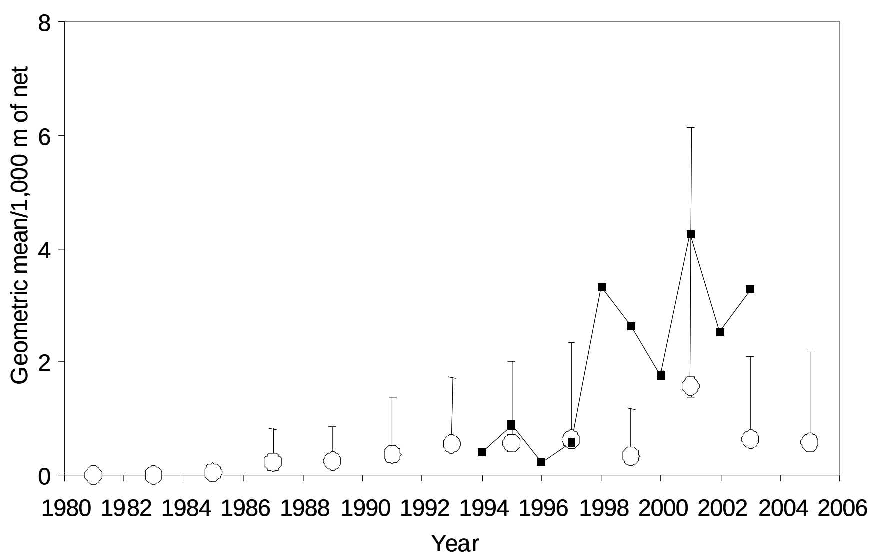
S.T. Schram and M.J. Seider. Wisconsin Department of Natural Resources, PO Box 589, 141 South Third Street, Bayfield, WI 54814, USA.

W.P. Mattes. Great Lakes Indian Fish and Wildlife Commission, 72682 Maple Street, Odanah, WI 54861, USA.

[3]Corresponding author (e-mail: henry_quinlan@fws.gov).

Good progress toward lake sturgeon rehabilitation has been made since last reported in the 2000 state-of-the-lake report (Quinlan 2007). Abundance is increasing along the south shore of Lake Superior owing to natural reproduction and stocking (Fig. 3; Schram et al. 1999; Auer and Baker 2007; WPM, unpublished data). Hydroacoustic surveys of spawning fish in the Sturgeon River, Michigan, and age structure analysis of fish in the Bad River, Wisconsin, showed that these populations meet rehabilitation criteria for self-sustaining populations (Auer and Baker 2007; HRQ, unpublished data).

Fig. 3. Abundance (bar = 95% CI) of adult lake sturgeon (open circles) in western Wisconsin waters during 1981-2005 based on gillnet surveys by the Wisconsin Department of Natural Resources and abundance of juvenile lake sturgeon near the mouth of the Bad River, Wisconsin, (closed squares) during 1994-2003 based on gillnet surveys by the Great Lakes Indian Fish and Wildlife Commission.



Initial surveys to assess the status of lake sturgeon spawning runs in the Pic, White, Michipicoten, Batchawana, Chippewa, Black Sturgeon and Goulais Rivers in Ontario; the Pigeon River at the Minnesota/Ontario border; and the White River in Wisconsin during 2001-2005 indicated that most runs were very small. The largest spawning runs were in the Pic, Black Sturgeon and White (Wisconsin) Rivers, and abundance was estimated at fewer than 200 individuals (Friday 2004; Fisheries and Oceans Canada 2008; HRQ, unpublished data). Initial site surveys in inshore (embayments) and nearshore waters included Pigeon Bay, Minnesota, (2005) off the mouth of the Ontonagon River, Michigan, (2005), and in Keweenaw Bay, Michigan, (2004-2005). Sub-adult lake sturgeon (>599 but <1,000-mm total length) were captured in Pigeon Bay, stocked juveniles were collected off the mouth of the Ontonagon River, and sub-adults and adults were found in Keweenaw Bay (G. Mensch, unpublished data; HRQ, unpublished data; S. Moore, Grand Portage Band of Chippewa Indians, personal communication, 2006).

Progress has been made in addressing some of the recommendations from the previous state-of-the-lake report (Quinlan 2007). Substrate type, quantity, and water depth were mapped using hydroacoustics in the Kaministiquia River, Ontario (Biberhofer and Prokopec 2005), and Bad River, Wisconsin (Cholwek et al. 2005), in support of studies of nursery and juvenile habitat preferences. Habitat preference of stocked sturgeon is being studied in the Ontonagon River, Michigan, and the St. Louis River, Minnesota, using radio telemetry (Fillmore 2003). A multi-year study was initiated in the Kaministiquia River to examine lake sturgeon spawning migrations and reproductive success while flow conditions were controlled in sections historically used for spawning. Minimum flows necessary for adult spawning migrations upstream and larval drift downstream on the Kaministiquia River have been estimated at 23 and 17 $m^3 \bullet s^{-1}$, respectively (Friday 2005, 2006). Population genetic structure has been described for all extant spawning populations, and these studies suggest that Lake Superior populations retain high genetic diversity and are significantly different from other Great Lake populations (Welsh et al. 2008).

Despite decades of progress toward restoration of lake sturgeon in Lake Superior, abundance remains reduced from historical levels. Spawning populations are still absent from 13 of 22 tributaries historically used for spawning. Only two of the nine tributaries with spawning populations currently meet rehabilitation criteria. Available evidence suggests that spawning no longer occurs in the Michipicoten River, Ontario, likely resulting from changes in hydropower operations (TCP, unpublished data).

Recommendations

1. Attempt to re-establish populations in those tributaries that no longer support spawning populations meeting rehabilitation objectives.
2. Quantify the amounts of spawning and nursery habitat in those tributaries currently containing populations that meet rehabilitation objectives so as to enable development of a quantitative habitat objective for lake sturgeon.
3. Establish standardized surveys for monitoring the relative abundance and life-history status of every population.
4. Minimize and mitigate the impact of hydropower operations on lake sturgeon populations.
5. Establish harvest regulations that will protect all extant populations from overharvest.

INSHORE FISH COMMUNITY: BROOK TROUT

Henry R. Quinlan, Marilee Chase, and Thomas C. Pratt

…maintain widely distributed, self-sustaining populations in as many of the historical habitats as is practical.

Prior to European settlement, migratory and lake dwelling (coaster) brook trout were associated with at least 118 tributary streams in Lake Superior, but, since that time, most of these populations have been extirpated (Newman et al. 2003). In an effort to restore some or all of these coaster populations, a lakewide rehabilitation plan was prepared (Newman et al. 2003) and the above fish-community objective (FCO) was developed (Horns et al. 2003). Presently, coaster brook trout remain rare and restricted geographically in Lake Superior. Self-sustaining populations are present in at least eight tributaries to Nipigon Bay and the Nipigon River, Ontario; in the Salmon Trout River, Michigan; and in Washington and Tobin Harbors and Siskiwit Bay, Isle Royale, Michigan (Fig. 1). From 2001 to 2005, coaster abundance increased in the Nipigon River, tributaries to Nipigon Bay, and Siskiwit Bay, was stable or decreasing in Tobin Harbor, and was highly variable in the Salmon Trout River (Fig. 4).

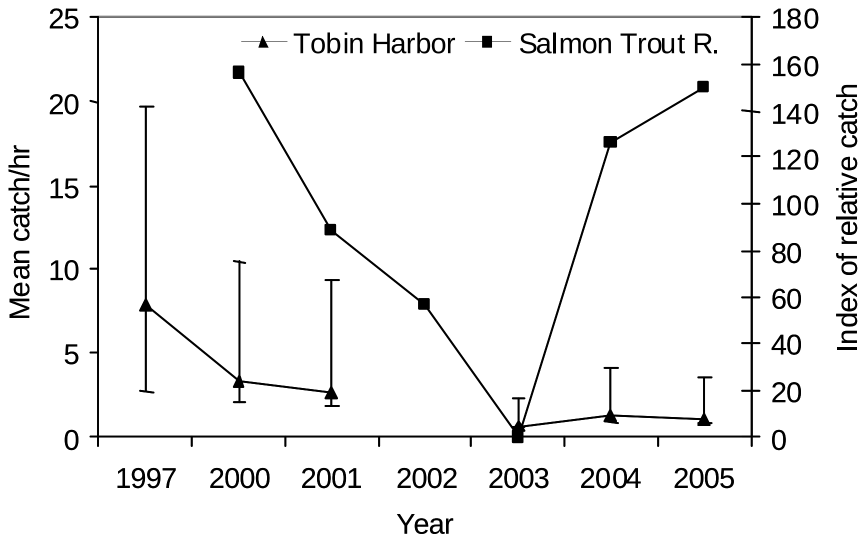
H.R. Quinlan.[4] U.S. Fish and Wildlife Service, Ashland National Fish and Wildlife Conservation Office, 2800 Lake Shore Drive East, Ashland, WI 54806, USA.

M. Chase. Ontario Ministry of Natural Resources, Upper Great Lakes Management Unit, 435 James Street South, Suite 221e, Thunder Bay, ON P7E 6S8, Canada.

T.C. Pratt. Fisheries and Oceans Canada, Great Lakes Laboratory for Fisheries and Aquatic Sciences, 1219 Queen Street East, Sault Sainte Marie, ON P6A 6W4, Canada.

[4]Corresponding author (e-mail: henry_quinlan@fws.gov).

Fig. 4. Mean (bar = 95% CI) catch of coaster brook trout by boat electrofishing in Tobin Harbor, Isle Royale, Michigan (HRQ, unpublished data) and index of relative catch of adfluvial brook trout (>30 cm) in the Salmon Trout River, Marquette County, Michigan (Huckins and Baker 2008).



Stocking programs and harvest regulations continue to be used to establish and protect populations and to increase the geographic distribution of coaster brook trout in Lake Superior. During 2001-2005, nearly 2.2 million Lake Superior basin-strain brook trout were stocked in lake tributaries accessible to migratory fish. Restrictive harvest regulations have been implemented for Lake Superior waters by U.S. states and the Province of Ontario, and "catch and release only" sport-fishing regulations were established by the U.S. National Park Service and Michigan Department of Natural Resources and Environment for waters in and around Isle Royale National Park. Restrictive harvest regulations are in effect on all Minnesota and Ontario tributaries and on selected Michigan and Wisconsin tributaries. In the Nipigon Bay area, creel-survey data showed that brook trout catch-per-unit effort (CPUE) was significantly higher in 2003 compared to the mid-1990s, but, due to restrictive regulations, harvest rates declined over the same time period

(Houle 2004). Conservative harvest regulations, completion of water- and forest-management plans, creation of spawning refuges, and public outreach are key components to the resurgence of coaster populations in this area.

Studies conducted in several areas of Lake Superior detected movement of brook trout in and out of tributary streams (Carlson 2003; Stimmell 2006; Pratt et al. 2006; Mucha and Mackereth 2008) and their extensive use of shallow (<7-m deep) inshore waters (Mucha and Mackereth 2008; Gorman et al. 2008a). In the Nipigon Bay area, the size and age structure of fish moving to the lake did not differ from those remaining in the stream, and individual fish were tracked moving into multiple tributary streams (Pratt et al. 2006; D'Amelio et al. 2008). The presence of coaster brook trout in Pictured Rocks National Lakeshore streams resulted in the postponement of stocking Isle Royale-strain fish in 2005, pending additional assessment and genetic analysis of stream-resident fish (L. Loope, Pictured Rocks National Lakeshore, personal communication, 2006). Genetic research on Lake Superior brook trout indicated the presence of at least five regional metapopulations, with Isle Royale and Nipigon Bay being distinct populations despite their geographic proximity (Wilson et al. 2005; Scribner et al. 2006).

In addition to the lakewide rehabilitation plan and FCO (Horns et al. 2003; Newman et al. 2003), much new collaborative research, planning, and field work has been done to promote coaster brook trout recovery. A workshop to synthesize information on the restoration of coaster brook trout in Lake Superior was held in October 2003 (Schreiner et al. 2004). In Ontario, a brook trout committee was formed to implement components of the lakewide rehabilitation plan (Ontario Ministry of Natural Resources 2004). More local management and rehabilitation plans have been developed for Wisconsin (Wisconsin Department of Natural Resources and U.S. Fish and Wildlife Service 2005) and Minnesota waters (Schreiner et al. 2006).

Recommendations

1. Develop and implement routine assessments and standardized reporting.
2. Conduct outreach for Native American subsistence fishers to inform them about rehabilitation efforts and to gather additional information on coasters.
3. Assess the impact of non-native salmonids on rehabilitation of brook trout.

INSHORE FISH COMMUNITY: ECOLOGICAL INTERACTIONS

Thomas C. Pratt, Henry R. Quinlan, Gary D. Czypinski, Stephen T. Schram, and Owen T. Gorman

A self-sustaining assemblage of prey dominated by indigenous species at population levels capable of supporting desired populations of predators and a managed commercial fishery.

…prevent the introduction of any non-indigenous aquatic species that is not currently established in Lake Superior; 2) prevent or delay the spread of non-indigenous nuisance species, where feasible; and 3) eliminate or reduce populations of non-indigenous nuisance species, where feasible.

…protect and sustain the diverse community of indigenous fish species not specifically mentioned earlier (burbot, minnows, yellow perch, northern pike, and suckers). These species add to the richness of the fish community and should be recognized for their ecological importance and cultural, social, and economic value.

T.C. Pratt.[5] Fisheries and Oceans Canada, Great Lakes Laboratory for Fisheries and Aquatic Sciences, 1219 Queen Street East, Sault Sainte Marie, ON P6A 2E5, Canada.

H.R. Quinlan and G.D. Czypinski. U.S. Fish and Wildlife Service, Ashland Fish and Wildlife Conservation Office, 2800 Lake Shore Drive East, Ashland, WI 54806, USA.

S.T. Schram. Wisconsin Department of Natural Resources, PO Box 589, 141 South Third Street, Bayfield, WI 54814, USA.

O.T. Gorman. U.S. Geological Survey—Lake Superior Biological Station, 2800 Lakeshore Drive East, Ashland, WI 54806, USA.

[5]Corresponding author (e-mail: thomas.pratt@dfo-mpo.gc.ca).

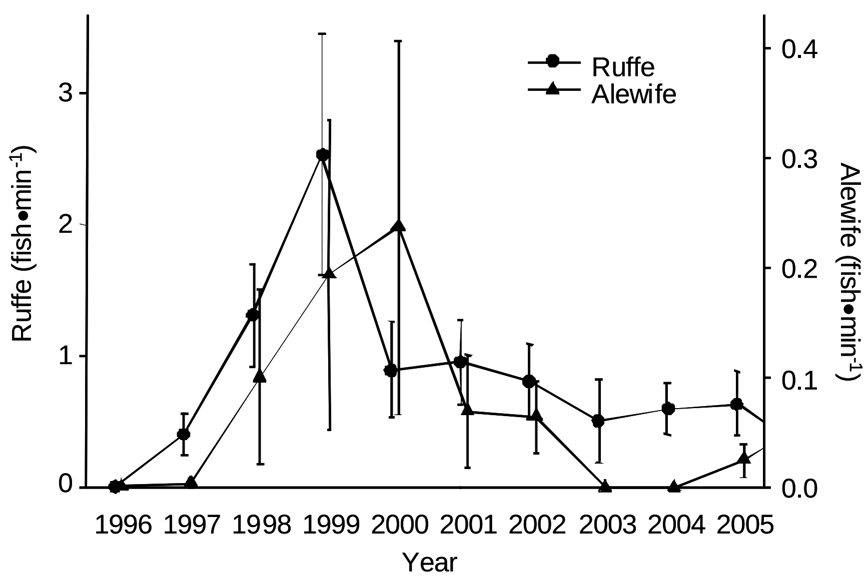
The above three fish-community objectives (Horns et al. 2003) apply to the inshore waters of Lake Superior, which includes nearly all the lake's degraded habitats owing to alterations associated with settlement of the drainage (Bronte et al. 2003). More specifically, the inshore zone is defined as lake waters ≤15 m in depth and comprises approximately 7% of the surface area of the lake, including open shoreline and embayments, coastal wetlands, tributary estuaries (reaches subject to seiches), and upstream tributary reaches not subject to seiches. Rehabilitation plans for three of the most economically and socially important inshore species—walleye, lake sturgeon, and brook trout—all identify habitat impairment as an important contributor to their population declines and an important impediment to population recovery (Hoff 2002; Auer 2003; Newman et al. 2003).

Principal Species and Assemblages

Fish-community assemblages in inshore areas include a mix of warm-water, cool-water, and cold-water species (Hoff and Bronte 1999). In embayment and tributary areas of the inshore zone, important piscivores include walleye, lake trout, northern pike, and smallmouth bass; key omnivores include brook trout, white sucker, and yellow perch; while important algivores and insectivores are juvenile yellow perch, log perch, johnny darter, rainbow smelt, trout-perch, and various Cyprinidae (i.e., spottail shiner, mimic shiner, emerald shiner) (Ogle et al. 1996; Bronte et al. 1998; Hoff and Bronte 1999; Devine et al. 2005). Inshore areas along the open lake (coastal shoreline) have simpler assemblages that include some of the same species. Burbot is the top predator, white sucker is the most abundant omnivore, and slimy sculpin, ninespine stickleback, trout-perch, and lake chub are the most widespread primary and secondary consumers (Gorman and Moore 2006; Gorman et al. 2008a). Additional species of economic and ecological importance to inshore habitats include lake trout, brook trout, rainbow trout, rainbow smelt, and lake whitefish (Keough et al. 1996; Bronte et al. 1998; Devine et al. 2005; Gorman et al. 2008a), but, of these, only brook trout is considered to be a year-round resident. Overall, most fish species found in the inshore zone complete their entire life cycle there.

Non-native fishes are found primarily in Lake Superior's inshore zone (Bronte et al. 2003). The establishment of ruffe, a Eurasian percid, in some areas of western Lake Superior during the 1990s was a serious concern to management agencies. However, abundance of ruffe and most other non-native fishes (alewife, fourspine stickleback, and white perch) has either declined or remained stable during this reporting period (2001-2005)—the only exception being an increased abundance of threepine stickleback (Fig. 5). Survey data from three different assessments indicate that fish-community structure in embayment habitats of the inshore zone has remained relatively stable and that native species continue to predominate in inshore habitats (Figs. 5, 6; Table 2).

Fig. 5. Relative abundance of five non-native fishes based on catch-per-unit effort fish•min^{-1}) at bottom-trawling stations in inshore areas of Lake Superior during 1996-2005. Data were collected as part of the U.S. Fish and Wildlife Service's ruffe surveillance program and by Fisheries and Oceans Canada.



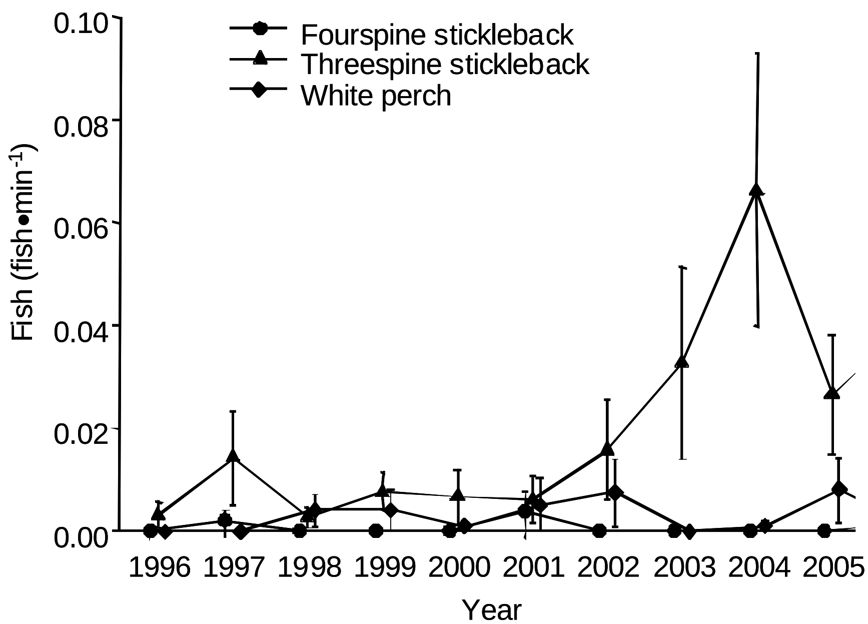
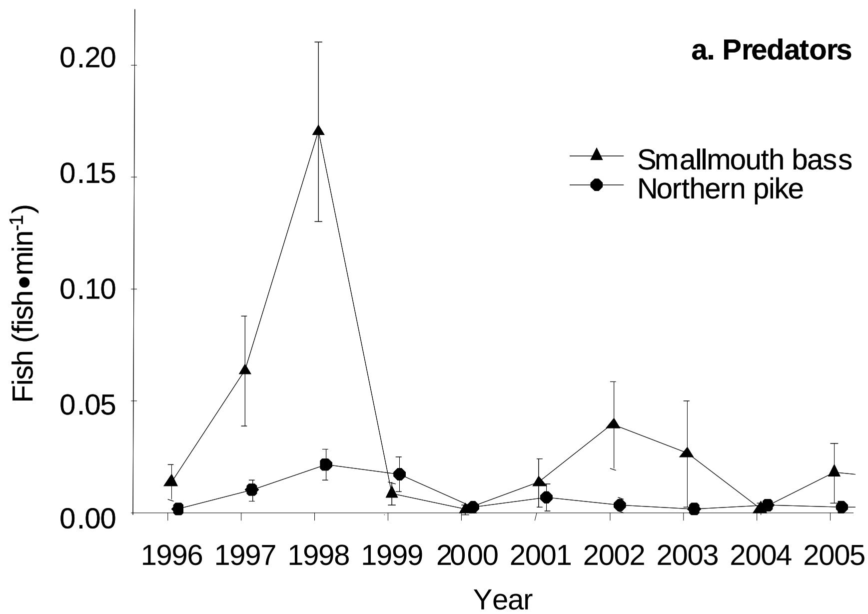

Fourspine stickleback
Threespine stickleback
White perch
Fish (fish•min-1)
0.10
0.08
0.06
0.04
0.02
0.00
1996 1997 1998 1999 2000 2001 2002 2003 2004 2005
Year

Fig. 6. Relative abundance of important inshore (native) predators (a) and prey fish (b) based on catch-per-unit effort (fish•min^{-1}) at bottom-trawling stations along the south shore of Lake Superior, 1996-2005. Data were collected as part of the U.S. Fish and Wildlife Service's ruffe surveillance program.



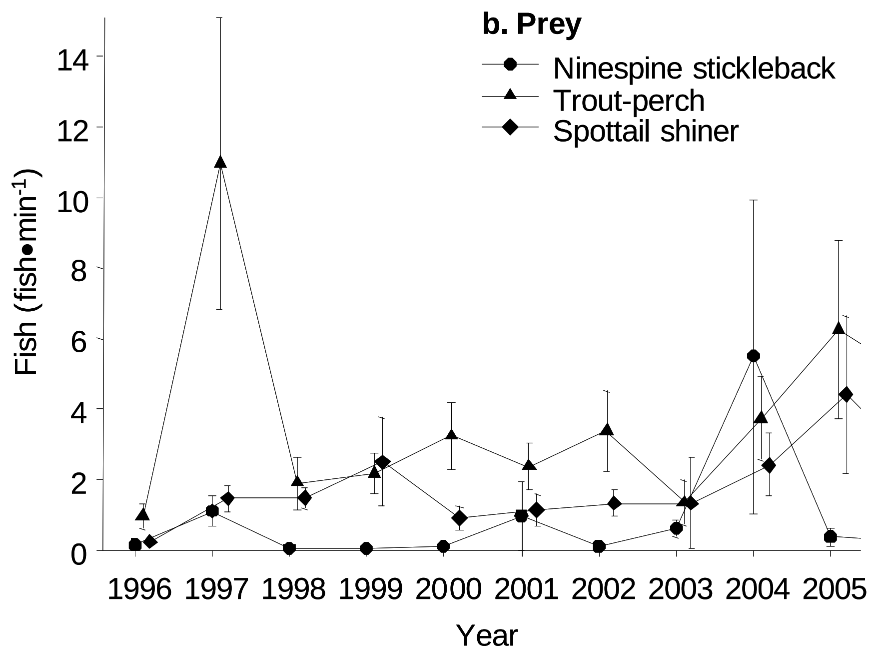

b. Prey
Ninespine stickleback
Trout-perch
Spottail shiner
Fish (fish•min-1)
0
2
4
6
8
10
12
14
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
Year

Table 2. Native species diversity (Shannon-Weiner index, H') and evenness (probability of interspecific encounter (PIE)) in areas of the Lake Superior inshore habitat zone during 1996-2005. PIE is a measurement of the chance that two individuals drawn at random from a population represent different species (Hurlbert 1971). Data from U.S. Fish and Wildlife Service ruffe surveillance bottom-trawl program (trawl), Wisconsin Department of Natural Resources St. Louis River seining (seine), and Minnesota Department of Natural Resources St. Louis River gillnetting (gillnet).

	Trawl		**Seine**		**Gillnet**	
Year	H'	**PIE**	H'	**PIE**	H'	**PIE**
1996	0.96	0.50	1.43	0.74	1.74	0.84
1997	0.95	0.46	1.53	0.74		
1998	1.15	0.58	1.56	0.74	1.84	0.89
1999	1.07	0.53	0.98	0.46		
2000	0.95	0.49	1.22	0.64	1.79	0.82
2001	0.97	0.48	1.51	0.67		
2002	1.05	0.49	1.48	0.65	1.84	0.84
2003	0.76	0.42	1.48	0.62	1.58	0.83
2004	1.04	0.53	2.15	0.87	1.63	0.75
2005	1.22	0.58	2.03	0.85	1.86	0.88

Lake Superior has the highest ratio of non-native to native fish species (24%) of all the Laurentian Great Lakes (Mills et al. 1993), yet it is the least impacted by non-native species (Grigorovich et al. 2003). Low temperatures and productivity have likely reduced the reproductive rate and subsequent spread of non-native species. Inshore habitats are the most susceptible to invasion and contain a number of well-established populations of non-native fishes. Although no new fishes have established in Lake Superior during the 2001-2005 reporting period, the previously established ruffe and round goby have expanded their range (less so for the round goby) along Lake Superior's south shore (GDC, unpublished data), and five additional non-native invertebrates (*Sphaerium corneum*, *Pisidium amnicum*, *P.*

moitessierianum, *Potamopyrgus antipodarum*, and *Echinogammarus ischnus*) previously established in the lower Great Lakes were recently found in Lake Superior (Grigorovich et al. 2003). Two Chinese mitten crabs (*Eriocheir sinensis*) were also captured in Thunder Bay Harbour: one in September 2005 and one in October 2006 (Veilleux and de Lafontaine 2007). Whether non-native species have negatively impacted native species in the inshore zone has not been conclusively determined (Ogle et al. 1996; Bronte et al. 1998), but all reasonable efforts should be made to eliminate future introductions.

Diet, Food Webs, and Habitat Coupling

A recent survey of predator diets in Chequamegon Bay identified the rainbow smelt, a non-native species, as the dominant prey for walleye and lake trout, whereas ninespine stickleback, trout-perch, and various cyprinids and sculpins were important prey for burbot, smallmouth bass, and northern pike (Devine et al. 2005). Predator diets in the St Louis River estuary were similar, except that yellow perch was more important and rainbow smelt less important (Ogle et al. 1996; Mayo et al. 1998).

The movements of Lake Superior fishes and the associated impacts of this movement on trophic structure and energy transfer in nearshore and offshore habitats is becoming better understood (Hrabik et al. 2006a; Jensen et al. 2006), but comparable insights for inshore habitats have been primarily limited to lower trophic levels (Sierszen et al. 2006b). In general, the interchange in nutrients and biological interactions between inshore and more-open-water habitats can be important, even in large lakes, and littoral-zone benthic production is an important energy source to whole-lake food webs (Hobson and Welch 1995; Vadeboncoeur and Steinman 2002; Vadeboncoeur et al. 2002).

Stable isotopes show that inshore benthic foodwebs are supported by benthic algae, unlike nearshore and offshore habitats where isotopic analysis suggests phytoplankton are the primary basal energy source for benthic foodwebs (Strand 2005; Sierszen et al. 2006a). In contrast, Lake Superior wetlands derive their carbon from both phytoplankton and benthic sources (Keough et al. 1996; Brazner et al. 2004a, 2004b; Sierszen et al. 2006b). Important trophic connections between wetland and embayment areas have been identified recently (Sierszen et al. 2006b), and tributaries, wetlands, and inshore areas expressed distinguishable isotopic patterns, suggesting that each is energetically distinct (Keough et al. 1996; Strand 2005).

Isotopic patterns of inshore fish assemblages suggest energy transfer between inshore embayments and the nearshore zone. Fishes, such as rainbow smelt, use inshore embayment areas as nursery habitat before shifting to nearshore habitats as adults (Keough et al. 1996). Isotopic signatures also indicate that fish move between coastal wetlands and the nearshore zone to feed (Sierszen et al. 2006b; M. Sierszen, U.S. Environmental Protection Agency, personal communication, 2006). Although the small area of Lake Superior's inshore zone likely means that it plays a minor role in system-wide energetics (Keough et al. 1996; Strand 2005), it is critical for maintaining lakewide fish diversity and production because many species are restricted to this habitat, and it provides spawning and nursery habitat for species such as rainbow smelt and cisco.

Future Directions

Despite increased knowledge of the function and status of the inshore aquatic ecosystem over the last few years, the inshore zone remains one of the least studied habitats of the lake, especially that portion along the open shoreline of the lake proper (see Gorman and Moore 2006; Gorman et al. 2008a). Because the inshore zone is critical in supporting early life stages of native fishes that live primarily in nearshore and offshore zones, the presence and expanding range of non-native species in this zone should be viewed as alarming and prompt further study.

Recommendations

1. Develop and implement a program to assess fish populations in the inshore zone.
2. Determine inshore food webs and linkages between inshore, nearshore, and offshore habitat zones.
3. Determine interactions between native and non-native fishes.
4. Continue efforts to protect and restore habitats in the inshore zone, especially in tributaries.

NEARSHORE FISH COMMUNITY: PREY FISHES

Daniel L. Yule, Jason D. Stockwell, Owen T. Gorman, and Thomas C. Pratt

A self-sustaining assemblage of prey dominated by indigenous species at population levels capable of supporting desired populations of predators and a managed commercial fishery.

In this chapter, we report on achievement of the above fish-community objective (Horns et al. 2003) by evaluating the status and trends of a sub-set of nearshore prey species (cisco, bloater, rainbow smelt, slimy sculpin, spoonhead sculpin, ninespine stickleback and pygmy whitefish) using results from a 29-yr bottom-trawl survey. Also, we summarize some recent studies evaluating the effectiveness of this survey and discuss recent efforts to evaluate the impacts of commercial roe fisheries on cisco.

D.L. Yule.[6] U.S. Geological Survey—Lake Superior Biological Station, 2800 Lakeshore Drive East, Ashland, WI 54806, USA.

J.D. Stockwell. Gulf of Maine Research Institute, 350 Commercial Street, Portland, ME 04101, USA.

O.T. Gorman. U.S. Geological Survey—Lake Superior Biological Station, 2800 Lakeshore Drive East, Ashland, WI 54806, USA.

T.C. Pratt. Fisheries and Oceans Canada, Great Lakes Laboratory for Fisheries and Aquatic Sciences, 1219 Queen Street East, Sault Sainte Marie, ON P6A 6W4, Canada.

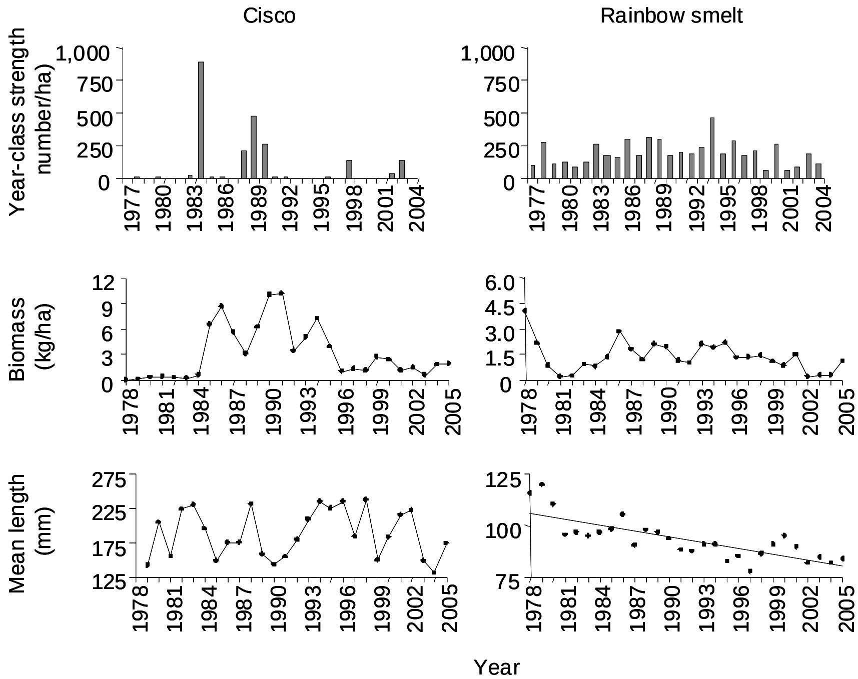
[6]Corresponding author (e-mail: dyule@usgs.gov).

Most data in this report were from the annual May-June daytime bottom-trawl survey conducted annually in 15-80-m depths in U.S. (since 1978) and Canadian (since 1989) waters by the U.S. Geological Survey—Great Lake Science Center (USGS—GLSC) (Stockwell et al. 2007). For this report, we assume that the annual bottom-trawl survey provides a measure of the relative density and biomass of prey species (not absolute estimates) over time. Year-class strength (number of yearlings•ha^{-1}) is reported for rainbow smelt and cisco only, whereas biomass (kg•ha^{-1}) and mean total length (mm) are reported for all of the principal forage species. Least-squares linear regression lines were fitted to plots of mean total length to determine the presence (slopes significantly different from zero) or absence of trends.

Cisco

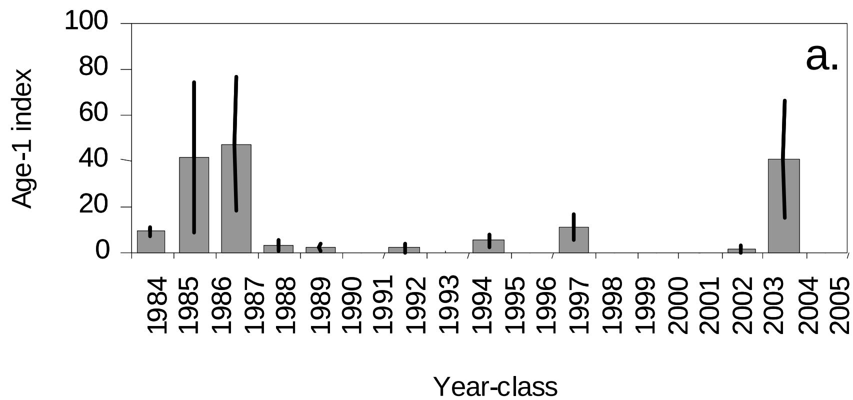
The annual bottom-trawl catch of yearling cisco indicates that strong year-classes occurred in 1984, 1988, 1989, 1990, 1998, and 2003 (Fig. 7). In the years after these strong year-classes were produced, the trawl-estimated biomass increased for a short time (2-3 yr) and then gradually decreased (Fig. 7). This decrease was likely due to the dominant year-class becoming pelagic after age 5 and, thus, unavailable to bottom trawls (Stockwell et al. 2007). Therefore, the biomass presented in Fig. 7 is that of juvenile cisco (ages 1-5), and this biomass has been low since 1994 due to fewer strong year-classes being produced after 1990.

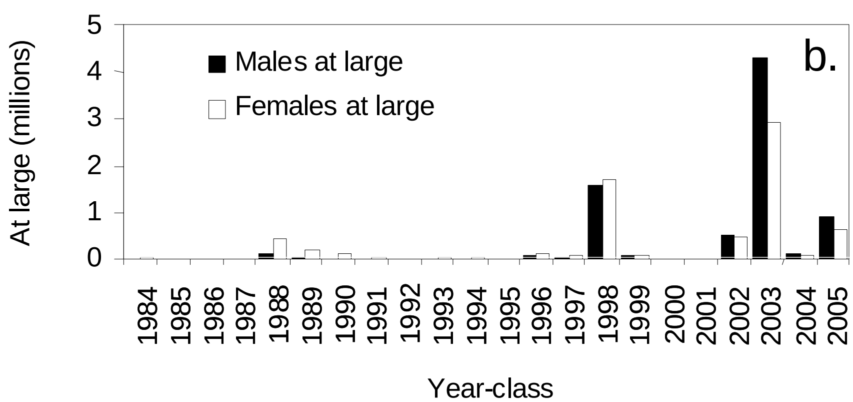
Fig. 7. Year-class strength, estimated biomass, and mean total length of cisco and rainbow smelt based on fish captured in the annual U.S. Geological Survey—Great Lakes Science Center bottom-trawl survey of the Lake Superior fish community, 1978-2005. Year-class strength was measured as the density (number•ha^{-1}) of age-1 fish. The trend line for rainbow smelt mean length was fit by least-squares linear regression.

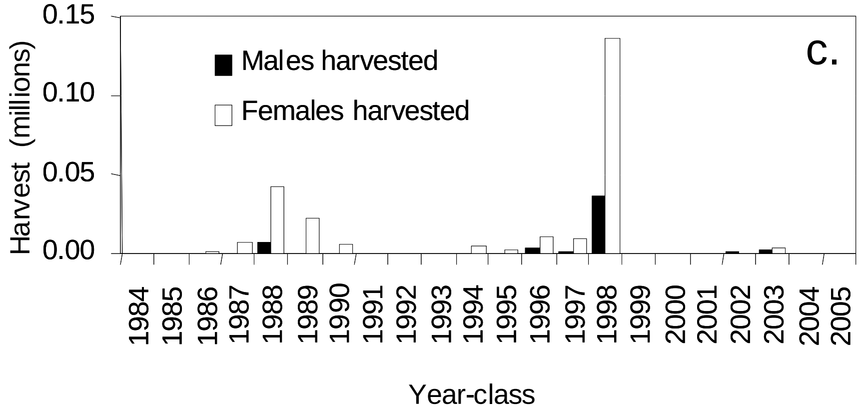


Most cisco are commercially harvested for their roe during November when the fish form prespawning aggregations in nearshore waters. Determining the sustainability of cisco roe fisheries has been identified as a high research priority by the Lake Superior Technical Committee (Great Lakes Fishery Commission 2006). Hrabik et al. (2006b) conducted acoustic and mid-water-trawl surveys in Minnesota waters during the summers of 2003 and 2004 and estimated biomass of spawning-size cisco (>305 mm) at 4.3 kg•ha^{-1} during 2003 and 11.0 kg•ha^{-1} during 2004. The biomass of spawning cisco in Ontario's Thunder Bay (Fig. 1) during mid-November 2005 was estimated at 22.8 kg•ha^{-1} based on USGS—GLSC acoustic and mid-water-trawl surveys (Yule et al. 2008a). The strong year-classes of cisco detected at age 1 in the annual May-June bottom-trawl surveys in Thunder Bay represented the bulk of the adult fish at large and of those harvested in the Thunder Bay commercial roe fishery during November 2005 (Fig. 8; Yule et al. 2008a). Exploitation rates of mature female cisco were estimated at 2.3% for a Wisconsin roe fishery in 2004 (Yule et al. 2006) and 8.5% in the Thunder Bay roe fishery in 2005 (Yule et al. 2008a), suggesting that these harvests are sufficiently low to allow sustainable fisheries. However, exploitation rates should be determined for these and the other principal roe fisheries on a regular basis.

Fig. 8. Year-class strength (±SE, number•ha^{-1}) at age 1 of cisco estimated from annual U.S. Geological Survey (USGS) bottom trawling each spring (May-June) at four fixed stations in Thunder Bay, 1989-2005 (a); estimated number of male and female cisco of different year-classes at large in Thunder Bay, based on USGS acoustic and mid-water trawling, during November 2005 (b); and year-class composition of cisco harvested by the November 2005 roe fishery (c). Graphs from Yule et al. (2008a).







Bloater

Coregonines (bloater and cisco) have recently accounted for about 10% of the lean lake trout diet in nearshore waters (Ray et al. 2007). Based on the annual bottom-trawl survey, bloater biomass was low (<1 kg•ha^{-1}) during 1978-1983; was slightly higher, but more variable during 1984-2000 (0.5-8.5 kg•ha^{-1}); and was intermediate during 2001-2005 (0.5-1.5 kg•ha^{-1}) (Stockwell et al. 2006b).

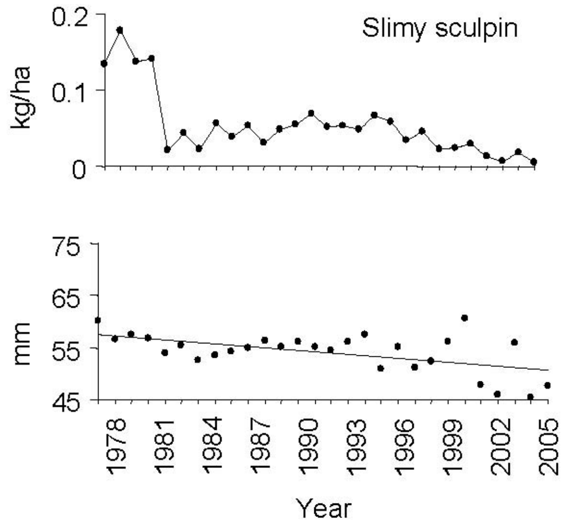
Rainbow Smelt

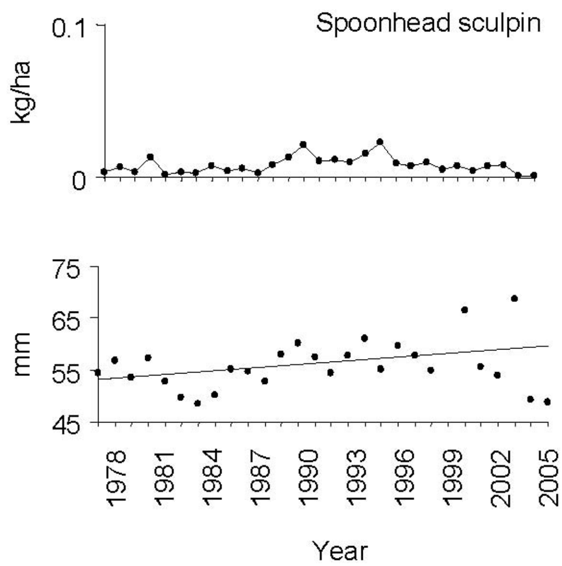
Rainbow smelt have been a principal prey of lean lake trout since at least the 1950s, but their numerical contribution to the diet of lake trout has declined from ~80% numerical contribution in 1986 to ~60% numerical contribution by 2001 (Ray et al. 2007). Unlike cisco, rainbow smelt have produced measurable year-classes during 1977-2004 (Fig. 7; Gorman 2007). However, year-class strength, biomass, and mean length have declined in recent years (Fig. 7). Three of the seven weakest year-classes produced during 1977-2004 have occurred since 2000 (2001, 2002, and 2004). The decline in mean length, which occurred gradually, was significant ($P < 0.0001$).

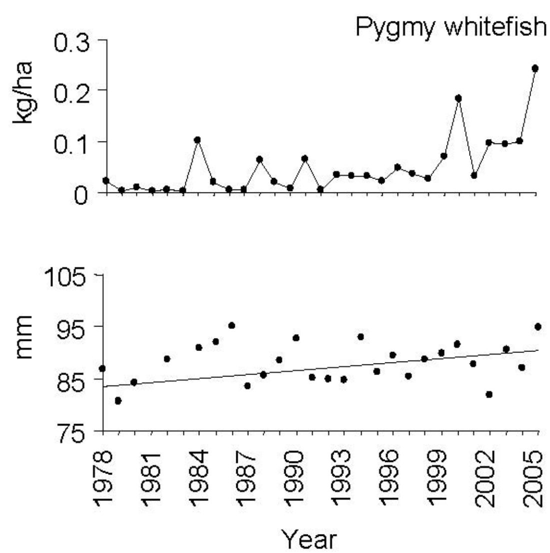
Important Benthic Prey Species

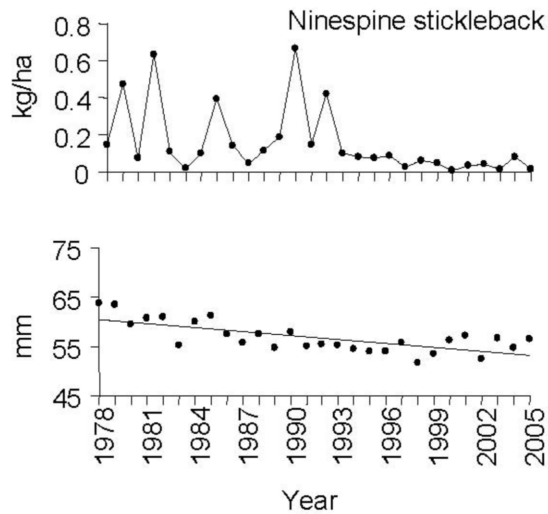
Sculpins accounted for about 10% of the biomass consumed by lake trout in recent years (Ray et al. 2007). Slimy sculpin biomass decreased dramatically in 1982 (Fig. 9), largely due to decreased catches in the Whitefish Bay region (Fig. 1) of eastern Lake Superior (DLY, unpublished data). Biomass increased somewhat in the mid-1980s to early 1990s but has since declined steadily. The average length of slimy sculpin also decreased significantly ($P = 0.003$) since 1978, and interannual variation in average length has been high in recent years (Fig. 9). Spoonhead sculpin often occupy depths deeper than those routinely sampled by the annual bottom-trawl survey, making biomass estimates conservative (Bronte et al. 2003). The biomass of spoonhead sculpin, in concert with that of slimy scuplin, has declined since the mid-1990s (Fig. 9). The apparent increase in average length in recent years was not significant ($P = 0.09$), but interannual variation has been high since 1999. In contrast to the biomass of other prey species, the biomass of pygmy whitefish has increased since 1978; mean length has also increased slightly during this period ($P = 0.06$) (Fig. 9). Pygmy whitefish were not found in the diet of lean lake trout during 1986-2001 (Ray et al. 2007). Ninespine stickleback biomass has declined steadily since 1992, and mean total length has declined significantly (Fig. 9; $P < 0.0001$). Prior to 1992, biomass was generally higher but highly variable.

Fig. 9. Mean biomass (kg/ha) and mean total length (mm) of slimy sculpin, spoonhead sculpin, pygmy whitefish, and ninespine stickleback. Data are from the annual U.S. Geological Survey bottom-trawl survey of the Lake Superior fish community during May-June, 1978-2005. Trend lines for mean total length were fit by least-squares linear regression.




Spoonhead sculpin
kg/ha
0.1
0
mm
75
65
55
45
1978
1981
1984
1987
1990
1993
1996
1999
2002
2005
Year


Pygmy whitefish
kg/ha
0.3
0.2
0.1
0
mm
105
95
85
75
1978
1981
1984
1987
1990
1993
1996
1999
2002
2005
Year



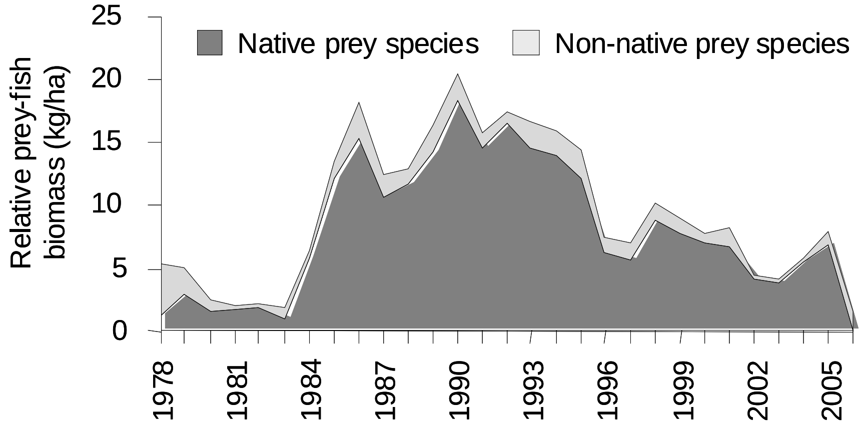
Improving Prey-Fish Assessment

The recent declines in prey-fish abundance and biomass have prompted increased interest in using new technology, new methodology, and simulation models to better understand predator-prey relationships and the role they play in management of fish populations (Negus 1995; Kitchell et al. 2000; Cox and Kitchell 2004). Negus (1995) compared predator food demand to prey-fish biomass estimates for Minnesota waters and found an apparent gross shortage of forage fish (predator demand exceeded prey supply). She concluded that the annual bottom-trawl survey likely underestimated the biomass of pelagic prey species like cisco and rainbow smelt, and she recommended the initiation of a more comprehensive assessment survey that combined acoustic techniques, mid-water trawls, and bottom trawls. Mason et al. (2005) conducted summer nighttime acoustic and mid-water-trawl surveys of Minnesota and Wisconsin waters during 1997 and found a much greater biomass of cisco and rainbow smelt than were estimated from the spring 1997 bottom-trawl survey. The prey discrepancy noted by Negus (1995) was accounted for by the greater biomass of pelagic species measured with acoustic methods (Mason et al. 2005). Stockwell et al. (2006a) found that night acoustic estimates of cisco far exceeded biomass estimates obtained by day bottom trawling, and Yule et al. (2008b) showed that catches of most benthic and demersal prey species were greater in night bottom-trawl samples in paired night-day tows. The USGS—GLSC is developing a new lakewide survey employing multiple gears for future assessment of prey fish in Lake Superior.

Community Stability

Although the biomass of most nearshore prey species has declined in recent years, the prey-fish community continues to be dominated by native species (Fig. 10). Given that native prey fishes evolved with the dominant predator, lake trout, the community should remain resilient when high predation pressure reduces prey-fish abundance. Recent declines in biomass and mean sizes of most nearshore prey species suggests the community is being regulated by size-selective predation, likely by lake trout (Gorman 2007). There is also evidence that growth rates of lake trout have slowed and that their numbers are no longer increasing (Sitar and He 2006). Additional information on species, like cisco, that account for the bulk of prey consumed by lake trout is given in the chapter on offshore prey fishes.

Fig. 10. Mean relative biomass (kg/ha) of native and non-native prey species. Data are from the annual U.S. Geological Survey bottom-trawl survey of the Lake Superior fish community during May-June, 1978-2005. Native prey-species biomass includes bloater, cisco, lake whitefish, longnose sucker, ninespine stickleback, slimy sculpin, spoonhead sculpin, and trout-perch; non-native species biomass is rainbow smelt only.



Recommendations

1. Develop a multiple-gear lakewide survey for assessing status and trends of prey fishes.
2. Use results of newly completed lakewide acoustic surveys to model lake trout growth potential across different regions of Lake Superior.
3. Determine exploitation rates for all important cisco roe fisheries.

NEARSHORE FISH COMMUNITY: LAKE TROUT

Shawn P. Sitar, Stephen C. Chong, Mark P. Ebener, Theodore N. Halpern, William P. Mattes, Michael J. Seider, and Matthew J. Symbal

Achieve and maintain genetically diverse self-sustaining populations of lake trout that are similar to those found in the lake prior to 1940, with lean lake trout being the dominant form in nearshore waters, siscowet lake trout the dominant form in offshore waters, and humper lake trout a common form in eastern waters and around Isle Royale.

S.P. Sitar.[7] Michigan Department of Natural Resources and Environment, 484 Cherry Creek Road, Marquette, MI 49855, USA.

S.C. Chong. Ontario Ministry of Natural Resources, 1235 Queen Street East, Sault Sainte Marie, ON P6A 2E5, Canada.

M.P. Ebener. Chippewa Ottawa Resource Authority, 179 West Three Mile Road, Sault Sainte Marie, MI 49783, USA.

T.N. Halpern. Minnesota Department of Natural Resources, 5351 North Shore Drive, Duluth, MN 55804, USA.

W.P. Mattes. Great Lakes Indian Fish and Wildlife Commission, 72682 Maple Street, Odanah, WI 54861, USA.

M.J. Seider. Wisconsin Department of Natural Resources, PO Box 589, 141 South Third Street, Bayfield, WI 54814, USA.

M.J. Symbal. Red Cliff Band of Lake Superior Chippewas, 88385 Pike Road, Highway 13, Bayfield, WI 54814, USA.

[7]Corresponding author (e-mail: sitars@michigan.gov).

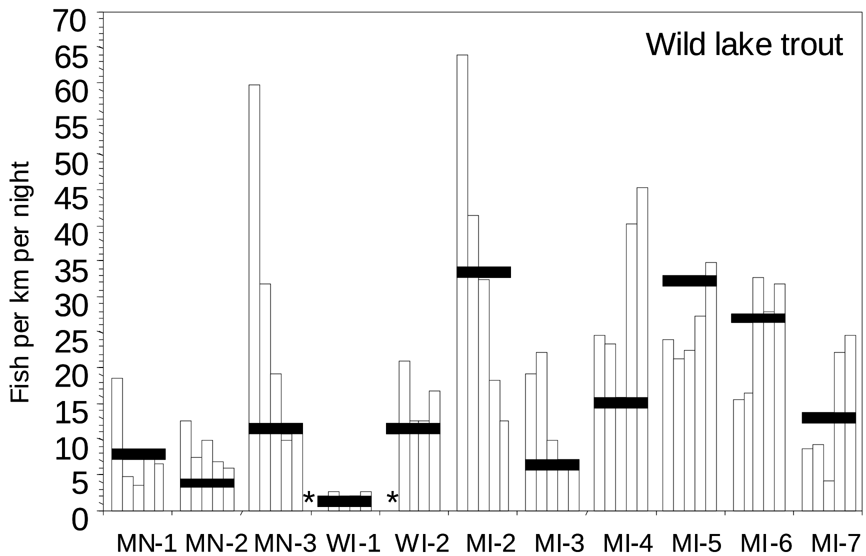
Of the three forms of lake trout recognized in the above fish-community objective (FCO) (Horns et al. 2003), we address here the lean form in nearshore waters. Although siscowet lake trout do at times occupy nearshore waters, their status is addressed in the chapter on the offshore fish community. No surveys have been done in recent years to assess the status of humper lake trout, which also occupy both nearshore and offshore waters.

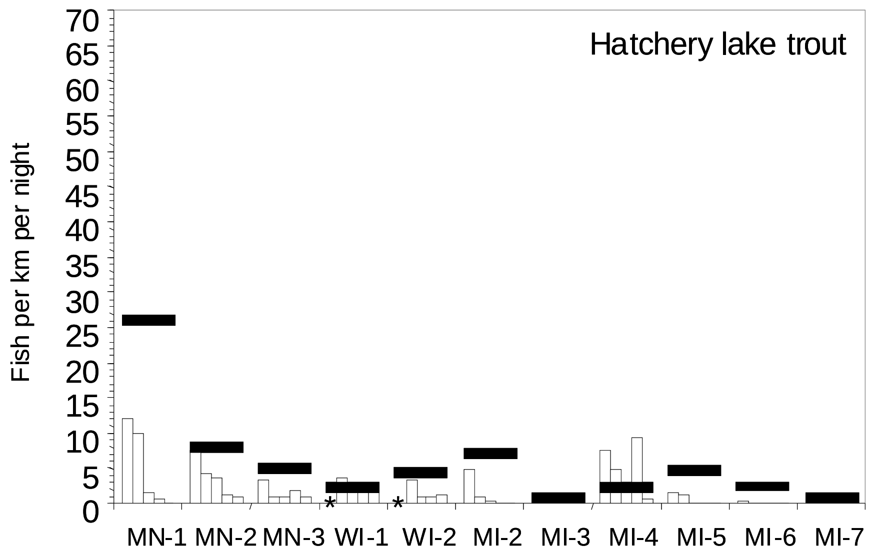
Lake trout recovery in U.S. waters of Lake Superior during the last 20 yr was geographically successional. Wild lake trout abundance increased and hatchery lake trout abundance declined first in Michigan waters, then in Wisconsin waters, and then in Minnesota waters. By 2001, in Michigan waters, abundance and recruitment of most lake trout populations were near historical highs (Wilberg et al. 2003; Richards et al. 2004). Although a continuous time-series of fishery-independent data (agency surveys) was not available for much of the Canadian waters of Lake Superior, we assumed, based on the limited information that was available, that wild lake trout recovery there was similar to patterns observed in U.S. waters. The ongoing recoveries have resulted from the three-pronged management approach of controlling fishing, reducing sea lamprey abundance, and stocking. Stocking has been discontinued in much of the lake and will be discontinued elsewhere as populations continue to recover and rehabilitation criteria are met. The sea lamprey control program continues to suppress lamprey abundance, and most fishery agencies continue to closely regulate their lake trout fisheries.

Abundance and Stocking

Although abundance was trending downward in MI-1 and 2, wild lake trout abundance in MI-2 through 4 (western Michigan waters, Fig. 1), during 2001-2005 was higher than during 1993-2000 (Fig. 11). Among eastern Michigan management units, wild lake trout abundance during 2001-2005 increased by 46% in MI-5 and by twofold in MI-6 and 7, where it exceeded the 1993-2000 average. Abundance in MI-5 was below the 1993-2000 mean, but within 2001-2005 the trend was upward. However, in Minnesota waters, annual relative abundance of wild lake trout has declined since 2001 in all three management units. In contrast, average abundance of wild lean lake trout in Wisconsin generally increased from 2001 to 2005.

Fig. 11. Relative abundance of wild and hatchery-origin (lean) lake trout in U.S. management units of Lake Superior (Fig. 1) expressed as the annual geometric mean number caught per km of gillnet per night fished (fish•km^{-1}•night^{1}) from standardized annual spring (April-June) bottom-set, gillnet surveys during 2001-2005 (vertical bars in chronological order). Horizontal black bars represent the geometric mean catch-per-unit effort for 1993-2000 (Sitar et al. 2007). Asterisks indicate years when no surveys were conducted.





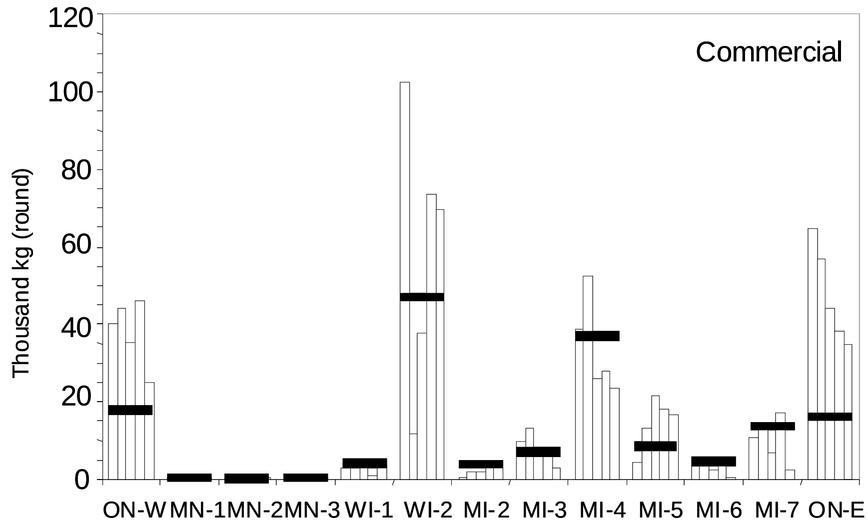
In all U.S. jurisdictions, hatchery lake trout abundance declined due to a reduction in numbers stocked and high mortality of stocked fish (Linton et al. 2007). In Minnesota waters, criteria used to determine when to cease stocking (Hansen 1996) were met by 2001 in MN-3, and stocking ceased in 2003. These criteria have also been met in MN-2, and stocking there ceased in 2007. In U.S. waters, stocking continues only in MN-1, WI-1, and MI-4 (Fig. 1). In Ontario waters, the average number of lake trout stocked increased during 2001-2005 and was higher than in the previous 5 yr. However in southeastern Ontario waters (management units 31 and 33; Fig. 1), stocking of hatchery lake trout will be discontinued in 2006 because of high fishery exploitation. Natural recruitment in this region has been weak, and, accordingly, attempts to rehabilitate lake trout have been deferred, just as they were in the U.S. waters of Whitefish Bay (MI-7) in 2001.

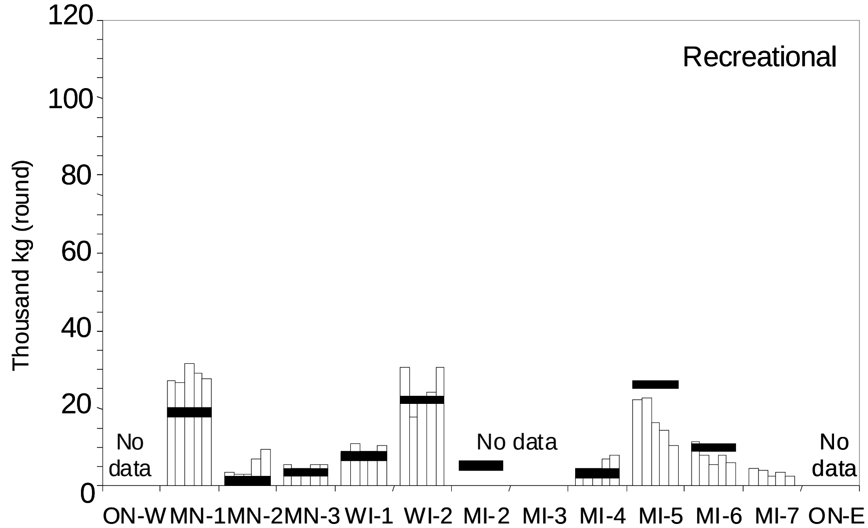
Of the two river-spawning lake trout populations in eastern Ontario waters, the population associated with the Dog River is recovering and considered to be in an early recovery status, whereas the population associated with the Montreal River does not appear to be recovering. A survey in 2005 produced 180 wild-origin spawning fish in the Dog River and only 9 in the Montreal River. By way of comparison, only 15 river-run lean lake trout were collected in 1977 in the Dog River, and all were of hatchery origin (Kerr 1977). Therefore, the apparent turnabout in the Dog River population is encouraging.

Fishery Harvest

The regions with the highest level of commercial lake trout yield during 2001-2005 were eastern Wisconsin's WI-2 (average 59,000 kg•year^{-1}), eastern Ontario (includes management units 23-34, 48,000), western Ontario (includes units 1-22, 38,000), and Michigan's MI-4 (average 34,000) and MI-5 (average 15,000). With respect to the previous reporting period of 1993-2000, average yield during 2001-2005 was lower in Wisconsin and Michigan waters and higher in Ontario waters (Fig. 12). However, Ontario's commercial yield (all units) declined nearly 50% from 2001 to 2005. In Michigan, commercial landings during 2001-2005 declined in MI-3, 4, and 7 but increased more than fourfold in MI-2 and 5. In Wisconsin, during the same period, more than 90% of the commercial yield was taken in WI-2, and the harvest increased more than fivefold from 2001 to 2005. There is no commercial fishery for lake trout in Minnesota, although small amounts are harvested as bycatch in other commercial fisheries.

Fig. 12. Annual commercial and recreational yield (kg round weight) of lake trout during 2001-2005 (vertical bars in chronological order) and the 1993-2000 mean commercial and recreational yield (horizontal black bars) from Lake Superior management units based on creel-survey and commercial reports. ON-W includes Canadian management units 1-22 and ON-E includes management units 23-34 (Fig. 1). Creel surveys were not conducted in MI-7 during 1993-2000, in MI-2 during 2001-2005, and in MI-3 in either period.


Commercial
Thousand kg (round)
120
100
80
60
40
20
0
ON-W MN-1 MN-2 MN-3 WI-1 WI-2 MI-2 MI-3 MI-4 MI-5 MI-6 MI-7 ON-E


Recreational
Thousand kg (round)
120
100
80
60
40
20
0
No data
No data
No data
ON-W MN-1 MN-2 MN-3 WI-1 WI-2 MI-2 MI-3 MI-4 MI-5 MI-6 MI-7 ON-E

Yield in the recreational fishery during 2001-2005 was higher than during 1993-2000 in most U.S. management units (Fig. 12). The highest annual harvests were in MN-1 and WI-2 (>25,000 kg•year^{-1}) and in MI-5 (>17,000 kg•year^{-1}). In both Minnesota and Wisconsin, recreational yield increased from 2001 to 2005, whereas recreational yield and effort declined in Michigan. One exception was in Keweenaw Bay (MI-4), where recreational yield almost tripled from 2001-2005.

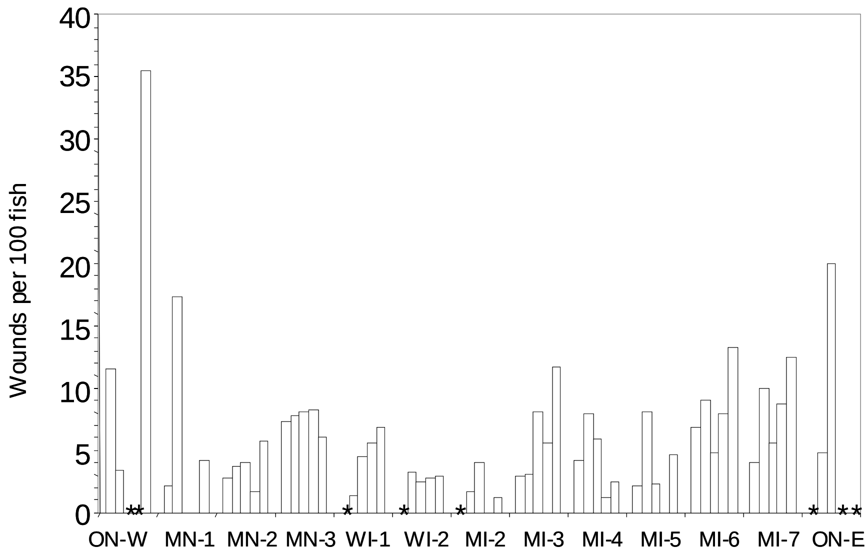
Food Habits

The diet of lean lake trout continues to be dominated in spring by rainbow smelt, although the proportion of coregonines has been increasing since the mid-1990s (Ray et al. 2007). As lake trout grow, the importance of larger native prey fishes increases, and the proportion of rainbow smelt (a smaller non-native fish) decreases (Mason et al. 1998). In U.S. waters during 2001-2005, the spring diet (by weight) of smaller lake trout (<600-mm total length) was 47-76% rainbow smelt, 4-35% coregonines, and <3% burbot, whereas the diet of larger lake trout (≥600 mm) was 20-32% rainbow smelt, 14-50% coregonines, and 9-23% burbot.

Mortality and Growth

Sea lamprey predation continues to be the major source of lake trout mortality, and it has steadily increased since the mid-1990s. Sea lamprey marking rates on the most abundant size-class of lake trout favored by lamprey (534-635 mm, total length) increased in most management units during 2001-2005 and were highest in Ontario waters and in Michigan management units MI-6 and 7 (Fig. 13). Marking rates decreased during this period in WI-2, MI-2, and MI-4. Recent estimates of total annual mortality rate in MN-1, MN-2, MN-3, WI-2, MI-5, MI-6, and MI-7 were below the upper bound of target values, although rates were increasing in some units, likely caused by increased sea lamprey-induced mortality (Bence and Ebener 2002; Schreiner et al. 2006; Linton et al. 2007).

Fig. 13. Annual sea lamprey marking rates for 534-635-mm (total-length) lean lake trout in Lake Superior management units during 2001-2005 (vertical bars in chronological order). Marking rates were the total number of Type A, Stages 1-3, marks per 100 lake trout. Asterisks indicate no data for that year. ON-W includes Canadian management units 1-22, and ON-E includes units 23-34.



Growth rates of lake trout continued to decline in most of Lake Superior as a result of increasing lake trout density and decreasing abundance of their key prey: rainbow smelt and cisco (Bronte et al. 2003). Mean length of age-7 lake trout decreased from >570 mm in 1980 to <545 mm during 2001-2005. Compared to 1993-2000 (the previous reporting period), mean length of age 7 lake trout in 2001-2005 was greater in Minnesota and Wisconsin waters but lower in Michigan waters (Sitar et al. 2007). Length at maturity in some areas has also changed in association with growth declines. In Michigan waters, Sitar and He (2006) reported that the length at which 50% of wild lake trout were mature declined from >630 mm during the hatchery-fish-dominant period (1970-1979) to <600 mm during the recent, wild-fish-dominant period (1986-2003).

Recommendations

1. Determine the distribution, abundance, and population dynamics of humper lake trout populations in nearshore and offshore waters.
2. Assess whether habitat is limiting achievement of the lake trout FCO relating to lean lake trout:
   i. Inventory, map, and classify lean lake trout habitat.
   ii. Model the relationships of habitat to lean lake trout production.
   iii. Determine if spawning habitat quantity is limiting river-run lean lake trout populations.
3. Develop long-term simulation models using current recovery and management biological reference points (e.g., 45% total annual mortality) to evaluate the production potential and sustainability of lean lake trout populations.

NEARSHORE FISH COMMUNITY: LAKE WHITEFISH

Stephen C. Chong, Mark P. Ebener, and William P. Mattes

Maintain self-sustaining populations of lake whitefish within the range of abundance observed during 1990-99.

The steady increase in relative abundance of lake whitefish based on commercial catch-per-unit effort (CPUE) over the past two decades suggests that the above fish-community objective (Horns et al. 2003) has been met or exceeded. Furthermore, commercial yields over the past two decades were near historical highs established since record keeping by all agencies began in the late 1890s. Although yields are high in terms of the historical record, the population is likely only a fraction of what the lake supported prior to European settlement (Lawrie and Rahrer 1973). The only management units in the lake where CPUEs were below the 1990-1999 minimum were in eastern waters, comprising management units MI-6, 7, and 8 in Michigan and management units 28-34 in Ontario (Fig. 1).

S.C. Chong.[8] Ontario Ministry of Natural Resources, 1235 Queen Street East, Sault Sainte Marie, ON P6A 2E5, Canada.

M.P. Ebener. Chippewa Ottawa Resource Authority, 179 West Three Mile Road, Sault Sainte Marie, MI 49783, USA.

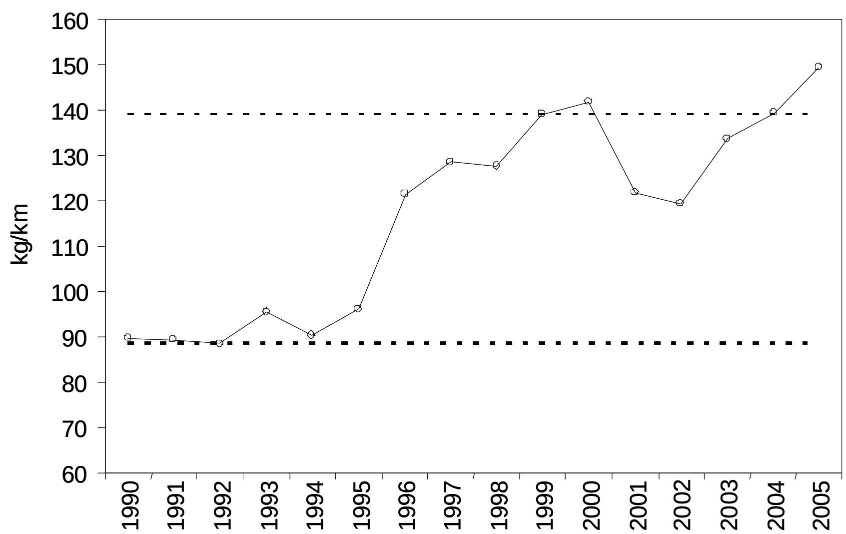
W.P. Mattes. Great Lakes Indian Fish and Wildlife Commission, 72682 Maple Street, Odanah, WI 54861, USA.

[8]Corresponding author (e-mail: stephen.chong@ontario.ca).

Abundance

A survey protocol for monitoring lake whitefish abundance and population characteristics on a lakewide basis remains to be established. Some agencies conduct fishery-independent surveys, but most agencies rely on commercial-fishery data to monitor trends in abundance. During 1990-1999, commercial gillnet CPUE ranged from a low of 89 kg•km^{-1} in 1992 to a high of 139 kg•km^{-1} in 1999. Commercial CPUE during 2001-2004 was within the 1990-1999 range and exceeded the range in 2005 when CPUE was 149 kg•km^{-1} (Fig. 14).

Fig. 14. Lake whitefish relative abundance based on gillnet CPUE (CPUE = kg•km^{-1} of gillnet) in the Lake Superior commercial fishery, 1990-2005. Dashed lines show the range of CPUE during 1990-1999, which is the fish-community-objective target.

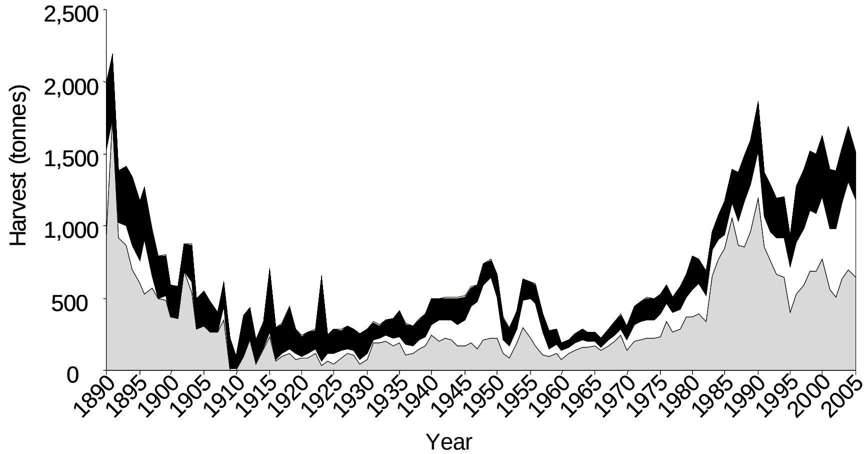


Although the annual U.S. Geological Survey spring forage-fish survey (day bottom trawling) in nearshore waters does not specifically target lake whitefish, it does provide estimates of year-class strength and biomass ($kg \bullet ha^{-1}$) of lake whitefish typically <430-mm total length (Yule et al. 2008b). These data, like the commercial data, indicated that overall abundance during 2001-2005 was within the fish-community target range and that biomass was greater in western than in eastern waters. In Ontario waters west of management unit 19 (Pic River, Fig. 1) during 2001-2005, biomass has been increasing since 2002 and is slightly above the 1990-1999 mean biomass for this region, whereas, in Ontario waters east of the Pic River, biomass declined after 2000 to below the 1990-1999 mean for this region. In Wisconsin waters, biomass was stable and close to the 1990-1999 regional mean. Based on the bottom-trawl surveys, biomass of lake whitefish in Wisconsin waters was more than 10 times greater than that observed in Michigan and eastern Ontario waters and roughly five times greater than in western Ontario waters. In Michigan waters, lake whitefish mean biomass, based on bottom trawling, has been below its 1990-1999 mean since 1995 (Yule et al. 2008b).

Harvest

Since the mid-1980s and during 2001-2005, harvest of lake whitefish, the primary target for commercial fishers in Lake Superior, has been close to the historical highs of the late 1800s (Fig. 15). Michigan accounts for approximately 40% of the lakewide harvest, Wisconsin ~35%, Ontario ~25%, and Minnesota virtually none. The Michigan and Wisconsin lake whitefish commercial fishery comprises small- and large-boat gillnet and trapnet operations. In Ontario, the fishery is conducted exclusively with small and large gillnet boats. Lakewide, commercial gillnet fishers are responsible for approximately 75% of the harvest. Notable sport fisheries occur near Munising and Grand Marais, Michigan, and Thunder Bay, Ontario, and in the upper St. Marys River (Fig. 1); however, the sport-fishing harvest is thought to be trivial in comparison with the commercial harvest.

Fig. 15. Commercial-fishery yield (metric tonnes) of lake whitefish from Ontario (black), Wisconsin (white), and Michigan (grey) waters of Lake Superior during 1889-2005.



Mortality, Mean Age, and Growth

Lake whitefish mortality rates during 2001-2005 were estimated using catch-curve analysis for all management units, except MI-5 through MI-8 where statistical catch-at-age analysis was used (Fig. 1; Bence and Ebener 2002; Table 5 in Petzold 2007). In Ontario units ON-1 and 33, mortality rates increased but were still well below the target maximum rate of 65%. Total annual mortality was higher in ON-1, ranging 21-31%, than in ON-33 where it ranged 30-50%. In Wisconsin unit WI-2, annual mortality remained below the target maximum and ranged from 23% to 57%. In Michigan waters, mortality rates exceeded 65% in MI-2, 3, and 4 in the 1990s but were less than 65% during 2001-2005. Annual mortality rates in MI-5, 6, 7, and 8 were well below 65% during 2001-2005.

Mean age of lake whitefish in the commercial catch in 2001-2005 was similar to that reported for the 1990s (Petzold 2007). Mean age in the majority of units ranged from 6.0 to 8.5 yr, except that, in WI-2 and ON-1, mean age was 11.7 and 10.7 yr, respectively. Both WI-2 and ON-1 have the highest densities of lake whitefish in the lake. The lowest average age was 6.4 yr in MI-2.

Growth of lake whitefish in Lake Superior in the past was density dependent, increasing with declines in density, as measured by CPUE (Bronte et al. 2003; Petzold 2007). In general, during 2001-2005, growth in most management units fluctuated without trend. The exceptions were in eastern MI-8 (Whitefish Bay) where growth has been declining since the early 1990s and in ON-1 where growth has declined along with density.

Recommendations

1. Continue to determine sustainable levels of harvest.
2. Develop methods for biomass estimation for all units.
3. Expand fishery-independent assessments.
4. Determine spatial delineation of stocks.

NEARSHORE FISH COMMUNITY: PACIFIC SALMON, RAINBOW TROUT, AND BROWN TROUT

Donald R. Schreiner, Michael J. Seider, Shawn P. Sitar, and Stephen C. Chong

Manage populations of Pacific salmon, rainbow trout, and brown trout that are predominantly self-sustaining but that may be supplemented by stocking that is compatible with restoration and management goals established for indigenous fish species.

The above fish-community objective (Horns et al. 2003) recognizes that most of the introduced salmonines in Lake Superior have naturalized and are a permanent component of the fish community. Furthermore, it acknowledges the potential risk to the rehabilitation of native species by continued supplemental stocking of non-native species. The balance between native and non-native species abundance is extensively debated among agencies and between agencies and their constituents. An acceptable balance that considers biological limitations, as well as social and economic needs, is continually being reformulated.

D.R. Schreiner.[9] Minnesota Department of Natural Resources, Lake Superior Area Fisheries Program, 5351 North Shore Drive, Duluth, MN 55804, USA.

M.J. Seider. Wisconsin Department of Natural Resources, PO Box 589, 141 South Third, Bayfield, WI 54814, USA.

S.P. Sitar. Michigan Department of Natural Resources and Environment, 484 Cherry Creek Road, Marquette, MI 49855, USA.

S.C. Chong. Ontario Ministry of Natural Resources, 1235 Queen Street East, Sault Sainte Marie, ON P6A 2E5, Canada.

[9]Corresponding author (e-mail: donald.schreiner@state.mn.us).

The introduction and widespread naturalization of non-native salmonines have had a significant impact on recreational fisheries in the inshore and nearshore habitat zones. Non-native salmonines have expanded sport-fishing opportunities for anglers, especially along shorelines and in tributaries of the inshore zone (Schreiner et al. 2008). Since most of the introduced salmonines are now naturalized, agencies are reevaluating the cost effectiveness of their stocking programs (Peck 1992; Schreiner and Schram 1997; Schreiner et al. 2006).

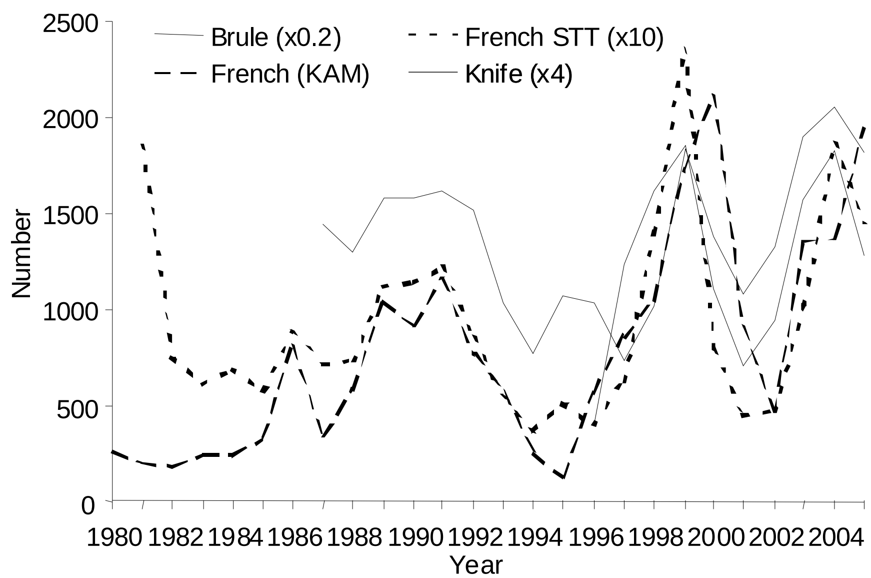
All agencies that stock trout and salmon now monitor, to some extent, the relative abundance of non-native salmonines and the contribution of stocked fish to recreational and commercial fisheries. Estimated angler catch and catch rates from creel surveys are the primary data for assessing the recreational fishery. Angler catch and catch rates presented herein are from annual creel surveys of the summer (May-September) open-water lake fishery. Spawning migrations of non-native salmonines in the Brule River in Wisconsin, the French and Knife Rivers in Minnesota, and the McIntyre River in Ontario are monitored using permanent traps or counting stations. Electrofishing surveys have been conducted in some tributaries to assess spawning success and juvenile production by naturalized salmonines.

Rainbow Trout (Steelhead)

All agencies have stocked various life stages of rainbow trout, but yearlings have been the predominant life stage stocked. Although there are many naturally reproducing populations in Lake Superior, some stocking continued during 2001-2005. The percentage of stocked rainbow trout caught by anglers has generally averaged 1% or less (Close and Hassinger 1981; Peck 1992; Schreiner et al. 2006). The contribution of stocked rainbow trout to spawning runs in individual streams varies widely, but meaningful contributions to fisheries occur only when the numbers stocked are substantial and the numbers of wild fish are small (Peck 1992). Stocking to supplement wild populations usually is inefficient and may pose genetic risks to wild populations (Krueger and May 1987; Krueger et al. 1994; Miller et al. 2004).

The abundance of wild- and hatchery-origin adults returning to spawn in western Lake Superior waters, as indicated by spawning runs in the Brule River, Wisconsin, and French and Knife Rivers, Minnesota, appear to be strongly influenced by environmental conditions in the lake (Fig. 16). Kamloops and steelhead strains of rainbow trout are stocked as yearlings in the French River and are little exposed to stream conditions, but fluctuations in abundance of their subsequent spawning runs were synchronous with spawning runs of wild fish. For example, a decline of spawning adults in the mid-1990s (Fig. 16) likely resulted from extremely cold lake temperatures during 1992-1993, which caused poor growth and low survival of year-classes emigrating as juveniles from streams. Abundance increased during the late 1990s and early 2000s likely because of relatively warm lake temperatures in 1998 and restrictive harvest regulations implemented in the early to mid-1990s by Wisconsin, Minnesota, and Ontario.

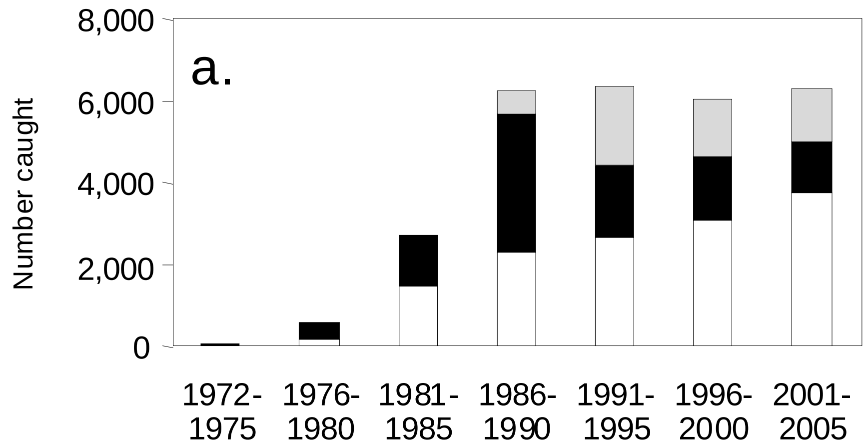
Fig. 16. Number of wild- and hatchery-origin spawning rainbow trout returning to the Brule River in Wisconsin and French and Knife Rivers in Minnesota, 1980-2005. Numbers were adjusted with multipliers to fit the y-axis scale as per the legend (KAM = Kamloops strain; STT = steelhead strain).

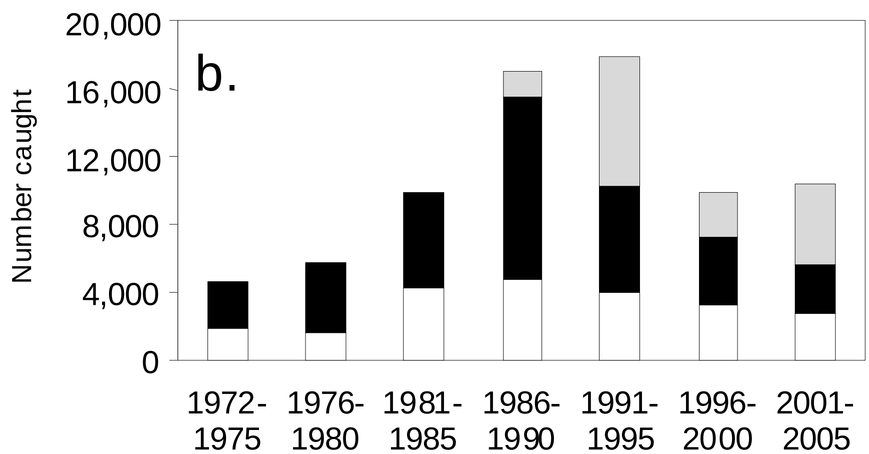


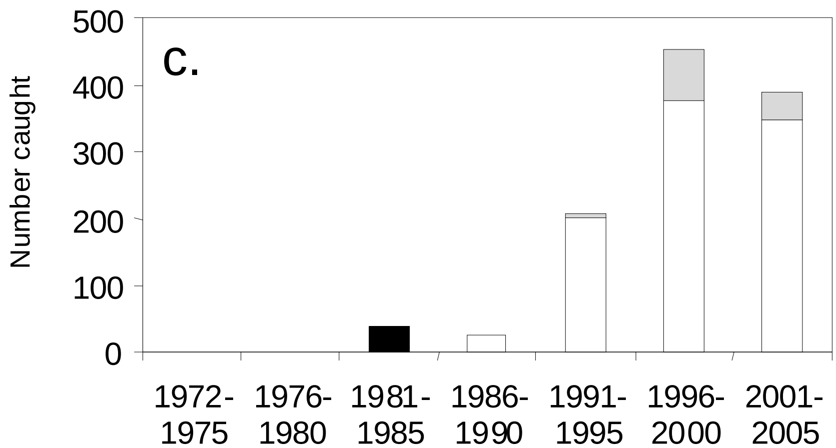
Chinook Salmon

Contemporary stocking of Chinook salmon into Lake Superior was initiated by Michigan in 1967 and followed by Minnesota in 1974, Wisconsin in 1977, and Ontario in 1988. All agencies stocked salmon fingerlings in the spring. Since the mid-1980s, the number of Chinook salmon stocked has declined, whereas the number of Chinook salmon caught in the summer fishery has remained relatively stable (Fig. 17a). The need for continued stocking was questioned because most Chinook salmon in Lake Superior are naturally reproduced. In a lakewide study of the Chinook salmon sport fishery in 1990-1994, over 75% of those harvested were naturally reproduced (Peck et al. 1999). In that study, stocked Chinook salmon made up 57% of the angler harvest in Minnesota, 32% in Wisconsin, 25% in Michigan, and 9% in Ontario. Chinook salmon stocked in each jurisdiction contributed to the fisheries in all other jurisdictions, indicating that the species moves considerable distances, ranging widely from stocking sites during the summer angling season. A more recent study conducted during 2003-2006 showed that Chinook salmon stocked in Minnesota comprised less than 5% of the Chinook salmon harvested in Minnesota waters (Schreiner et al. 2006), a sizeable decrease in survival from that reported ten years earlier (Peck et al. 1999). These studies suggested that, in Minnesota, returns of stocked fish were too low to justify further stocking, and, in 2007, Chinook salmon stocking was discontinued in the state's waters.

Fig. 17. Total average catch of (a) Chinook salmon, (b) coho salmon, and (c) pink salmon over 5-yr intervals in the summer sport fishery in Minnesota (white), Wisconsin (black), and Michigan (grey) waters of Lake Superior, 1972-2005. Michigan on-site lakewide creel surveys did not begin unil 1987. Creel surveys were done by mail in Michigan waters during the mid-to-late 1970s. On-site surveys began at Marquette in 1984 and were expanded to other sites in 1987.







Coho Salmon

Coho salmon were introduced by Michigan in 1966 and by Minnesota and Ontario during 1969-1972 and quickly became naturalized throughout Lake Superior. Coho salmon have reproduced successfully in most tributaries that are accessible during the spawning period, have suitable substrate, and maintain adequate winter groundwater flows. Michigan discontinued stocking of coho salmon in 1994 because stocked fish comprised less than 10% of the catch in the recreational fishery (Peck 1992). However, to address angler concerns during treaty negotiations, Michigan started stocking limited numbers of coho salmon in the Munising area (MI-6, Fig. 1) after 2000. Anglers exploit age-2 fish almost exclusively, which results in wide harvest fluctuations due to variations in year-class strength. In most years, coho salmon is the second most-harvested species, after lake trout, in the recreational fishery in U.S. waters. Since 1990, the total harvest has been remarkable, consistent within successive 5-yr periods, with slightly higher numbers being caught in Michigan than in Wisconsin and Minnesota (Fig. 17b). In general, a positive relationship exists between coho salmon catch rates in the lake and their abundance in spawning runs in the Brule River, Wisconsin, which was expected because both the fishery and spawning run depended on a single year-class. Because coho salmon populations were no longer supported by stocking after the mid-1990s, more restrictive harvest regulations were enacted in most jurisdictions at that time to provide for an adequate number of spawning fish.

Pink Salmon

In 1956, approximately 21,000 pink salmon fry were accidentally introduced into the Current River in Ontario (Nunan 1967), which resulted in the naturalization of the species in Lake Superior. Abundance of pink salmon has increased in Lake Superior during 1995-2005, as indicated by increased harvest in Minnesota and Michigan waters (Fig. 17c) and reports of increased numbers of spawning adults in tributaries. Spawning runs were only in odd years initially, but delayed maturity in some fish resulted in the establishment of even-year runs in many tributaries.

Brown Trout and Splake

Brown trout and splake are stocked in only a few isolated areas of Lake Superior, including Chequamegon Bay in Wisconsin and in the Copper Harbor, Marquette, and Munising areas of Michigan to provide anglers with a localized inshore and nearshore fishery. Lakewide, an average of 1,265 splake and about 800 brown trout were harvested anuually in the summer recreational fishery during 2001-2005. Prior to 1994, hatchery-reared brown trout made up 50% of the sport-fishery harvest in Wisconsin and 40% in Michigan (Peck et al. 1994). No recent studies have been conducted to determine the contribution of stocked brown trout to the fishery, but managers believe it has not changed dramatically. The Brule River, Wisconsin, supports the largest known spawning run of brown trout in Lake Superior, averaging ~4,000 fish during 2001-2005 (D. Pratt, unpublished data).

Non-native salmonines play a relatively minor role in the Lake Superior fish community (Kitchell et al. 2000; Bronte et al. 2003). Their thermal physiology relegates them to the inshore zone and pelagic portions of the nearshore and offshore zones of the lake. However, non-native salmonines have the potential to compete with brook trout for spawning and nursery habitat in the inshore zone, especially in tributaries (Fausch and White 1986; Huckins et al. 2008; Schreiner et al. 2008). Because non-native salmonines have naturalized and are of great social and economic importance to the sport fishery, a better understanding of their role in shaping the Lake Superior fish community is warranted.

Recommendations

1. Determine if non-native salmonines are having a negative effect on inshore populations of brook trout, especially in tributaries.
2. Develop a standardized database for harvest information collected by all agencies.
3. Inform the public of the cost-effectiveness of all stocking programs.
4. Apply the Great Lakes Fish Health Committee protocol and standards to all stocking programs.

NEARSHORE FISH COMMUNITY: SEA LAMPREY

Todd B. Steeves, Michael F. Fodale, Gavin C. Christie, and Mark P. Ebener

Suppress sea lampreys to population levels that cause only insignificant mortality on adult lake trout.

Sea lamprey control began in Lake Superior in 1958 in response to the increased mortality on lake trout that occurred after the invasion of sea lamprey in the late 1930s (Hansen et al. 1995). Since then, control efforts have been refocused from eradication to suppression to tolerable numbers (Heinrich et al. 2003). Suppressing sea lamprey abundance to a level of ≤35,000 spawners would be necessary to reduce sea lamprey-induced mortality to an insignificant level (>5%), indicated by ≤5 marks per 100 lake trout, thereby achieving the above sea lamprey fish-community objective for Lake Superior (Horns et al. 2003).

T.B. Steeves.[10] Fisheries and Oceans Canada, Sea Lamprey Control Centre, 1219 Queen Street East, Sault Sainte Marie, ON P6A 2E4, Canada.

M.F. Fodale. U.S. Fish and Wildlife Service, 3090 Wright Street, Marquette, MI 49855, USA.

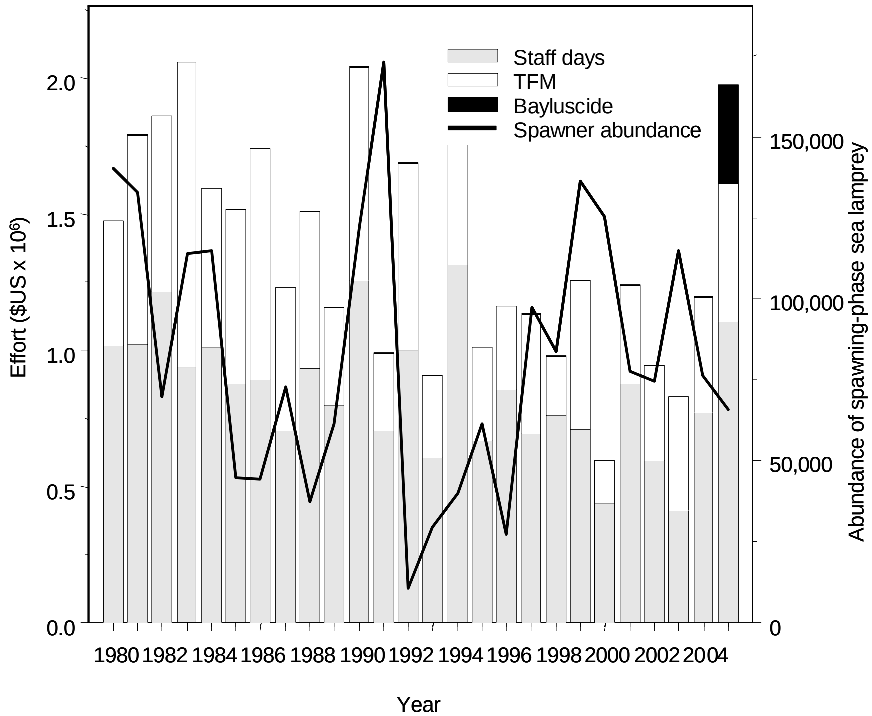
G.C. Christie. Great Lakes Fishery Commission, 2100 Commonwealth Boulevard, Suite 100, Ann Arbor, MI 48105-1563, USA.

M.P. Ebener. Chippewa Ottawa Resource Authority, 179 West Three Mile Road, Sault Sainte Marie, MI 49783, USA.

[10]Corresponding author (e-mail: mike.steeves@dfo-mpo-gc.ca).

From 1950 to 1954, the U.S. Fish and Wildlife Service and Fisheries and Oceans Canada evaluated 1,915 tributaries to Lake Superior for their potential to produce sea lamprey. Of these, 424 tributaries were found to have suitable spawning and nursery habitats. Sea lamprey have been collected from 137 of those tributaries, and, of these, 52 have spawning runs sufficiently large to warrant chemical treatment on a repetitive 3- to 5-yr cycle, and an additional 19 have been treated at least once in the last 10 yr (Heinrich et al. 2003). The estimated abundance of spawning-phase sea lamprey declined irregularly during the 1980s, reaching an all-time low of 11,200 in 1994. However, since then abundance rebounded, reaching a post-control high of 140,000 in 2001 (Fig. 18).

Fig. 18. Expenditures on effort (staff days), TFM, and granular Bayluscide (bars) to control sea lamprey in Lake Superior and corresponding annual estimates of spawning-phase sea lamprey abundance (line) from 1980 through 2005. The effects of sea lamprey-control efforts do not affect the estimates of spawner abundance for at least 2 yr.



TFM-Based Control

The average amount of the lampricide 3-trifluoromethyl-4-nitrophenol (TFM) used annually to treat tributaries declined from 14,780 kg in the 1980s to 9,560 kg in the 1990s. This reduction in TFM usage was the result of an effort to reduce dependency on lampricides by 20%, which involved an increase in the efficiency of TFM application in some rivers, a reduction in the amount applied in certain tributaries to protect non-target species, such as lake sturgeon or spawning salmonids, and a reduction in the number of rivers treated. Concurrent with reduced dependency, however, spawning-phase sea lamprey abundance increased (Fig. 18). In response, lampricide application was increased, both in the usage of TFM and of Bayluscide granules in embayments known to harbor larvae. In brief, spawning-phase abundance during 2001-2005 averaged 105,000, which was equivalent to abundance in the early 1980s (Mullett et al. 2003). Although this abundance is only ~17% of pre-control (pre-1958) abundance, it is well above the target maximum of 35,000. The mean marking rate of 9.5 per 100 lake trout >533 mm during 2001-2005 exceeded the target (5 marks) established by the Lake Superior Technical Committee.

Bayluscide-Based Control

Assessment of larval sea lamprey populations in embayments or lentic areas near sea lamprey-producing tributaries has increased since 2004. New technology has resulted in sonar-based quantification of substrates and improved evaluation of abundance and distribution of larvae. These assessments resulted in the 2005 treatment with granular Bayluscide of four lentic areas comprising 183 ha (Fig. 18). Larval sea lamprey abundance in these areas will continue to be monitored, and Bayluscide application will be scheduled regularly.

Barrier-Based Control

The strategic vision of the Great Lakes Fishery Commission (Great Lakes Fishery Commission 2008) contains a milestone seeking during this decade at least a 50% suppression of sea lamprey using alternative control technologies while, at the same time, reducing TFM use by 20%. At present, barriers that block spawning sea lamprey from tributaries is an important alternative-control method, and, as of 2005, 16 barriers were in place on Lake Superior tributaries (Heinrich et al. 2003; Young and Klar 2005). These barriers blocked 260 km of tributary spawning habitat, eliminating the need for lampricide application in these areas. Because barriers on tributaries reduce species richness above barriers (Dodd et al. 2003), those constructed on Lake Superior tributaries since 1990 have either been of variable-crest design, where the barrier crest can be lowered to the stream bed to enable fish passage when lamprey are not migrating, or have incorporated trap-and-sort fishways to provide passage for other fish species.

Recommendations

1. Estimate sea lamprey-induced mortality for other fishes, in addition to lake trout, that are preyed on extensively.
2. Monitor streams pre- and post-treatment to detect new recruitment and streams with large numbers of treatment survivors.
3. Increase control efforts on tributaries.
4. Evaluate lentic areas harboring treatable numbers of larvae.
5. Develop and implement new control technologies, such as the use of pheromones.
6. Develop methodology for improving abundance estimates for spawning-phase sea lamprey.

NEARSHORE FISH COMMUNITY: ECOLOGICAL INTERACTIONS

Owen T. Gorman, Jason D. Stockwell, Daniel L. Yule, Thomas R. Hrabik, Mark P. Ebener, and Thomas C. Pratt

A self-sustaining assemblage of prey dominated by indigenous species at population levels capable of supporting desired populations of predators and a managed commercial fishery.

The above fish-community objective (Horns et al. 2003) focuses on the nearshore habitat zone (15-80 m, ~16% of Lake Superior's surface area) because the fish community in this zone includes most of the lake's important predator and prey species. In addition, most survey work and fishery harvests have been in this zone.

O.T. Gorman.[11] U.S. Geological Survey—Lake Superior Biological Station, 2800 Lakeshore Drive East, Ashland, WI 54806, USA.

J.D. Stockwell. Gulf of Maine Research Institute, 350 Commercial Street, Portland, ME 04101, USA.

D.L. Yule. U.S. Geological Survey—Lake Superior Biological Station, 2800 Lakeshore Drive East, Ashland, WI 54806, USA.

T.R. Hrabik. University of Minnesota—Duluth, 1035 Kirby Drive, SSB11, Duluth, MN 55812, USA.

M.P. Ebener. Chippewa Ottawa Resource Authority, 179 West Three Mile Road, Sault Sainte Marie, MI 49783, USA.

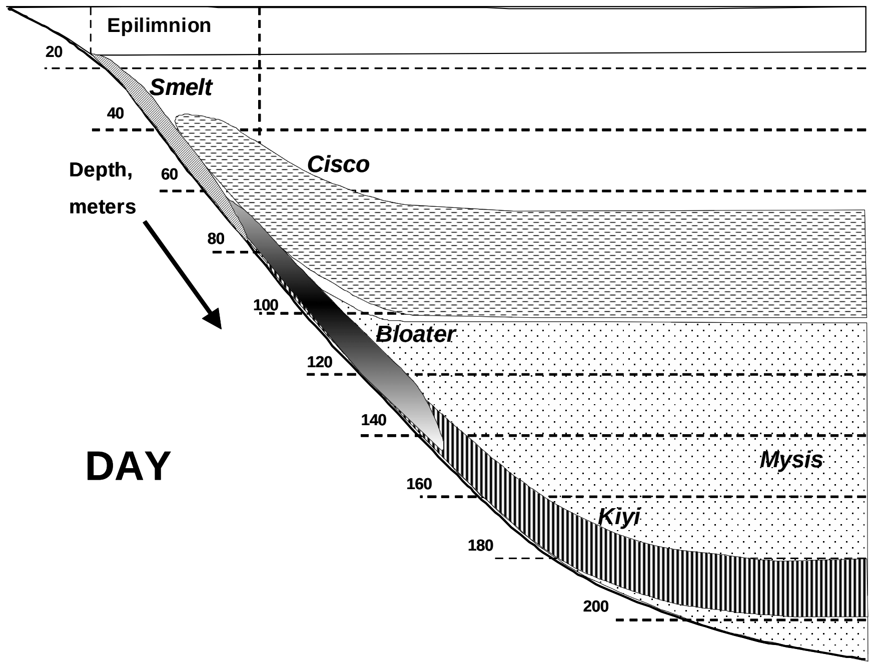
T.C. Pratt. Fisheries and Oceans Canada, Great Lakes Laboratory for Fisheries and Aquatic Sciences, 1219 Queen Street East, Sault Sainte Marie, ON P6A 6W4, Canada.

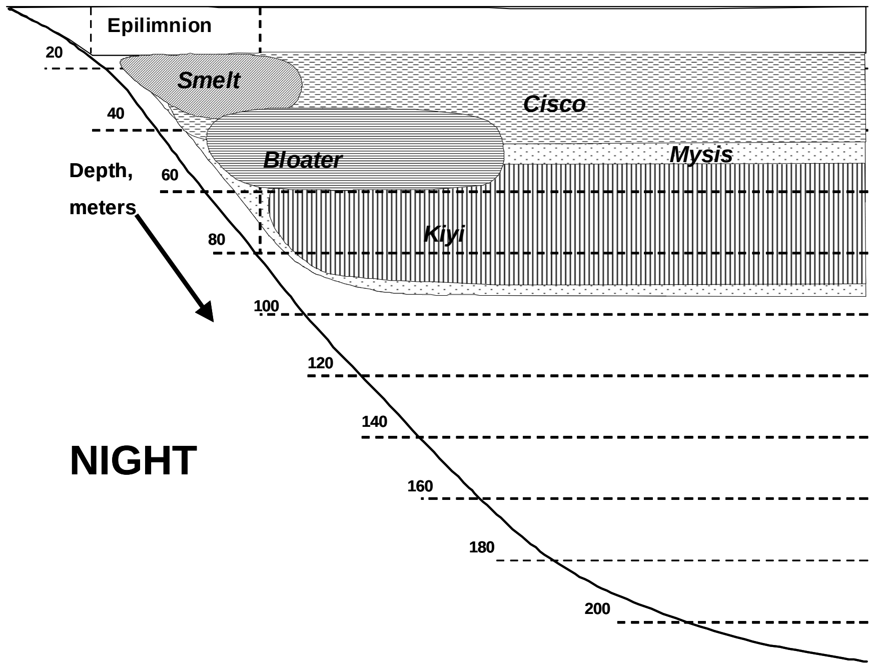
[11]Corresponding author (e-mail: owen.gorman@usgs.gov).

Lean and siscowet lake trout are the principal predators of the nearshore zone; other predators include, burbot, Pacific salmon, and sea lamprey. Principal prey species include cisco, bloater, lake whitefish, rainbow smelt, ninespine stickleback, and slimy sculpin. Sea lamprey prey mainly on lake trout, burbot, and lake whitefish. The principal invertebrate prey are crustaceans that include *Diporeia* spp. (hereafter, diporeia as a common name), *Mysis relicta*, calanoid copepods, cyclopoid copepods, and cladocerans.

Most animals in the nearshore zone (and offshore zone) engage in diel vertical migrations (DVMs) driven by foraging, predator avoidance, or both (Eshenroder and Burnham-Curtis 1999; Gal et al. 2006; Hrabik et al. 2006a; Jensen et al. 2006). The primary invertebrate crustaceans, such as *Mysis*, move up toward the surface at night and are followed and preyed upon by planktivorous fishes, such as cisco—both then move down during the day to decrease their vulnerability to predation (Hrabik et al. 2006a; Jensen et al. 2006). Lake trout also engage in DVMs that track the movement of their coregonine prey (Hrabik et al. 2006a). The bulk of the fish biomass in the nearshore zone comprises cisco, bloater, lake whitefish, rainbow smelt, and lake trout (Bronte et al. 2003; Gorman and Hoff 2009). During summer months (late June to mid-September), bloater, rainbow smelt, and juvenile cisco are largely demersal during the day and pelagic (i.e., in the water column) at night, whereas juvenile and adult lake whitefish are demersal both day and night and adult cisco are pelagic both day and night (Fig. 19; Stockwell et al. 2006a; Yule et al. 2007).

Fig. 19. Summer (late June to mid-September) day and night depth distributions of principal prey fishes and *Mysis relicta* in Lake Superior. Information for this diagram comes from Gorman et al. (2008b), Stockwell et al. (2006b), Yule et al. (2007), and unpublished data from T. Hrabik and the U.S. Geological Survey—Lake Superior Biological Station, Ashland, Wisconsin.


Epilimnion
20
Smelt
40
Depth,
meters
60
Cisco
80
100
Bloater
120
140
DAY
Mysis
160
Kiyi
180
200


Epilimnion
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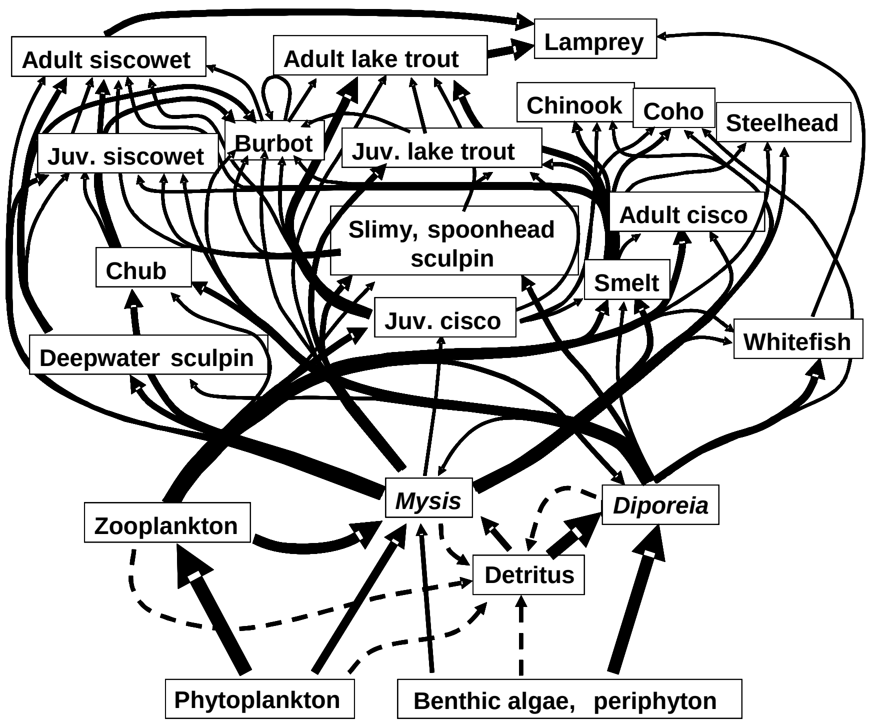
Depth,
meters
20
40
60
80
100
120
140
160
180
200
NIGHT

Stable isotope studies have shown that the Lake Superior ecosystem passes energy and nutrients through food chains leading to two major endpoints: lean and siscowet lake trout as top predators in the nearshore zone and siscowet trout as the top predator in the deep offshore zone (Harvey and Kitchell 2000; Harvey et al. 2003). The predominant prey fishes consumed by lean lake trout in nearshore waters are pelagic species (rainbow smelt and cisco) (Conner et al. 1993; Ray et al. 2007), which, in turn, consume pelagic zooplankton and *Mysis* (Anderson and Smith 1971). The major prey species consumed by siscowet lake trout include kiyi, bloater, and deepwater sculpin (Conner et al. 1993; Ray et al. 2007), which, in turn, rely on the benthic invertebrate diporeia and demersal-oriented *Mysis* as principal food resources (Anderson and Smith 1971). Although some overlap exists in the diet of lean and siscowet lake trout (Ray et al. 2007), the difference is sufficient to impart distinct stable isotope signatures in adult fish (Harvey and Kitchell 2000; Harvey et al. 2003).

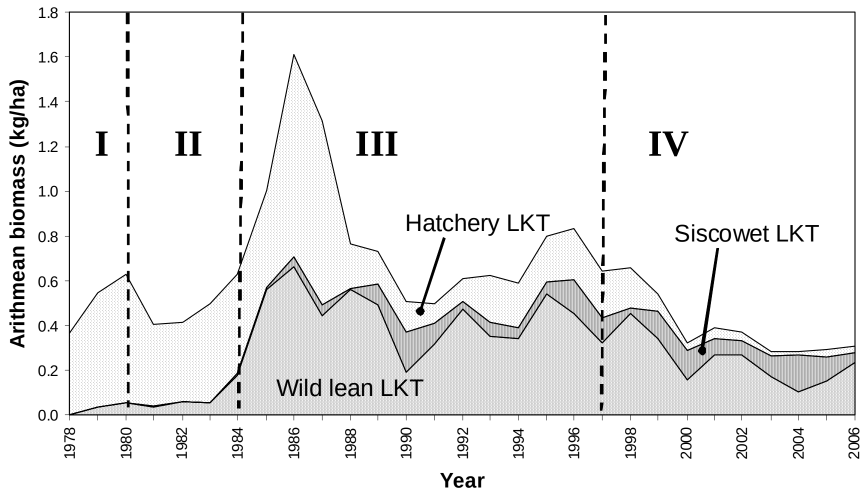
The nearshore food web of Lake Superior is characterized by four major trophic levels: lower-trophic producers (pelagic phytoplankton and benthic macrophytes, periphyton, and benthic algae), lower trophic consumers (invertebrates), mid-trophic consumers (prey fishes), and upper-trophic consumers (predator fishes). Energy enters the food web at the lower trophic level through a pelagic pathway that originates with pelagic primary-production input and moves upward through zooplankton and *Mysis* to cisco and rainbow smelt and finally to mainly lean lake trout at the upper trophic level (Fig. 20). An alternate pathway occurs through benthic primary production and detrital input to diporeia and *Mysis* and then moves upward to bloater, lake whitefish, and various sculpins (slimy, spoonhead, deepwater), terminating mainly in siscowet lake trout. A cross-linkage in the food web between the pelagic and benthic origins of energy is considerable, and multiple consumers are using single resources, e.g., several planktivore fishes consume *Mysis*. Consequently, the potential for complex predator-prey and competitive interactions is substantial (Gal et al. 2006). In the Lake Superior food web, lake trout exert strong top-down effects on community structure (Hairston et al. 1960; Hairston and Hairston 1993, 1997). However, sea lamprey, an invasive species, has the potential to destabilize this food web by reducing the abundance and size structure of lake trout, thereby reducing its influence on mid-trophic-level consumers. Destabilization of a top native predator can lead to a cascade of changes in community and food-web structure down to the lowest level (Carpenter and Kitchell 1988, 1993; Kitchell et al. 1988; Gal et al. 2006).

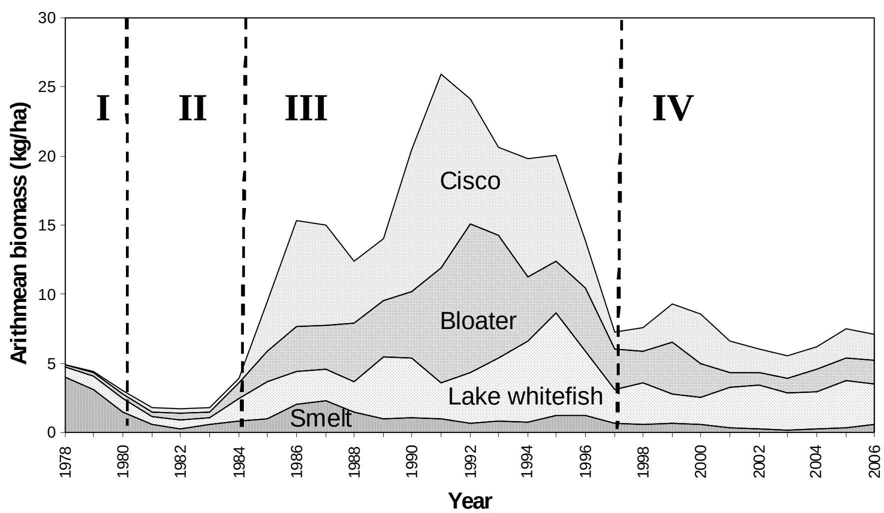
Fig. 20. An idealized food web of energy transference in the nearshore and offshore habitat zones of Lake Superior. Pathway thickness reflects relative amount of energy transferred. Dashed pathways indicate major links in the detrital component of the food web. “Chub” refers to deepwater cisco (bloater, shortjaw cisco, and kiyi). Structure of the food web is adapted from Kitchell et al. (2000).

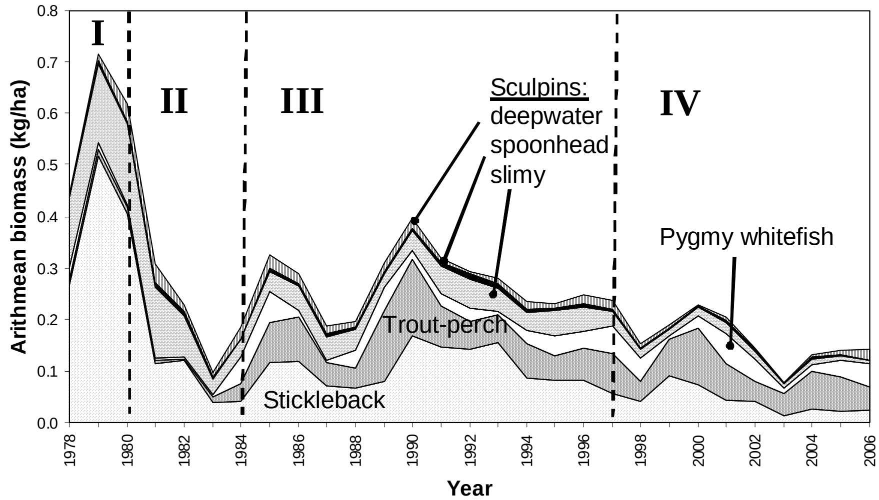


The Lake Superior fish community appears to have experienced four phases of major structural change in community composition since 1978 (Fig. 21; Bronte et al. 2003; Gorman 2007; Gorman and Hoff 2009). During Phase I, 1978-1979, the fish community was dominated by non-native rainbow smelt and strains of hatchery-origin lake trout. In Phase II, 1980-1983, fish-community biomass declined abruptly to <2 kg•ha^{-1} as rainbow smelt and hatchery-origin lake trout biomass declined. Phase III, 1984-1996, represents a recovery phase for several native fishes, most notably production of the largest year-class of cisco (1984) in the time series followed by three consecutive strong cisco year-classes (1988, 1989, and 1990). Strong recovery of cisco was paralleled by a resurgence of bloater and lake whitefish biomass and a rapid recovery of most wild lean lake trout populations. Rainbow smelt populations rebounded only moderately. Estimated mean biomass of prey fish exceeded 25 kg•ha^{-1} in 1991-1992, and wild lake trout biomass exceeded 0.5 kg•ha^{-1} in 1986, 1988, 1992, and 1995 (Fig. 21). Phase IV, 1997-2006, appears to be a fish-community equilibrium phase during which biomass of native prey fishes and rainbow smelt declined. Wild lake trout biomass declined moderately to ~0.3 kg•ha^{-1}, and increases in biomass of prey fish were of short duration and were driven by strong year-classes of cisco and bloater in 1998 and 2003. Lake trout appeared to become increasingly food limited (Sitar and He 2006; Gorman 2007), which is expected in systems where top predators and their prey are at equilibrium. Present evidence suggests that most wild lake trout populations in Lake Superior are fully recovered and are at, or exceed, historical levels of abundance (Wilberg et al. 2003; Sitar and He 2006).

Fig. 21. Trends in biomass of major fish species of the nearshore zone (15-80-m depth) of U.S. waters of Lake Superior, 1978-2006. Data is from U.S. Geological Survey annual spring (May-June) bottom-trawl assessments. Average annual biomass values were smoothed by averaging biomass (kg•ha^{-1}) for year *N* and year *N*-1. Roman numerals and vertical dashed lines delineate four distinct phases of the nearshore-zone fish community: I (1978-1979), II (1980-1983), III (1984-1996), IV (1997-2006).


I
II
III
IV
Hatchery LKT
Siscowet LKT
Wild lean LKT
Arithmean biomass (kg/ha)
Year


I
II
III
IV
Cisco
Bloater
Lake whitefish
Smelt
Arithmean biomass (kg/ha)
Year



Cox and Kitchell (2004) concluded that the abundant adult rainbow smelt population in Lake Superior prior to 1980 was a major factor in suppressing recovery of cisco populations, and the dominance of hatchery-origin lake trout as the primary predator prior to 1980 implicates them as being primarily responsible for the decline of rainbow smelt allowing the recovery of cisco, bloater, and lake whitefish populations (Gorman 2007; Gorman and Hoff 2009).

OFFSHORE FISH COMMUNITY: PREY FISHES

Jason D. Stockwell, Daniel L. Yule, and Owen T. Gorman

A self-sustaining assemblage of prey dominated by indigenous species at population levels capable of supporting desired populations of predators and a managed commercial fishery.

Until recently, very little attention has been paid to the offshore fish community, despite the above fish-community objective (Horns et al. 2003), because relatively few data were available from this habitat zone (>80-m depth). During May-October 2001-2005, data were collected from the offshore zone to a depth of 325 m using day and night bottom trawls, mid-water trawls, and acoustics, which provided density (fish•ha^{-1}) and biomass (kg•ha^{-1}) estimates for deepwater sculpin and kiyi and density estimates and length-frequency for cisco. These three species were the dominant prey species, by numbers and biomass, captured in offshore bottom and mid-water trawl tows during this period (e.g., Yule et al. 2009; Stockwell et al. 2010). Other prey species captured included rainbow smelt, bloater, shortjaw cisco, ninespine stickleback, spoonhead sculpin, and lake whitefish. Stockwell et al. (2006a) provide a description of the sampling methodologies.

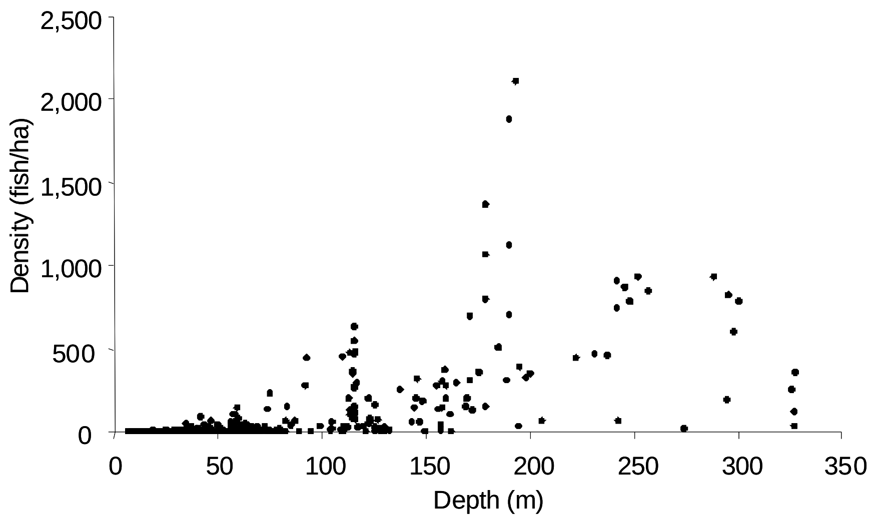
J.D. Stockwell.[12] Gulf of Maine Research Institute, 350 Commercial Street, Portland, ME 04101 USA.

D.L. Yule and O.T. Gorman. U.S. Geological Survey—Lake Superior Biological Station, 2800 Lakeshore Drive East, Ashland, WI 54806, USA.

[12]Corresponding author (e-mail: jstockwell@gmri.org).

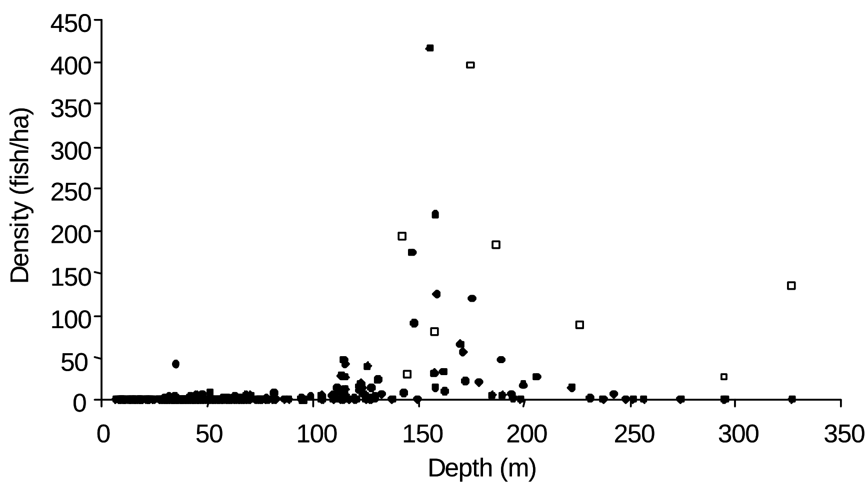
Deepwater sculpin, although occurring also in the nearshore zone, were most abundant in the offshore zone and were present at the maximum depth sampled (325 m; Fig. 22). Maximum estimated density of deepwater sculpin was 2,102 fish•ha^{-1}. Mean density (± SE) in the offshore zone was 274.0 ± 31.8 fish•ha^{-1}and biomass was 1.61 ± 0.201 kg•ha^{-1}. Conversely, mean density was only 4.0 ± 0.7 fish•ha^{-1}and biomass was 0.01 ± 0.006 kg•ha^{-1} in the nearshore zone. There was no significant difference in deepwater sculpin density or biomass estimates between day or night collections at a subset of offshore stations.

Fig. 22. Density estimates of deepwater sculpin as a function of bathymetric depths sampled in Lake Superior during May-October, 2001-2005.



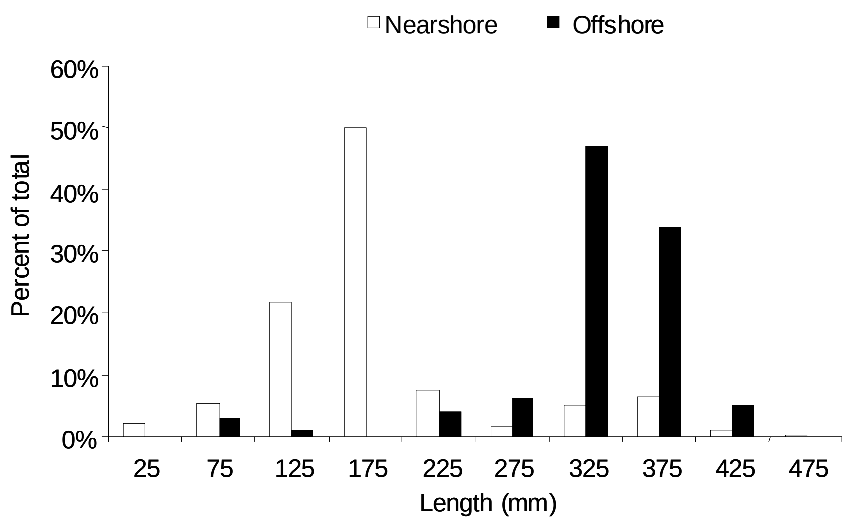
Kiyi captured with day bottom-trawl tows were found almost exclusively in the offshore zone (approximately 110 to 225 m; Fig. 23). Mean density and biomass estimates from day bottom trawls in all offshore depths sampled (80-325 m) were 21.0 ± 5.8 fish•ha^{-1} and 0.75 ± 0.170 kg•ha^{-1}, but estimates for 110-225 m were greater at 30.0 ± 8.0 fish•ha^{-1} and 1.04 ± 0.232 kg•ha^{-1}. Very few kiyi were caught in night bottom-trawl tows (mean density <1 fish•ha^{-1}), indicating kiyi undergo diel vertical migration. Mean density of kiyi in the pelagic zone at night, based on acoustics and mid-water trawl tows, was 126.0 ± 40.8 fish•ha^{-1}. Although kiyi were found in the pelagic zone over bathymetric depths >225 m at night, they were absent in day bottom trawls at these depths (Fig. 23), suggesting there may be a limit to their daytime bathymetric distribution. Because depths >225 m represent about 17% of Lake Superior, the combination of acoustics and mid-water trawls is likely the best strategy for assessing kiyi populations in the offshore zone.

Fig. 23. Density estimates of kiyi collected with day bottom trawls (circle) and night acoustics/mid-water trawls (square) at bathymetric depth sampled in Lake Superior during May-October, 2001-2005.



Previous studies indicated that cisco were pelagic and occupied the offshore zone (Koelz 1929; Dryer and Beil 1964; Selgeby 1982; Selgeby and Hoff 1996). These life-history characteristics were confirmed based on night acoustics and mid-water trawl sampling in the offshore zone during spring, summer, and fall of 2005 (Stockwell et al. 2006a, 2010; Yule et al. 2009). No cisco were captured in day bottom-trawl tows, suggesting cisco remain pelagic throughout the day. Most cisco captured in these mid-water trawl tows were adults (>250-mm total length), whereas most captured in nearshore mid-water tows were juveniles (Fig. 24). Density estimates of adult cisco in offshore waters in spring 2005 (39 fish•ha^{-1}) were higher than nearshore estimates of adults (21 fish•ha^{-1}), although the difference was not statistically significant (Stockwell et al. 2006a).

Fig. 24. Length-frequency distributions of cisco captured in night mid-water trawls in 2005 (spring, summer, and fall combined) in nearshore and offshore zones in Lake Superior. Sample size was 550 in nearshore waters (15-80 m) and 100 in offshore waters (>80 m).



Scaling our density estimates to the total area of the offshore zone (6 million ha) provides a preliminary estimate of total abundance for deepwater sculpin, kiyi, and cisco. Deepwater sculpin were most abundant, an estimated 1,706 million individuals, followed by kiyi at 784 million and cisco at 255 million. Multiplying abundance by mean mass of each species (deepwater sculpin = 5.0 g, kiyi = 43.4 g, and cisco = 249.0 g) generates a total biomass estimate for deepwater sculpin at 8,530 metric tonnes (t), kiyi at 34,026 t, and cisco at 63,495 t.

The data presented here indicate that the fish-community objective for prey fish ("to support predator populations and a managed commercial fishery") is being achieved in the offshore zone of Lake Superior. The principal predator (siscowet lake trout) has increased over the last few decades (Bronte et al. 2003), suggesting that prey resources were sufficient to support this increase. Negus et al. (2008) found that the biomass of coregonines greatly exceeded consumption by predators in deep offshore-zone waters of western Lake Superior in 2004, whereas predators consumed 50% of available coregonine biomass and nearly all rainbow smelt biomass in nearshore-zone waters. Negus et al. (2008) also suggested that the offshore zone might act as a potential refuge for prey fish from predators, and Stockwell et al. (2010) suggest that the refuge concept may be true especially for adult cisco. Lakewide commercial harvest of cisco in all habitat zones in 2005 was 480 t, which is <1% of the estimated cisco biomass (mostly adults) in the offshore zone alone. Although the sustainable level of cisco harvest has not been determined, our comparison of cisco biomass with harvest suggests exploitation is currently at a low level.

Recommendations

1. Assess deepwater sculpin day and night with bottom trawls throughout the offshore zone.
2. Because kiyi undergo diel vertical migrations but may remain pelagic during the day in waters >225 m, night sampling with mid-water trawls and acoustics is recommended to estimate kiyi abundance and to collect biological parameters in the offshore zone.
3. Adult cisco are mainly pelagic throughout the lake and, therefore, must be assessed using night mid-water trawls and acoustics.

OFFSHORE FISH COMMUNITY: BURBOT

Stephen T. Schram, Jason D. Stockwell, and Shawn P. Sitar

Protect and sustain the diverse community of indigenous fish species not specifically mentioned earlier (burbot, minnows, yellow perch, northern pike, and suckers). These species add to the richness of the fish community and should be recognized for their ecological importance and cultural, social, and economic value.

Burbot, one of the few minor species identified in the lake's fish-community objectives (Horns et al. 2003), are a native piscivore that inhabits all habitat zones of Lake Superior. They are caught incidentally in commercial and sport fisheries but are not actively sought by either fishery. Their historical abundance prior to the sea lamprey invasion is unknown. However, burbot abundance declined due to sea lamprey predation and then resurged following implementation of sea lamprey control (Smith 1968; Lawrie and Rahrer 1972; Smith and Tibbles 1980).

S.T. Schram.[13] Wisconsin Department of Natural Resources, PO Box 589, 141 South Third Street, Bayfield, WI 54814, USA.

J.D. Stockwell. Gulf of Maine Research Institute, 350 Commercial Street, Portland, ME 04101, USA.

S.P. Sitar. Michigan Department of Natural Resources and Environment, 484 Cherry Creek Road, Marquette, MI 49855, USA.

[13]Corresponding author (e-mail: stschram@charter.net).

Based on the catch-per-unit effort in summer graded-mesh gillnet surveys conducted during 2001-2005, burbot relative abundance was highest and increasing in the westernmost Minnesota management unit (MN-1), possibly owing to nearby river spawning habitat and rocky in-lake substrates that afford juveniles protection from predation by lake trout (Schram 2000). Abundance declined in MN-2 and MN-3. In Wisconsin waters, burbot abundance in management units (WI-1 and WI-2) has been low but stable during 2001-2005, although abundance in WI-1 prior to 2001 had been declining. In Michigan waters, burbot abundance was low in all management units, and the eastern units were the lowest of all in U.S. waters. Day bottom-trawl surveys indicated a slow, erratic decline in burbot abundance throughout the lake since the mid-1980s (Stapanian et al. 2008).

Diet studies in Michigan and Wisconsin found that burbot smaller than 400 mm consumed primarily *Mysis relicta* and sculpin (SPS, unpublished data; Schram et al. 2006). Burbot larger than 400 mm were almost exclusively piscivores (Schram et al. 2006). Small burbot are prey for lake trout, and this predation may be limiting burbot abundance in Lake Superior. Burbot comprise 3-80% by weight of the large siscowet lake trout diet and 43% of the large lean lake trout diet in Lake Superior (Fisher and Swanson 1996; Peck and Sitar 2000; see Fig. 4, Sitar et al. 2008). In the Apostle Islands area (Fig. 1; WI-2), a decline in burbot abundance was linked to increased abundance of siscowet and lean lake trout (Schram et al. 2006). However, lack of burbot abundance data for years prior to the demise of native lake trout by sea lamprey predation and commercial fishing (prior to 1940) precludes evaluating the causes of the decline.

Recommendations

1. Develop standardized assessment programs, accounting for catchability in assessment gear (gillnets and trawls), to adequately describe population characteristics (abundance and age and size composition).
2. Determine the location of spawning areas in the lake and tributaries.

OFFSHORE FISH COMMUNITY: SISCOWET

Mark P. Ebener, Shawn P. Sitar, William P. Mattes, Thomas R. Hrabik, and Melissa T. Mata

…achieve and maintain genetically diverse self-sustaining populations of lake trout that are similar to those found in the lake prior to 1940, with lean lake trout being the dominant form in nearshore waters, siscowet lake trout the dominant form in offshore waters, and humper lake trout a common form in eastern waters and around Isle Royale.

The above fish-community objective from Horns et al. (2003) placed greater biological interest on a heretofore somewhat neglected species. Siscowet lake trout originally inhabited all the Great Lakes, except Lake Ontario (Krueger and Ihssen 1995), but they are now found only in Lake Superior (Bronte et al. 2003). Siscowet-like lake trout have been reported also in Great Slave Lake in northwestern Canada (Zimmerman et al. 2006).

M.P. Ebener.[14] Chippewa Ottawa Resource Authority, 179 West Three Mile Road, Sault Sainte Marie, MI 49783, USA.

S.P. Sitar. Michigan Department of Natural Resources and Environment, 484 Cherry Creek Road, Marquette, MI 49855, USA.

W.P. Mattes. Great Lakes Indian Fish and Wildlife Commission, 72682 Maple Street, Odanah, WI 54861, USA.

T.R. Hrabik. University of Minnesota—Duluth. 2035 Kirby Drive, SSB11, Duluth, MN 55812, USA.

M.T. Mata. Michigan State University, 13 Natural Resources Building, East Lansing, MI 48824, USA.

[14]Corresponding author (e-mail: mebener@lighthouse.net).

Siscowet are distinguished from lean lake trout and humper lake trout by their short convex snout; high fat content in flesh and viscera; deep body shape; and a short, thick caudal peduncle (Eschmeyer and Phillips 1965; Burnham-Curtis and Smith 1994; Krueger and Ihssen 1995; Moore and Bronte 2001; Henderson and Anderson 2002; Bronte and Moore 2007). Although these morphological features are likely genetically based, overlap in some features is considerable, making it difficult to distinguish the three morphotypes confidently (Burnham-Curtis and Smith 1994; Burnham-Curtis and Bronte 1997; Moore and Bronte 2001). The siscowet's high fat content is believed to be an aid in buoyancy compensation associated with diel vertical migration to feed on coregonines (Henderson and Anderson 2002; Hrabik et al. 2006a; Zimmerman et al. 2006).

Multiple reproductively isolated stocks of siscowet inhabit Lake Superior, and some fish can be found spawning in every month of the year (Eschmeyer 1955; Bronte 1993; Krueger and Ihssen 1995). Based on mitochondrial DNA analysis, their populations are genetically diverse and their diversity appears to increase from east to west in the lake (M.K. Burnham-Curtis, unpublished data). However, genetic diversity of siscowet may be less than that of humper from Caribou Island and lean lake trout from Isle Royale (Burnham-Curtis and Bronte 1997). Recent work by Bronte and Moore (2007), using morphological characteristics, identified three geographic groups of siscowet in Lake Superior (Isle Royale, eastern Michigan, and western Michigan).

Fishery Yield

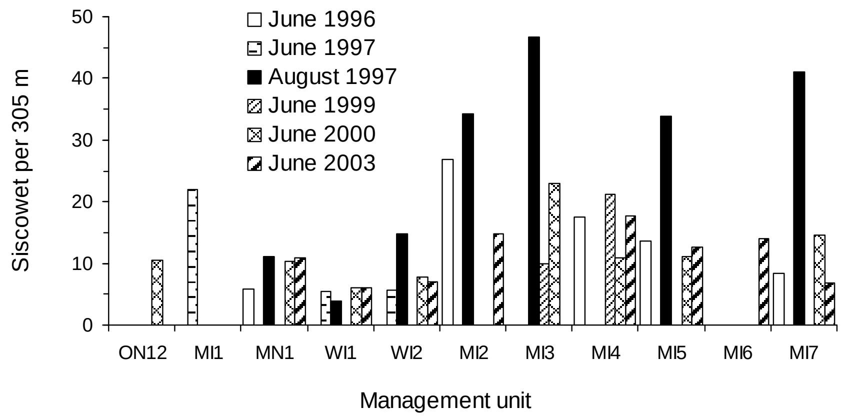
The siscowet harvest is mostly commercial and was not distinguished from the total lake trout yield in Michigan prior to 1970, in Wisconsin prior to 1982, and as yet is not distinguished in Ontario. Minnesota has no commercial fishery for siscowet. Commercial yield of siscowet averaged 117,000 kg•ha^{-1} during 1970-2005, and 60% of this yield was taken in Michigan waters. Yield averaged only 46,200 kg•ha^{-1} during 2001-2005 (the current reporting period) and was only slightly higher during 1996-2000 (73,200 kg•ha^{-1}). The peak yield was 441,000 kg•ha^{-1} in 1987, of which 63% came from Michigan. Commercial yield in Michigan declined dramatically after 1990 because residual levels of the pesticide chlordane were found to exceed the 0.3-ppm guideline for fish consumption (Bronte et al. 2003) Chlordane was still above the no-consumption advisory level (0.3 ppm) in the flesh of siscowet >457-mm total length during 2001-2005 (Bredin 1998; Lake Superior Binational Program 2006a). However, now data are needed to allow the determination of sustainable yield because of recent interest in developing a fishery capable of supporting industrial production of omega-3 fatty acid. Despite the high biomass of siscowet, its potential yield would be constrained by its life-history strategy, which features slow growth and late maturity (Bronte et al. 2003).

Abundance

Siscowet are the most abundant form of lake trout in Lake Superior, a finding based on lakewide gillnet surveys coordinated by the lake's technical committee and conducted in June of 1996, 1997, 1999, 2000, and 2003 and August/September of 1997 in management units MN-1, WI-1, WI-2, MI-1-7, and Ontario 12 (Fig. 1; Sitar et al. 2007; Sitar et al. 2008). Lakewide catch-per-unit effort (CPUE) (CPUE = number of fish per 305 m of gillnet) of siscowet in June averaged 16 compared with 2 for lake trout. The CPUE of siscowet in June declined from 16 in 1996 to 10 in 2003. The CPUE in August/September 1997 was 30, compared with 2 for lake trout.

Substantial spatial variability exists in abundance of siscowet. The CPUE of siscowet in June was consistently lowest in Minnesota and Wisconsin management units MN-1 and WI-1-2, intermediate in MI-4-7 management units, and highest in western Michigan management units MI-2-3 (Fig. 25). Siscowet CPUE in August/September 1997 was considerably greater than during June in all management units, except MN-1 and WI-1. The actual population size of siscowet in western Lake Superior (comprising all MN, WI, and MI-1-2 management units) during 1981-1994 (Ebener 1995) was 33 million age-1 and older fish. Negus et al. (2007) estimated abundance of age-1 and older siscowet in Wisconsin and Minnesota waters at 12 and 10 million in 2000 and 2004, respectively, using an approach similar to Ebener (1995). The difference between the two estimates was due to Ebener's inclusion of MI-2-3 where abundance was three times that in Minnesota and Wisconsin waters (Fig. 25). Lakewide abundance of siscowet in 2005 was estimated at 26 million based on the expansion of the density of fish caught in day bottom–trawl stations to the total area of Lake Superior (U.S. Geological Survey, Ashland Biological Station, unpublished data).

Fig. 25. Catch-per-unit effort (fish•305 m^{-1}) of siscowet caught in graded-mesh gillnet surveys in management units of Lake Superior averaged for June of 1996, 1997, 1999, 2000, and 2003 and August/September of 1997.



The fish-community objective for siscowet has been achieved. Siscowet are self-sustaining throughout the lake and are morphologically and genetically diverse. Although siscowet diversity may be less now than during the 1940s, it is the most abundant top predator in the lake. Despite its prominence, the siscowet has little dietary overlap with lean lake trout (Harvey and Kitchell 2000; Harvey et al. 2003; Ray et al. 2007).

OFFSHORE FISH COMMUNITY: ECOLOGICAL INTERACTIONS

Jason D. Stockwell, Daniel L. Yule, Thomas R. Hrabik, Michael E. Sierszen, Mary T. Negus, Owen T. Gorman, Donald R. Schreiner, and Mark P. Ebener

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J.D. Stockwell.[15] Gulf of Maine Research Institute, 350 Commercial Street, Portland, ME 04101, USA.

D.L. Yule. U.S. Geological Survey—Lake Superior Biological Station, 2800 Lakeshore Drive East, Ashland, WI 54806, USA.

T.R. Hrabik. University of Minnesota—Duluth, 1035 Kirby Drive, SSB11, Duluth, MN 55812, USA.

M.E. Sierszen. U.S. Environmental Protection Agency, Mid-Continent Ecology Division, 6201 Congdon Boulevard, Duluth, MN 55804, USA.

M.T. Negus. Minnesota Department of Natural Resources, Area Fisheries Office, 5351 North Shore Drive, Duluth, MN 55804, USA.

O.T. Gorman. U.S. Geological Survey—Lake Superior Biological Station, 2800 Lakeshore Drive East, Ashland, WI 54806, USA.

D.R. Schreiner. Minnesota Department of Natural Resources, Lake Superior Area Fisheries Program, 5351 North Shore Drive, Duluth, MN 55804, USA.

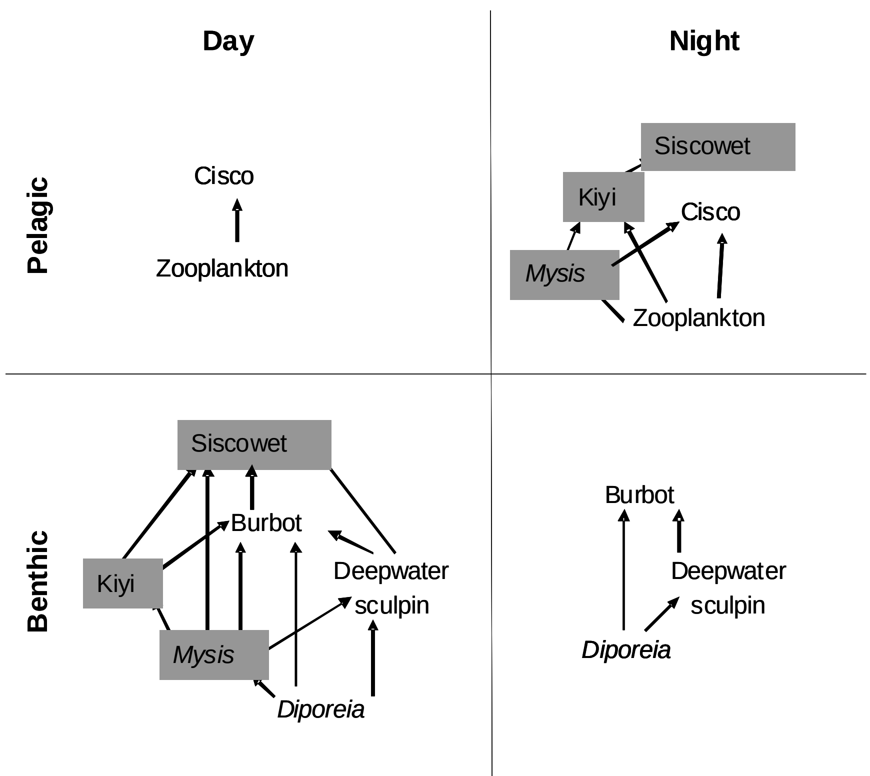
M.P. Ebener. Chippewa Ottawa Resource Authority, 179 West Three Mile Road, Sault Sainte Marie, MI 49783, USA.

[15]Corresponding author (e-mail: jstockwell@gmri.org).

The offshore (>80 m) fish community of Lake Superior is made up of predominately native species. The most prominent species are deepwater sculpin, kiyi, cisco, siscowet lake trout, burbot, and the exotic sea lamprey. Bloater and shortjaw cisco are also found in the offshore zone. Bloater is abundant in the offshore zone but appears restricted to depths shallower than 150 m (Selgeby and Hoff 1996; Stockwell et al. 2010), although it occuppied greater depths several decades ago (Dryer 1966; Peck 1977). Shortjaw is relatively rare in the offshore zone (Hoff and Todd 2004; Gorman and Hoff 2009; Gorman and Todd 2007). Lake whitefish is also known to frequent bathymetric depths >100 m (Yule et al. 2008b). In this chapter, we develop a conceptual model of the offshore food web based on data collected during 2001-2005 and on inferences from species interactions known for the nearshore fish community. We then develop a framework for examination of energy and nutrient movements within the pelagic and benthic habitats of the offshore zone and across the offshore and nearshore zones.

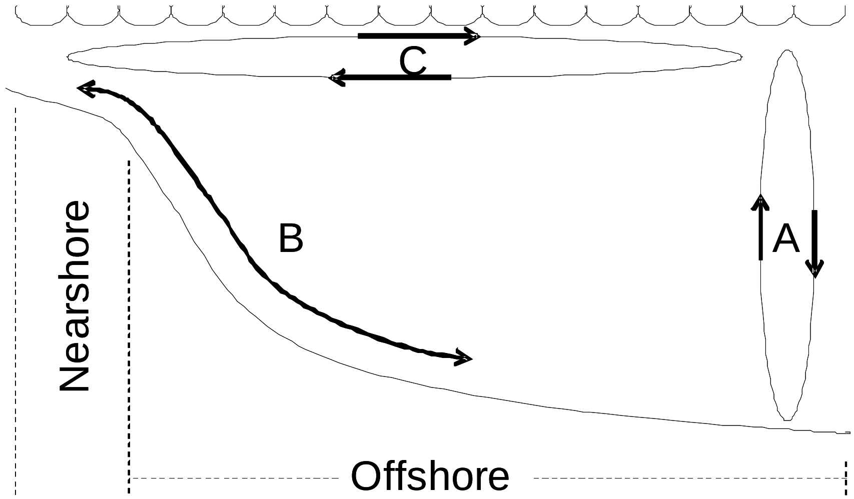
The template we use for our conceptual offshore-zone food web consists of benthic and pelagic habitats during day and night (Fig. 26). In the benthic habitat, the macroinvertebrate *Diporeia* spp. (hereafter, diporeia as a common name) represents the lowest trophic level day or night, and siscowet (day) and burbot (night) represent the highest trophic level. In the pelagic habitat, zooplankton represents the lowest trophic level day or night, and cisco (day) and siscowet (night) represent the highest level. Cisco is zooplanktivorous day and night (Johnson et al. 2004). Deepwater sculpin and kiyi feeds on the macroinvertebrates diporeia and *Mysis relicta* during the day, and sculpin feeds on them at night (Anderson and Smith 1971; Bowers 1988; Auer and Kahn 2004; Scharold et al. 2004). Burbot and siscowet feed on all lower trophic levels (Bailey 1972; Fisher and Swanson 1996), and evidence suggests burbot is a prominent prey of siscowet (Harvey et al. 2003). At night, *Mysis*, kiyi, and siscowet migrate vertically and become part of the pelagic food web (Bowers 1988; Hrabik et al. 2006a; Jensen et al. 2009; Stockwell et al. 2010) with *Mysis* feeding on zooplankton, kiyi on *Mysis*, and siscowet on coregonines (Anderson and Smith 1971; Hrabik et al. 2006a; Jensen et al. 2006). Stockwell et al. (2010) hypothesized that the large size of cisco inhabiting offshore waters (Fig. 24) lessens its predation risk to siscowet because of gape limitations (Yule and Luecke 1993; Keeley and Grant 2001). This inference suggests kiyi is the primary coregonine prey of siscowet in the offshore pelagic habitat. The role of sea lamprey in shaping community dynamics in the offshore zone is poorly understood. Although siscowet is much more abundant that lean lake trout, sea lamprey marking rates on siscowet are comparable to those for lean lake trout (Fig. 13; Bronte et al. 2003; Sitar et al. 2008), suggesting either that sea lamprey are much more abundant and mortality by sea lamprey is much higher in the offshore zone than previously thought, or that marking rates on siscowet are higher because the cold water in the offshore zone slows mark healing.

Fig. 26. Conceptual food web of the Lake Superior offshore-zone community. Arrows indicate flow of energy from lower to high trophic levels. Shaded boxes indicate those species that undergo diel vertical migration.



Our conceptual offshore food web can be used as a framework to examine how food-web structure and migratory behavior in the Lake Superior ecosystem affects the spatial distribution of predation and other processes as organisms, energy, and nutrients move within and across habitats (Fig. 27). First, we hypothesize that the diel vertical migration (DVM) behavior of *Mysis*, kiyi, and siscowet provides a critical energy transfer link between benthic and pelagic offshore habitats (Fig. 27: A). Hrabik et al. (2006a) and Jensen et al. (2006) found that, under low predator densities, coregonines followed a shallower DVM trajectory, which afforded higher growth opportunities but also included greater predation risk. Under high predator density, they found that prey fish followed a deeper DVM trajectory, which reduced predation risk but also decreased growth potential. In a subsequent study where coregonines were identified to species, Stockwell et al. (2010) attributed the different DVM strategies to differences between cisco and kiyi life histories rather than to different predator densities. Cisco appear to have a size refuge from siscowet, and kiyi DVM appears more consistent with the DVM patterns of *Mysis*, its primary prey. Therefore, *Mysis*, by causing DVM at higher trophic levels, may be a key driver of the vertical movement of energy and nutrients across the offshore benthic and pelagic habitats.

Fig. 27. Diagram showing proposed major migration-driven energy and nutrient transportation pathways in Lake Superior. (A) The offshore link between pelagic and benthic habitats based on diel vertical migration of *Mysis relicta*, kiyi, and siscowet lake trout. (B) The offshore-nearshore link of benthic habitat based on up-the-bank migrations of species such as lake whitefish and siscowet lake trout. (C) The link between offshore pelagic habitat and nearshore benthic habitat based on ontogenetic shifts of juvenile cisco to offshore pelagic habitat and on spawning migrations of adult cisco in the fall from offshore pelagic habitat to nearshore habitat.



Second, we propose a link between offshore and nearshore benthic habitats through diel up-the-bank migrations by benthic fishes (Fig. 27: B). Yule et al. (2008b) found that larger lake whitefish in the Apostle Islands area occupied water deeper than that inhabited by smaller lake whitefish during the day; at night, lake whitefish sizes were well mixed in shallower water as those in deeper water migrated up the bank and returned before morning. They also found a similar migration pattern for siscowet lake trout. These shifts represent huge fluxes of biomass, and presumably of energy and nutrients, between deeper and shallower waters. Because diporeia have depth-specific isotopic signatures in Lake Superior (Sierszen et al. 2006a), specimens from stomachs of lake whitefish and other fish species could be used as natural tags to determine where and when foraging occurs relative to capture location, enabling a better understanding of energy and nutrient flow across habitats.

Lastly, we propose a link between the offshore pelagic habitat and nearshore benthic habitat through movement in late fall of adult cisco from offshore to nearshore for spawning (Fig. 27: C). The abundance of adult cisco (>250 mm) decreased 67% between November 2005 and May 2006 in Thunder Bay, Ontario (Stockwell et al. 2007), and abundance of adult cisco increased substantially in the western arm of Lake Superior between October and November 2006 (Yule et al. 2009). We hypothesize that cisco eggs, derived from offshore zooplankton production, represent through winter a major resource subsidy from the offshore pelagic habitat to the nearshore benthic habitat.

The pathways proposed above provide a framework to examine the gains and losses of energy and nutrients within and across habitats and zones and the effects on community dynamics of the different time scales inherent in these processes. Up-the-bank and vertical migrations occur daily and offshore-nearshore migrations of cisco occur seasonally and annually. The long life span of cisco coupled with their extremely variable and sporadic recruitment patterns (Yule et al. 2008a; Stockwell et al. 2009) may also affect this energy pathway on a time scale of years or even decades (Carpenter and Kitchell 1987). Collectively, these functions and processes may influence the abundance and composition of future fish-community assemblages. The flows of energy and nutrients are issues that must be considered to ensure that the fish-community objectives for Lake Superior are realistic (Kitchell et al. 2000).

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