

## Deepwater Demersal Fish Community Collapse in Lake Huron

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**Abstract.**—Long-term fish community surveys were carried out in the Michigan waters of Lake Huron using bottom trawls from 1976 to 2006. Trends in abundance indices for common species (those caught in 10% or more of trawl tows) were estimated for two periods: early (1976–1991) and late (1994–2006). All common species significantly decreased in abundance during the late period with the exception of the johnny darter *Etheostoma nigrum* and spottail shiner *Notropis hudsonius*, which showed no significant trends, and the round goby *Neogobius melanostomus*, which increased in abundance. Percentage decreases in abundance indices between 1994–1995 and 2005–2006 ranged from 66.4% to 99.9%, and seven species decreased in abundance by more than 90%. The mean biomass of all common species in 2006 was the lowest observed in the time series and was less than 5% of that observed in the mid-1990s. The mean number of common species captured per trawl has also decreased since the mid-1990s. Several factors, including recent invasion of the lake by multiple exotic species, may have contributed to these declines, but insufficient published data are currently available to determine which factors are most important. Our observations suggest that significant changes have occurred in the ecology of Lake Huron since the mid-1990s. The extent of these changes indicates that the deepwater demersal fish community in Lake Huron is undergoing collapse.

Lake Huron is the second largest of the Laurentian Great Lakes and the fifth-largest freshwater lake in the world in terms of surface area. The lake historically supported valuable commercial fisheries for lake trout *Salvelinus namaycush*, lake whitefish *Coregonus clupeaformis*, and deepwater ciscoes *Coregonus* spp. and continues to support economically important fisheries, particularly for lake whitefish (Brown et al. 1999). The native deepwater (water depth > 25 m: Busch and Lary 1996) fish community of Lake Huron was historically dominated by lake trout, which probably fed primarily on deepwater ciscoes and sculpins *Cottus* spp. and *Myoxocephalus* spp. (Eshenroder and Burnham-Curtis 1999). Other species that occurred in deep waters of the lake were the burbot *Lota lota*, lake whitefish, round whitefish *Prosopium cylindraceum*, ninespine stickleback *Pungitius pungitius*, trout-perch *Percopsis omiscomaycus*, spottail shiner *Notropis hudsonius*, lake chub *Couesius plumbeus*, white sucker *Catostomus commersonii*, and longnose sucker *Catostomus catostomus* (Argyle 1982; Spangler and Collins 1992).

The deepwater fish community of Lake Huron has undergone drastic changes over the past century (Berst and Spangler 1972; Ebener et al. 1995). Commercial fishing and the invasion by sea lampreys *Petromyzon marinus* caused the lake trout population in Lake

Huron to collapse by 1950 (Coble et al. 1990; Eshenroder 1992). Two other exotic fish species, the alewife *Alosa pseudoharengus* and rainbow smelt *Osmerus mordax*, have become abundant in the lake since the 1930s and have been implicated in the declines of native species (Smith 1970; Berst and Spangler 1972; Argyle 1982; Evans and Loftus 1987). With the exception of the bloater *Coregonus hoyi*, deepwater ciscoes were drastically reduced in abundance or extirpated from the lake by the 1960s (Brown et al. 1987; Eshenroder and Burnham-Curtis 1999). Lake trout have been stocked annually since the 1970s in an attempt to restore the species, but this effort has been only marginally successful to date (Eshenroder et al. 1995; Whelan and Johnson 2004). Since the late 1960s, nonnative Pacific salmon *Oncorhynchus* spp. have been stocked into the lake (Tanner and Tody 2002) and sea lamprey abundance has declined due to an extensive control program (Smith and Tibbles 1980). Chinook salmon *Oncorhynchus tshawytscha* now reproduce naturally in the basin (Carl 1982; Powell and Miller 1990) and support an economically valuable sport fishery (Bence and Smith 1999).

Since the late 1980s, a new wave of exotic species—including the zebra mussel *Dreissena polymorpha*, quagga mussel *Dreissena bugensis*, round goby *Neogobius melanostomus*, and spiny water flea *Bythotrephes longimanus* (a predatory zooplankton)—has invaded Lake Huron (Ricciardi and MacIsaac 2000; Vanderploeg et al. 2002; Dobiesz et al. 2005). These recent invaders have been responsible for a number of ecological changes in the Great Lakes, from negative

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interactions with individual species (Lauer et al. 2004; Steinhart et al. 2004a) to large-scale ecosystem engineering (Hecky et al. 2004). A number of significant changes have been observed in the Lake Huron ecosystem in recent years, including increased water clarity (Budd et al. 2001); increased occurrence of toxic algal blooms (Vanderploeg et al. 2001); an increase in outbreaks of botulism in fish and birds (EC and USEPA 2006; Yule et al. 2006); a drastic reduction in abundance of benthic amphipods *Diporeia* spp. (Nalepa et al. 2003, 2005, 2007); decreased abundance and altered community structure of zooplankton (R. Barbiero, Loyola University, personal communication); an increase in the occurrence of natural reproduction by lake trout (Riley et al. 2007); decreases in abundance, size at age, and condition of lake whitefish (Mohr and Ebener 2005) and Pacific salmon; and precipitous declines in Chinook salmon harvest (J. E. Johnson, Michigan Department of Natural Resources, Alpena Fisheries Station, personal communication). Here we examine long-term trends in the abundance of deepwater demersal fishes in the Michigan waters of Lake Huron to determine the nature of any changes that may have occurred in the deepwater demersal fish community.

### Methods

The U.S. Geological Survey (USGS) Great Lakes Science Center (GLSC) has monitored fish abundance annually from 1973 to 2006 using bottom trawls (12-m headrope: 1973–1991; 21-m headrope: 1992–2006) along fixed transects at up to 11 depths (9, 18, 27, 36, 46, 55, 64, 73, 82, 92, and 110 m) at five ports (Detour, Hammond Bay, Alpena, Au Sable Point, and Harbor Beach) in the Michigan waters of Lake Huron (Figure 1). Both types of trawl used a cod end with 4.76-mm square mesh. The same fixed transects were sampled each year from the USGS RV *Kaho* during 1973–1977 and from the USGS RV *Grayling* during 1978–2006; some transects were fished from the USGS RV *Cisco* in 1990.

Single, 10-min trawl tows were conducted during daylight at each transect in each year. Tow duration was occasionally less than 10 min; for these tows, catch was standardized to 10-min tows (see correction formula below). Trawl catches were sorted by species, and each species was counted and weighed in aggregate. Large catches (>20 kg) were subsampled; a random sample was sorted, counted, and weighed, and the remainder of the catch was weighed for extrapolation of the sample.

We applied correction factors to standardize trawl data among depths because the actual time on bottom for each trawl increased with depth (Fabrizio et al.

1997). Relative abundance was standardized to catch per effort (CPE; fish/10 min on bottom) as

$$C_t = 10N/K_tT,$$

where  $C_t$  is CPE for trawl type  $t$ ,  $N$  is the catch,  $T$  is tow time, and  $K_t$  is a correction factor that varies with fishing depth ( $D$ , m) and trawl type ( $K_{12} = 0.00400D + 0.8861$  for the 12-m trawl;  $K_{21} = 0.00385D + 0.9149$  for the 21-m trawl). Catches were expressed in terms of density (fish/ha) and biomass (kg/ha) by dividing CPE by the area swept by the trawl. The area swept was estimated as the product of distance towed (speed  $\times$  tow time) and trawl width. Trawl width estimates were depth specific and were based on trawl mensuration data collected from the RV *Grayling* in 1991, 1998, and 2005 (USGS, unpublished data).

To make density estimates from the two trawls comparable, we multiplied density estimates from the 12-m trawl (1976–1991) by species-specific fishing power corrections (FPCs) developed from a comparative trawl experiment based on 150 trawl tows conducted in Lake Huron using both trawl types (75 tows each) in 1979, 1980, and 1988 (USGS, unpublished data). Comparative trawl tows were conducted over the entire depth range (9–110 m) at all ports in Lake Huron, but not all depth–port combinations were included. The FPCs were estimated using generalized linear models with a gamma distribution and a log link; FPCs expressed catches from the 12-m trawl as though they were made with the 21-m trawl. We applied FPCs greater than 1.0 to the density and biomass of alewives, rainbow smelt, bloaters, lake whitefish, and lake trout; FPCs less than 1.0 were applied to the density and biomass of ninespine sticklebacks, slimy sculpin *Cottus cognatus*, and deepwater sculpin *Myoxocephalus thompsonii*. Catches of trout-perch were not significantly different between the two trawl types. Insufficient data were available to estimate FPCs for burbot, spottail shiners, and johnny darters *Etheostoma nigrum*; density estimates were not corrected for these species. Because of the nature of the analyses applied to these data (i.e., abundance indices were compared only within time periods; see below), the FPC value did not affect the results reported here.

Trawl surveys on Lake Huron were completed annually between 3 October and 15 November. In 1992 and 1993, however, trawl surveys occurred in early to mid-September; these data were not used in our analyses, because the distribution of many deepwater species in the Great Lakes is highly variable among seasons (Dryer 1966; Wells 1968; Argyle 1982) and data collected in September may not be comparable with the rest of the time series. In 1998, sampling was conducted in a nonstandard manner, and these data

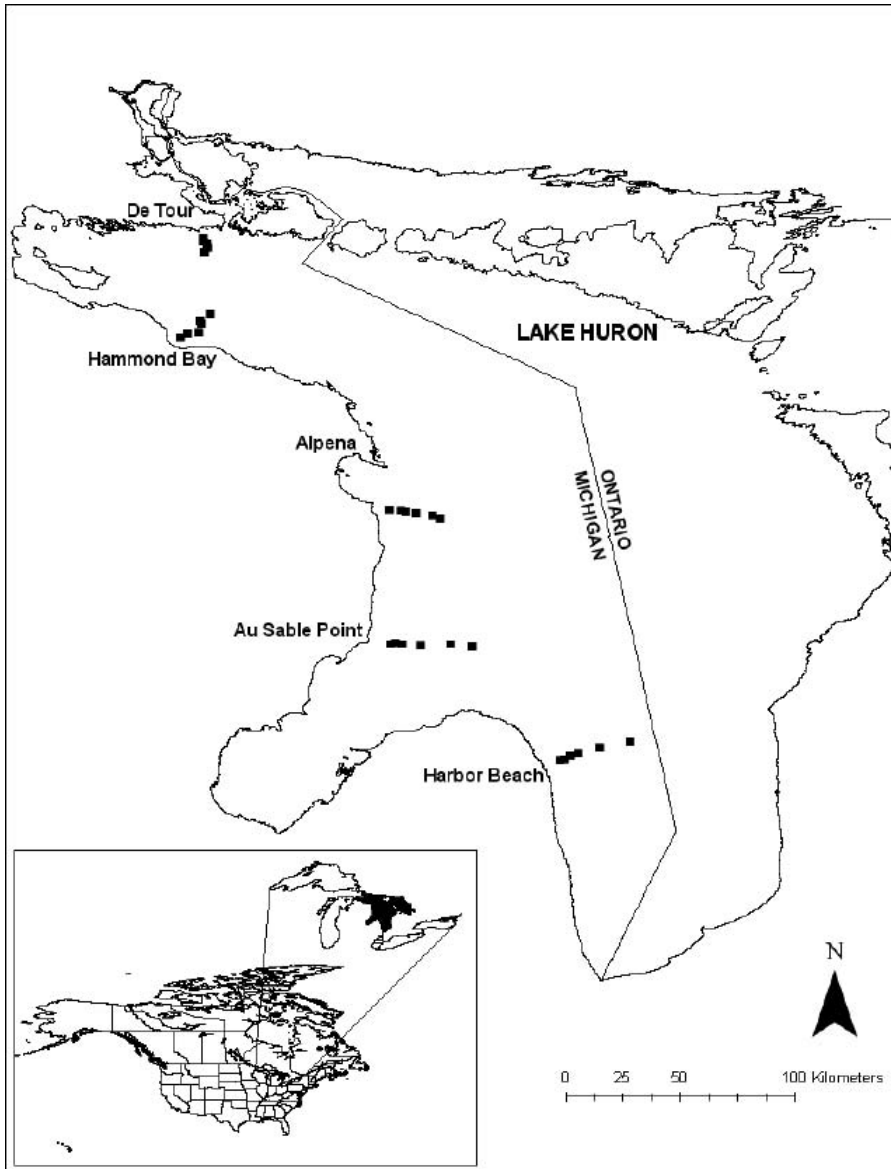


FIGURE 1.—Fall bottom trawl transect locations (black squares) used by the U.S. Geological Survey's Great Lakes Science Center in Michigan waters of Lake Huron. Locations of transects at 27–73-m depths occur in order from near shore to off shore at all ports.

were also excluded from analysis. The fall survey was not conducted in 2000. We did not use data collected prior to 1976, because ports and depths were not consistently sampled until 1976.

We restricted our analysis to trawl catches at six depths (27, 37, 46, 55, 64, and 73 m) that were sampled at all ports in nearly all years. There were 15 missing tows for this range of depths over the time series. Trawls were not completed at 27 m at Detour in 1977,

1999, 2001, 2002, and 2004–2006; at Harbor Beach in 2002; and at Alpena during 2002–2006. Tows were not conducted at 73 m at Harbor Beach in 1996 and 1999. The data set consisted of 795 trawl tows from 27 individual years spanning a period of 31 years.

Using length frequency data, we partitioned the total catch of alewives, rainbow smelt, and bloaters into size-based age-classes. Year-specific length cutoffs were determined from length frequency data and were

used to apportion the catch into two age-classes (age 0 and age 1 and older). Our analyses focused on age-1 and older alewives, rainbow smelt, and bloaters, because many age-0 fish of these species are pelagic and unavailable to the trawls. We similarly excluded age-0 lake trout (<90 mm) from analysis.

*Data analysis.*—Analysis was restricted to species that were common in trawl catches (i.e., those which were captured in at least 10% of all tows). Thirteen species were common in Lake Huron bottom trawl catches: rainbow smelt, alewife, bloater, deepwater sculpin, trout-perch, lake whitefish, ninespine stickleback, slimy sculpin, lake trout, spottail shiner, johnny darter, burbot, and round goby. Species that were occasionally captured but not considered further included the threespine stickleback *Gasterosteus aculeatus*, white perch *Morone americana*, white bass *Morone chrysops*, freshwater drum *Aplodinotus grunniens*, round whitefish, longnose sucker, white sucker, emerald shiner *Notropis atherinoides*, logperch *Percina caprodes*, yellow perch *Perca flavescens*, walleye *Sander vitreus*, and mottled sculpin *Cottus bairdii*.

We calculated an abundance index for each common species as the mean density (fish/ha) from all depths (27–73 m) and ports for each year ( $n = 30$  tows in most cases). We estimated means and standard errors for each species and year by assuming that each tow was an independent replicate. Because abundance indices were means of densities from fixed ports and depths, variability due to these factors was included in residual variation and thus the standard errors and confidence intervals may have overestimated actual uncertainty. We also calculated the annual proportion of trawl tows that included catches of each common species, the mean number of common species captured in trawl tows, and the mean combined biomass of all common species per tow.

We examined trends in abundance indices using linear regression of  $\log_e$  transformed mean density for each species, and year was used as the independent variable. We also used linear regression to examine trends in the arcsine-transformed proportion of tows that captured each common species, the mean number of common species captured in each tow, and mean combined biomass per tow (all common species). The null hypothesis for regression analyses was that there was no trend over time in abundance, proportion of tows, mean number of common species, or biomass (i.e., regression slope = 0). Regression slopes were considered to be significant at  $\alpha$  equal to 0.05;  $\alpha$  was corrected for multiple tests using the step-up sequential Bonferroni procedure of Hochberg (1988). All statistical analyses were conducted using the Statistical Analysis System (SAS; SAS Institute 1996).

We performed regression analyses for two time periods: early (1976–1991) and late (1994–2006). These time periods were chosen because of the change in trawls that occurred in 1992 and the lack of usable data in 1992 and 1993. Determining separate trends for these time periods alleviated potential problems with comparing data from different trawls. For a given time period, we estimated the percentage change in density for all species by estimating the difference in mean density between the first and last 2 years of the series (early period: 1976–1977 and 1990–1991; late period: 1994–1995 and 2005–2006).

Before conducting regression analysis, we tested the data for first-order autocorrelation (Bence 1995; Pyper and Peterman 1998) using the Durbin–Watson test in SAS. Autocorrelation was evident ( $P < 0.05$ ) for only a few variables (alewife abundance and lake whitefish abundance in the early period; round goby abundance in the late period; proportion of tows containing bloaters in the early period; proportion of tows containing lake whitefish and lake trout in the late period); in such cases, we estimated regression parameters using the Yule–Walker method by fitting regression models augmented with autoregressive models to account for autocorrelation (SAS Institute 1996).

*Caveats.*—Fish abundance indices reported here are likely to be negatively biased, primarily due to variability in the catchability of fish by the trawl, which may reflect the vulnerability of fish to the gear or the off-bottom distribution of fish. Many individuals of some demersal species may be pelagic at some times and not available to our trawls (Argyle 1982; Stockwell et al. 2006). Results reported here should therefore not be interpreted as absolute abundance estimates.

Some of the observed fluctuations in abundance of individual species may have resulted from changes in catchability caused by altered fish distributions. For example, catchability of a given species might differ from year to year due to changes in temperature or food distribution (e.g., O’Gorman et al. 2000), and observed changes in abundance might result from a decrease in fish catchability by bottom trawls in recent years, although USGS fall trawl data show little evidence of changes in depth distributions for most species in Lake Huron (USGS, unpublished data). The presence of dreissenid mussels in Lake Huron may also have affected the efficiency of the trawl, as has been observed in Lake Ontario (O’Gorman et al. 2005). Data reported here were collected at a restricted range of depths; trawling occurred only in the Michigan waters of Lake Huron’s main basin in areas that were free of obstructions and were characterized by sandy or gravel substrates. It is therefore possible that USGS

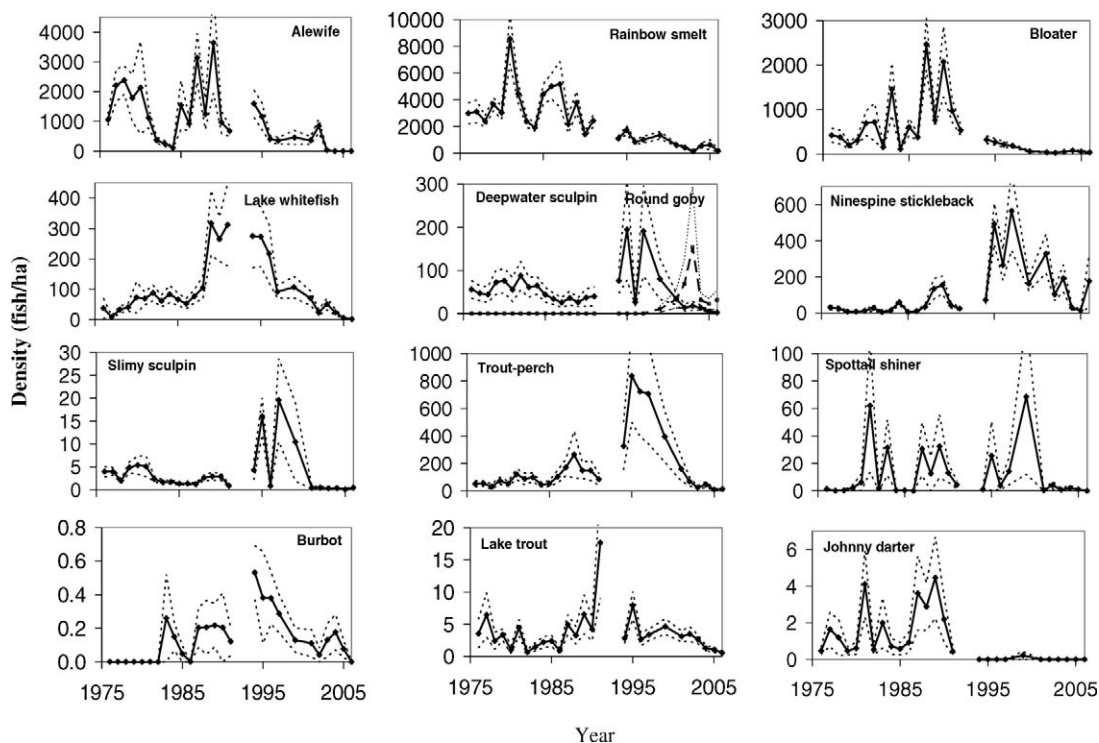


FIGURE 2.—Mean (solid line) abundance indices (fish/ha; dotted lines show 95% confidence interval) for common fish species (those caught in at least 10% of bottom trawl tows) captured in Michigan waters of Lake Huron, 1976–2006. Round goby abundance is represented by the dashed line in the panel depicting deepwater sculpin abundance. Data from 1998 were not used, and the trawl survey was not conducted in 2000 (see Methods).

trawl data did not fully characterize the deepwater demersal fish community. There are no other published long-term data on deepwater demersal fish abundance in Lake Huron that would allow us to investigate the representativeness of the trawl data. Despite the foregoing constraints, however, these data are currently the best available for assessing the Lake Huron deepwater demersal fish community.

### Results

Trends in abundance indices for individual species were variable, but the majority of species (except round goby) apparently decreased in abundance after approximately the mid-1990s (Figure 2). Three species (the bloater, lake whitefish, and burbot) significantly increased in abundance during the early period (1976–1991), while deepwater and slimy sculpin decreased, and seven species (alewife, rainbow smelt, lake trout, ninespine stickleback, trout-perch, spottail shiner, and johnny darter) showed no significant trends; round goby were not present in the lake during this period (Table 1). During the late period (1994–2006), only round goby abundance significantly

increased and abundance of johnny darters and spottail shiners showed no significant trends; abundance trends for all other species were significantly negative. During the early period, seven species showed positive percentage changes in abundance, while four showed negative changes ranging from 25% to 50%. Percentage changes in abundance indices between 1994–1995 and 2005–2006 were negative for all species (round goby were not present in 1994–1995) and ranged from 66.4% to 99.9% (Table 1); seven species decreased in abundance by over 90%.

The mean biomass of all common species declined drastically since 1994 (Figure 3), reaching an all-time low in 2006. Combined mean biomass (common species) in 2005–2006 was less than 5% of that observed in 1994–1995. Trends in combined mean biomass and mean number of common species captured in trawls were significantly positive in the early period and significantly negative in the late period (Figure 3; Table 1).

The proportion of tows in which bloaters, lake whitefish, and burbot were caught increased significantly during the early period, whereas the proportion

TABLE 1.—Slopes of linear regression analyses of  $\log_e$  transformed fish abundance and arcsine-transformed proportion of bottom trawl tows that captured each common deepwater demersal fish species (those caught in at least 10% of tows) during early (1976–1991) and late periods (1994–2006; year = independent variable in regressions); and percent change in common species abundance (comparison of first 2 years and last 2 years within each period) in Michigan waters of Lake Huron. Slopes for total biomass and total number of common species (both arcsine transformed) are given under the slopes for abundance. Bold type indicates significant slopes (Bonferroni-adjusted  $P < 0.05$ ).

Species or variable	1976–1991			1994–2006		
	Slope (abundance)	Slope (proportion of tows)	Percent change in abundance	Slope (abundance)	Slope (proportion of tows)	Percent change in abundance
Age-1+ alewife	-0.015	0.004	-49.9	<b>-0.389</b>	<b>-0.057</b>	-99.94
Age-1+ rainbow smelt	-0.040	0.001	-37.1	<b>-0.244</b>	<b>-0.043</b>	-71.25
Age-1+ bloater	<b>0.228</b>	<b>0.046</b>	87.4	<b>-0.191</b>	<b>-0.029</b>	-83.79
Lake whitefish	<b>0.128</b>	<b>0.023</b>	114.5	<b>-0.247</b>	<b>-0.039</b>	-98.58
Lake trout	0.024	0.005	119.6	<b>-0.050</b>	-0.017	-85.38
Deepwater sculpin	<b>-0.025</b>	-0.002	-24.9	<b>-0.135</b>	<b>-0.016</b>	-97.25
Slimy sculpin	<b>-0.031</b>	-0.012	-52.1	<b>-0.081</b>	<b>-0.021</b>	-97.23
Ninespine stickleback	0.073	0.014	21.2	<b>-0.215</b>	<b>-0.045</b>	-66.43
Trout-perch	-0.017	<b>-0.019</b>	123.8	<b>-0.169</b>	-0.005	-97.99
Johnny darter	0.010	0.002	24.2			
Spottail shiner	0.025	0.003	109.5	-0.022	-0.004	-95.82
Burbot	<b>0.007</b>	<b>0.006</b>		<b>-0.019</b>	<b>-0.020</b>	-91.55
Round goby				<b>0.129</b>	<b>0.042</b>	
Total biomass	<b>0.028</b>			<b>-0.160</b>		
Species count	<b>0.083</b>			<b>-0.160</b>		

of tows in which trout-perch were caught decreased significantly (Table 1). All species showed significant negative trends in the proportion of tows in which they were caught since 1994; the exceptions were lake trout,

trout-perch, and spottail shiners, which showed no significant trends, and round goby, which showed a significant positive trend.

**Discussion**

The deepwater demersal fish community in Lake Huron has undergone significant changes since the mid-1990s. Population trends for the majority of species captured in bottom trawls have decreased significantly since 1994. Mean biomass of trawl catches and mean number of common species per trawl have also significantly declined since 1994. The fact that we observed these significant decreases for such a wide variety of species with different ecological requirements suggests that drastic changes have occurred in the ecology of the lake. Several factors might be responsible for these changes, including the effects of multiple exotic species, increased predation by fish or double-crested cormorants *Phalacrocorax auritus*, fisheries, physical factors (e.g., climate change, nutrients), or disease. Unfortunately, long-term data on the majority of these factors are lacking for Lake Huron. Thus, despite extensive long-term sampling, we were not able to quantitatively determine the factors that contributed to the observed community changes; this highlights the need for comprehensive monitoring across all trophic levels. Although the data currently available are insufficient to quantify the effects of these factors, we discuss each below.

We note that the timing of the fish community changes implicates the recent invasion of the lake by

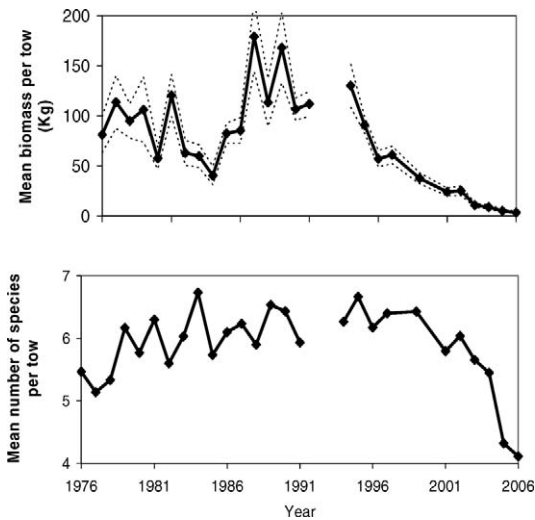


FIGURE 3.—Mean biomass (kg/tow; top panel; dotted lines show 95% confidence interval) of common fish species (those caught in at least 10% of bottom trawl tows) and number of common species captured (species/tow; bottom panel) during fall trawling surveys conducted by the U.S. Geological Survey’s Great Lakes Science Center at five ports in Michigan waters of Lake Huron, 1976–2006. Biomass estimates prior to 1991 were adjusted (see Methods).

exotic species—particularly dreissenid mussels, round goby, and spiny water fleas—as a potentially important factor. In Lake Huron, dreissenids first became abundant in Saginaw Bay in 1991 (Nalepa et al. 1995), but the population dynamics of zebra and quagga mussels in the main basin since their invasion are not well documented (Nalepa et al. 2007). Dreissenid mussels are now found at all ports sampled by the USGS fall trawl survey, and quagga mussels have become much more abundant recently, particularly at deeper transects (USGS, unpublished data). There are no published long-term data on dreissenid abundance in the Michigan waters of Lake Huron that would allow us to correlate fish community changes with mussel densities. A number of changes have been observed in Great Lakes fish populations since the invasion of dreissenid mussels, including changes in diet or body composition of lake whitefish (Pothoven et al. 2001) and slimy sculpin (Owens and Dittman 2003), shifts in depth distributions of alewives and rainbow smelt (O’Gorman et al. 2000), reduction in the feeding efficiency of benthic predators (Beekey et al. 2004), and changes in the seasonal energy dynamics of alewives (Madenjian et al. 2006). Dreissenids may cause changes in the composition of benthic communities (Dermott and Kerec 1997; Ricciardi et al. 1997; Nalepa et al. 2003, 2007; Ward and Ricciardi 2007) and phytoplankton communities (Holland 1993; Bastviken et al. 1998; Nicholls et al. 2002), and these changes may result in the alteration of food web dynamics. Dreissenids have drastically modified the nutrient and energy flows in Great Lakes ecosystems (Hecky et al. 2004), and their alteration of food webs may have been severe enough to affect abundances of some deepwater demersal species.

Round goby were first recorded in Lake Huron in 1994 at Goderich, Ontario, and they have been recorded from most areas of the lake since then (Schaeffer et al. 2005). Round goby first appeared in USGS trawl catches in 1997 and now occur at 40% of USGS trawl sites (2004–2006). Round goby have proliferated widely throughout the Great Lakes, and there is concern that they could displace native species (Mills et al. 1998; Fuller et al. 1999; Lauer et al. 2004; Balshine et al. 2005). Populations of mottled sculpin, logperch, and johnny darters have declined dramatically in areas colonized by round goby (Jude et al. 1995; Lauer et al. 2004), and these nonnative fish are known to prey on the eggs and fry of lake trout (Chotkowski and Marsden 1999) and other species (Steinhart et al. 2004a). This invasive species may also have affected the abundance of deepwater demersal species in Lake Huron.

The invasion of Lake Huron by the spiny water flea

(Barbiero et al. 2001) may also have affected the ecology of the deepwater fish community. Spiny water fleas have been present in Lake Huron since 1984 (Mills et al. 1993) and have been shown to cause reduced zooplankton abundance and biomass in lakes (Boudreau and Yan 2003; Strecker and Arnott 2005). Zooplankton abundance in Lake Huron appears to have decreased in recent years (R. Barbiero, personal communication), which may have reduced food availability for some fish species.

Increased predation by birds or fish may also be a factor affecting the deepwater demersal fish community. Double-crested cormorants have increased in abundance in Lake Huron (Weseloh et al. 1995; Diana et al. 1997; Dobiesz et al. 2005), and a significant proportion of their diet in the lake is contributed by alewives, rainbow smelt, sticklebacks, trout-perch, and sculpins (Diana et al. 1997; Neuman et al. 1997). However, double-crested cormorant abundance began to increase greatly in the early to mid-1980s (Weseloh et al. 1995), which does not coincide with the observed declines in fish abundance. The effects of double-crested cormorant predation are more likely to be important in nearshore waters less than 20 m in depth (Stapanian et al. 2002; M. Ridgway, Ontario Ministry of Natural Resources, Peterborough, personal communication).

Decreasing abundance of some species (especially the alewife, rainbow smelt, and deepwater sculpin) in Lake Huron might be due to the effects of fish predation, because these species constitute a major part of the diets of important offshore fish predators (i.e., Chinook salmon, lake trout, and burbot) in the lake (Diana 1991). Predation by restored lake trout populations in Lake Superior is thought to be responsible for recent declines in rainbow smelt abundance (Bronte et al. 2003). Declines in rainbow smelt and alewife abundance in Lake Huron since the 1990s may have coincided with increased abundance of Chinook salmon in the lake (Dobiesz et al. 2005), and sea lamprey control efforts conducted in the St. Mary’s River during the late 1990s (Schleen et al. 2003) may have resulted in greater abundance of predators. Gill-net surveys suggest that the abundance of large lake trout, which have low catchability in trawls, has increased in Lake Huron during recent years (M. Ebener, Chippewa–Ottawa Resource Authority, personal communication). There are no fishery-independent surveys of salmon in the lake, but recreational catch data suggest that abundance and condition of Chinook salmon are currently low (J. E. Johnson, personal communication). It is therefore difficult to assess the importance of predation by fish

as a factor in the recent fish community changes in Lake Huron.

Commercial fisheries for lake whitefish, lake trout, and bloaters in Lake Huron have recovered since the 1950s, when the majority of fisheries collapsed (Brown et al. 1999). Lake whitefish are the most heavily fished species in Lake Huron, and fishery yield and effort have remained fairly stable for the last two decades (M. Ebener, personal communication). Fishing mortality is unlikely to have contributed to the observed declines in abundance of most of the species assessed here.

Disease and physical factors may also have contributed to the abundance declines in Lake Huron. Several recent fish mortality events in Lake Huron have been attributed to viral hemorrhagic septicemia (MDNR 2007) and botulism (EC and USEPA 2006; Yule et al. 2006), but it is unknown whether the incidence of fish disease has increased in Lake Huron and the effects of disease on Great Lakes fish populations are poorly understood (Riley et al., in press). King et al. (1997) reported that climate change may be affecting water temperatures in Lake Huron, but evidence for significant increases in surface and bottom water temperatures at the USGS trawl transects is equivocal, particularly in deeper water (USGS, GLSC, unpublished data). Nutrient levels in Lake Huron have remained stable since the 1970s (Neilson et al. 2003; Dobiesz et al. 2005; EC and USEPA 2006), but phosphorus levels appear to have been declining in offshore waters of Lake Huron over the past decade (R. Barbiero, personal communication).

Most deepwater demersal fish species in Lake Huron exhibited negative abundance trends in the late period, whereas most species showed no significant trend during the early period. Because the USGS fall trawl survey began in the early 1970s after the collapse of major fisheries, the extirpation of several coregonids, and the introduction of Pacific salmon, fish abundance levels from the early period may not be representative of the natural state of the lake and abundance of some species may have been higher than historic or natural levels. Because comparable trawl data were not collected prior to major anthropogenic alterations in Lake Huron, it is difficult to compare current fish abundance indices with expectations for the lake in its natural state. The focus of our analysis was on trends in abundance rather than absolute abundance estimates, and the negative trends that we observed for most species in recent years suggest that major changes have taken place in the Lake Huron ecosystem.

Significant changes in the fish communities of the other Laurentian Great Lakes have been noted in recent years, including declines in abundance of alewives,

lake whitefish, and slimy sculpin in Lake Ontario (Owens et al. 2003, 2005; Mills et al. 2005) and declines in alewives, bloaters, rainbow smelt, and lake whitefish in Lake Michigan (Bunnell et al. 2006). Alewives, rainbow smelt, and bloaters appear to have decreased in abundance throughout the Great Lakes during recent years (Shear 2006; USGS, unpublished data), but to our knowledge only Lake Huron has exhibited significant concurrent declines in abundances of nearly all deepwater demersal species. These concurrent declines may be a symptom of ecosystem distress or instability (Rappport et al. 1985; Lehman and Tilman 2000).

Recent work has highlighted the effects of overfishing on marine fish communities, whereby fishing selectively removes species at higher trophic levels and results in "fishing down the food web" (Christensen et al. 2003; Myers and Worm 2005; Pauly and Palomares 2005). Here, we have reported similarly drastic abundance declines in the majority of deepwater demersal fish species within one of the world's largest lakes; however, these declines are not limited to a single trophic level and are unlikely to have been caused by fishing. The extent and scope of these changes suggest that the deepwater demersal fish community in Lake Huron is collapsing. The timing of the changes suggests that the recent invasion of the lake by multiple exotic species at several trophic levels is a major factor responsible for these recent declines, but a lack of published data on other components of the Lake Huron ecosystem precludes the confirmation of this hypothesis. Long-term monitoring of multiple trophic levels in the lake is required to understand the causes and significance of the recent changes in the deepwater demersal fish community. The effects of continued change in this community on future ecosystem services from the lake (including fisheries for lake whitefish, lake trout, and Pacific salmon) are difficult to predict.

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