

Status of Burbot Populations in the Laurentian Great Lakes

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ABSTRACT.—Burbot *Lota lota* populations collapsed in four of the five Laurentian Great Lakes between 1930 and the early 1960s. Collapses in Lakes Michigan, Huron, and Ontario were associated with sea lamprey *Petromyzon marinus* predation, whereas the collapse in Lake Erie was likely due to a combination of overexploitation, decreased water quality, and habitat degradation. We examined time series for burbot population density in all five lakes extending as far back as the early 1970s to present time and characterized the long-term trends after the initial collapses. Burbot population density in Lake Superior has remained relatively low and stable since 1978. Recovery of the burbot populations occurred in Lakes Michigan and Huron during the 1980s and in Lake Erie during the 1990s. Control of sea lampreys was a requirement for recovery of burbot populations in these three lakes. Declines in alewife *Alosa pseudoharengus* abundance appeared to be a second requirement for burbot recovery in Lakes Michigan and Huron. Alewives have been implicated in the decline of certain Great Lakes fish stocks that have pelagic larvae (e.g., burbot) by consuming the pelagic fry and possibly by outcompeting the fry for food. Relatively high populations of adult lake trout *Salvelinus namaycush* compared to burbot served as a buffer against predation by sea lampreys in Lakes Huron and Erie, which fa-

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cilitated recovery of the burbot populations there. Although sea lampreys have been controlled in Lake Ontario, alewives are probably still too abundant to permit burbot recovery.

Introduction

Burbot *Lota lota* and lake trout *Salvelinus namaycush* are the two native coldwater piscivores of the Laurentian Great Lakes (Smith 1968). Burbot occur in all of the Great Lakes, but in Lake Erie, the species is restricted to the colder and deeper eastern portion of the lake (Trautman 1957). Commercial harvest of burbot throughout North America is generally restricted to incidental catches from fishing for other species (e.g., Branion 1930; Hewson 1955; but see Muth and Smith 1974; Rudstam et al. 1995). In the Great Lakes, burbot are occasionally commercially targeted only in Green Bay, Lake Michigan, and there are few recreational fisheries for burbot throughout the basin.

In Lakes Michigan, Huron, Erie, and Ontario, burbot populations collapsed between 1930 and the early 1960s, and the collapses in Lakes Michigan, Huron, and Ontario have been attributed to predation by sea lamprey *Petromyzon marinus* (Berst and Spangler 1973; Christie 1973; Wells and McLain 1973; Baldwin et al. 2002). A synthesis on the fish community changes in Lake Erie from the 1880s to 1970 suggested that the decline in burbot abundance in Lake Erie during the 1950s and early 1960s was likely due to habitat degradation, decreased water quality, and perhaps overexploitation (Hartman 1973; Stapanian et al. 2006). Apparently, habitat degradation in Lake Erie and its tributaries was so extensive that sea lampreys could not become firmly established until the 1970s, when habitat and water quality substantially improved as a consequence of the Water Quality Agreement Act of 1972 (Sullivan et al. 2003). We have not found any evidence to indicate that bur-

bot abundance in Lake Superior underwent any historical decline.

Burbot have pelagic larvae (Clady 1976; Jude et al. 1979; O'Gorman 1983; Ghan 1990). Alewife *Alosa pseudoharengus* predation has been implicated in the decline of certain Great Lakes fish stocks, mainly by preying on their pelagic fry (Smith 1970; Brandt et al. 1987; Brown et al. 1987; Eck and Wells 1987; Luecke et al. 1990; O'Gorman and Stewart 1999). Eshenroder and Burnham-Curtis (1999) concluded that when alewives are abundant in the Great Lakes, they inhibit the natural succession of native species in the Great Lakes.

Since the decline of burbot many changes have occurred in the Great Lakes, including reductions in sea lamprey through control efforts, reductions in alewives, stocking native and nonnative salmonines, and controls on commercial fishing. Perhaps the most important management effort, in terms of its influence on the fishery of the Great Lakes, has been sea lamprey control (Smith and Tibbles 1980). Sea lamprey abundance has been dramatically reduced in all five of the Great Lakes as a result of control efforts. Sea lamprey control in Lake Superior began in 1962, and by the mid-1960s, abundance of spawning-phase sea lampreys had been reduced by about 85% (Smith and Tibbles 1980; Heinrich et al. 2003). Lampricide applications in Lake Michigan began in 1960 and by the mid-1960s, the number of spawning-phase sea lampreys in Lake Michigan had decreased by nearly 95% (Smith and Tibbles 1980; Lavis et al. 2003). Sea lamprey control in Lake Huron tributaries began in 1965, with weirs on the Ocqueoc River (Smith and Tibbles 1980; Morse et al. 2003). Sea lamprey abundance immediately declined by about 94% from the

levels recorded during 1947–1964 and remained relatively low through 1978. In Lake Erie, sea lamprey control began in 1986 and by 1989 abundance of spawning-phase sea lampreys declined by more than 80% (Sullivan et al. 2003). Spawning-phase sea lampreys declined by about 67% in Lake Ontario from control efforts during 1978–1985 and by 1999, sea lampreys were eliminated in 20 of the 57 tributaries with historical records of production (Larson et al. 2003).

Major salmonine stocking programs began in the 1960s and 1970s in the Great Lakes (Madenjian et al. 2002; Bronte et al. 2003; Mills et al. 2003; Dobiesz et al. 2005). Most of the species stocked were lake trout, Chinook salmon *Oncorhynchus tshawytscha*, coho salmon *O. kisutch*, rainbow trout *O. mykiss*, and brown trout *Salmo trutta*. Salmonine stocking and subsequent predation led to reductions in alewife abundances in Lakes Michigan, Huron, and Ontario (Madenjian et al. 2002, 2005a, 2005b; Mills et al. 2003; Dobiesz et al. 2005). However, alewife abundance in Lake Ontario has remained considerably higher than alewife abundances in Lakes Michigan and Huron (O’Gorman and Stewart 1999; Madenjian et al. 2003). Alewife abundance in Lake Erie has remained low, owing mainly to the species’ intolerance to the adverse water temperature regimes that exist under typical winter conditions in Lake Erie (Ryan et al. 1999).

Given that burbot and lake trout are the top two native coldwater predators in the Great Lakes, some degree of competition for food may be expected (Stapanian et al. 2006). However, environmental conditions that favor burbot may also favor lake trout, at least over a large range of population densities of both species (e.g., Carl 1992; Stapanian et al. 2006). High populations of adult lake trout in the Great Lakes have been shown to serve as a buffer species against sea lamprey predation and thus contribute to the recovery of

other native species, including burbot (e.g., Swink and Fredericks 2000; Madenjian et al. 2002; Stapanian and Madenjian 2007).

In this paper, we examine recent time series for burbot abundances from the Great Lakes and document the temporal trends in burbot abundances for the past 20–30 years. We provide evidence from the literature of how the abundances of sea lamprey, alewife, and lake trout influenced burbot populations in each lake. We then synthesize this information to explain similarities among lakes in terms of ecological processes influencing burbot population abundance. Such basin-wide synthesis may be useful for understanding Great Lakes food webs.

Methods

Lake Superior

The U.S. Geological Survey (USGS) has conducted a bottom trawl survey to track changes in the fish community in Lake Superior since 1978 (Figure 1; Bronte et al. 2003; Stockwell et al. 2005). Stations were first established in U.S. waters and expanded to Canadian waters in 1989. Currently, 86 fixed sampling stations are distributed around the perimeter of Lake Superior. A single tow was made at each station using a 12-m headrope and 16-m footrope bottom trawl towed cross-contour during daylight hours. Sampling typically occurred from early May to mid-June. Most (80%) of the trawl tows started at the 15-m contour (range 13–28 m) and extended to a median end depth at the 65-m contour (range 22–138 m, interquartile range 48–85 m). Median tow duration was 25 min (range 6–60 min) and tow speed was 3–4 km/h. Refer to Bronte et al. (1991) and Stockwell et al. (2005) for full details of trawl locations and assessment methods. For each year, density (expressed as mean number of fish per hectare) of burbot was estimated using area-swept calculations for U.S. and Canadian waters of Lake Superior.

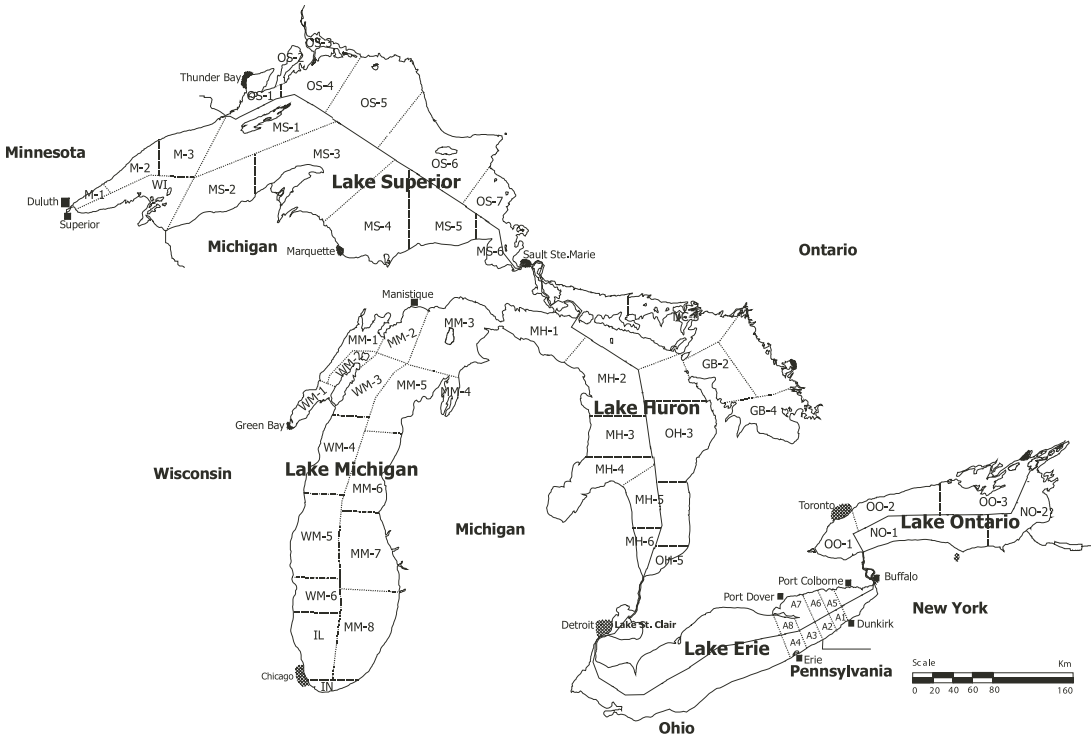


FIGURE 1. The Laurentian Great Lakes, with statistical districts and study areas.

Lake Michigan

The USGS has conducted a lakewide survey of the fish community in Lake Michigan during the fall of each year since 1973 (Madenjian et al. 2003). A 10-min tow using a bottom trawl (12-m headrope) dragged on contour was the basic unit of sampling in the USGS survey (Hatch et al. 1981). Towing speed has averaged 3.4 km/h. Depth of the tows ranged from 9 to 110 m, in 9-m depth increments. Since 1973, the following seven transects have been regularly sampled: Frankfort (Michigan), Ludington (Michigan), Saugatuck (Michigan), Waukegan (Illinois), Port Washington (Wisconsin), Sturgeon Bay (Wisconsin), and Manistique (Michigan). The number of burbot caught in each tow was determined. For each year, the density (expressed as mean number of fish per hectare) of burbot in Lake Michigan was estimated using area-swept

calculations. These estimates corresponded with the area of Lake Michigan proper between the 5-m and 114-m depth contours. Refer to Madenjian et al. (2003, 2005a) for more details pertaining to methods.

Lake Huron

Burbot were caught in bottom-set, graded-mesh gill-net surveys in the main basin of Lake Huron and Georgian Bay during 1970–2004. The Michigan Department of Natural Resources and Chippewa Ottawa Resource Authority conducted gill-net surveys in the spring of 1970–2004 at annual index sites in statistical districts MH-1 through MH-5 (Johnson and VanAmberg 1995), across contours at depths ranging from 10 to 46 m. The Ontario Ministry of Natural Resources conducted gill-net surveys in June–August of 1989–2004 at six annual index sites at depths

ranging from 20 to 55 m in statistical districts GB-4, OH-3, and OH-5 (Figure 1). Gill nets were made up of nine panels, each 30.5-m long and 2.4-m high, with mesh sizes ranging from 51 to 151 mm in 12.5-mm increments. All nets were lifted after one night in the water, unless precluded by adverse weather conditions. Refer to Johnson and VanAmberg (1995) and Mohr et al. (1997) for complete survey details. We reported the mean number of burbot caught per kilometer of gill net during the time series in statistical districts in Michigan and Ontario waters. Ages of burbot caught in the gill nets were estimated by examining otoliths (Evanson 2000). Otoliths were cross-sectioned, dipped in mineral oil, and the annuli were counted. Age-specific and year-class specific relative abundance were estimated from the otolith data and fishing effort.

Lake Erie

Burbot in Lake Erie occur almost exclusively in the eastern portion (Trautman 1957). Data for burbot in Lake Erie were obtained from annual gill-net assessments of coldwater predator fishes conducted by agencies of the Coldwater Task Group of the Lake Erie Committee of the Great Lakes Fishery Commission (Stapanian et al. 2006). The assessment has been conducted in August of each year in eight areas of the eastern basin of Lake Erie (Figure 1) since 1985 in New York waters and since 1992 in Pennsylvania and Ontario waters. Refer to Stapanian et al. (2006) for detailed descriptions of the assessment methods. Briefly, gill nets consisted of nine panels, each 15.2 m long and 2.4 m high, with mesh sizes ranging from 51 to 151 mm in 12.5-mm increments. We did not include in the analysis the results from additional panels with mesh sizes of 38 mm, 178 mm, and 203 mm that were added during the survey (Stapanian et al. 2006). Nets were set perpendicular to northwest/southeast-oriented inte-

ger 58000 series Loran C Lines of Position, along depth contours and below the 8°C to 10°C isotherm. All nets were lifted after one night in the water, unless precluded by adverse weather conditions. Ages of burbot at capture were estimated by examining otoliths according to Evanson (2000). Burbot were not fully recruited to the gear until they were at least 4 years of age (Stapanian and Madenjian 2007). We reported the mean number of burbot caught per kilometer of gill net in each year during 1985–2004. Detailed statistical analyses of population trends were provided elsewhere (Stapanian et al. 2006).

Lake Ontario

Burbot populations in U.S. waters of Lake Ontario were monitored by the USGS and New York State Department of Environmental Conservation from annual gill-net assessments of lake trout during September 1983–2004 and from trawling activity during 1978–2002. Assessment gill nets consisted of nine panels, each 15.2 m long and 2.4 m high, with mesh sizes ranging from 51 to 151 mm in 12.5-mm increments. Nets were fished overnight within 17 areas during 1983–1993 and 14 areas during 1994–2004. Sampling sites encompass the entire U.S. shoreline of Lake Ontario. Refer to Elrod et al. (1995), Schneider et al. (1996), O’Gorman et al. (1998), and Owens et al. (2003) for detailed description of the assessments and procedures. We reported burbot population density from these annual surveys as mean number of burbot caught per kilometer of gill net. Ages of burbot at capture were estimated by examining otoliths (Evanson 2000).

Trawl surveys in Lake Ontario were conducted from mid-April to early November in U.S. waters. Refer to O’Gorman and Schneider (1986), O’Gorman et al. (1987), Elrod and Schneider (1987), and Owens and Bergstedt (1994) for detailed descriptions of the methods and assessments. Trawl locations

were spaced at about 25-km intervals along the southern and eastern shores of the lake, starting east of the mouth of the Niagara River and finishing near the head of the St. Lawrence River. Density was calculated by dividing the catch per tow by the area swept based on 10-min time on bottom during a standard tow. During 1978–1996, a 12-m headrope, three-quarter-Yankee bottom trawl was fished. In 1997, for all but the October/November assessment, the 12-m trawl was replaced with an 18-m (headrope), 3-seam 3-in-1 bottom trawl equipped with rollers along the footrope in order to avoid biofouling by exotic dreissenid mussels *Dreissena* spp., which spread throughout the lake in the early 1990s (Mills et al. 2003). This new configuration fished lighter on bottom and was less effective at catching fish tightly associated with the bottom (Owens et al. 2003). Densities were reported as mean number per hectare.

Results

Lake Superior

Estimated population density of burbot in Lake Superior remained relatively low and fairly constant from 1978 to about 1995, and declined thereafter to a low in 2003. In U.S. waters during 1978–2004, the estimated density averaged 0.29 fish/ha (Figure 2). Burbot declined from around 0.35 fish/ha during 1978–1996 to about 0.02 fish/ha in 2003. Density appeared to rebound in 2004 and returned to the average level before the steady decline that began in the mid-1990s. Average density was higher in Ontario waters during 1989–2004 (0.35 fish/ha) compared to U.S. waters (0.23 fish/ha) during the same time period (Figure 2). Densities varied more in Ontario waters compared to U.S. waters. Mean total lengths of burbot captured in trawl tows generally ranged from 300 to 500 mm during

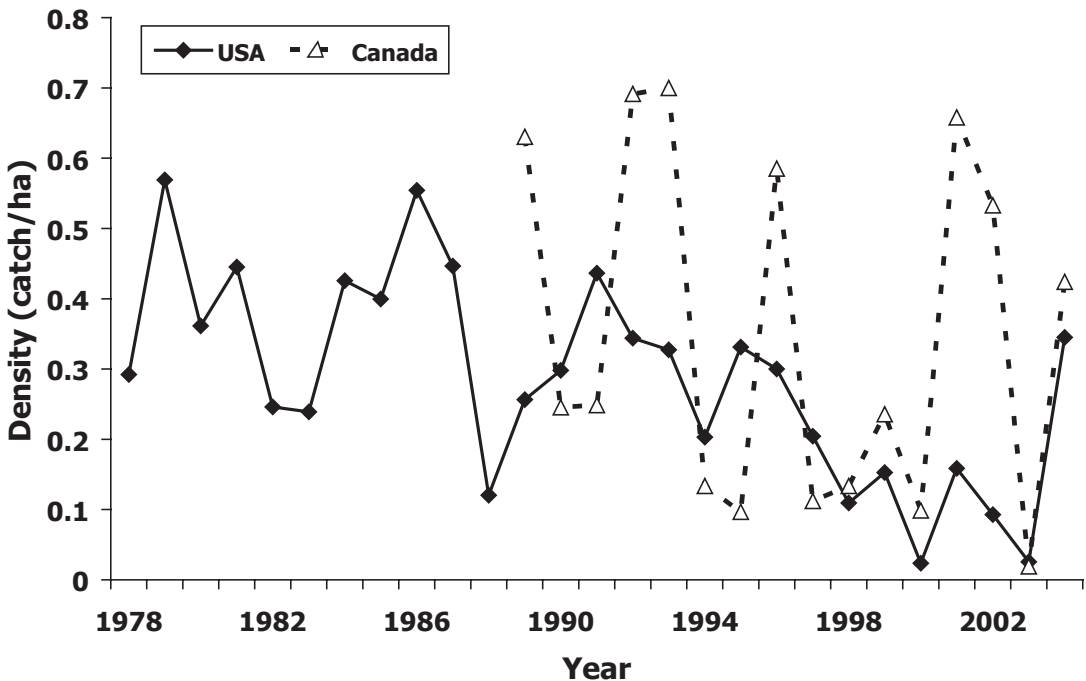


FIGURE 2. Density (catch/ha) of burbot caught in bottom trawl assessments in U.S. and Canadian waters of Lake Superior.

1978 to 1904, suggesting that mostly older fish were susceptible to the trawls and that either recruitment was sporadic or that younger fish were not available to the trawls.

Lake Michigan

Estimates of burbot population density in Lake Michigan were zero for all years between 1973 and 1983, except for years 1973, 1981, and 1982, when the estimates ranged from 0.01 to 0.05 fish/ha (Figure 3). Burbot density rose sharply from 1983 to 1987, with density in 1987 estimated at more than 1 fish/ha. Density remained relatively high throughout the 1990s, peaking in 1997 at about 3.6 fish/ha. Burbot density trended downward during 1997–2004. Density of burbot averaged 1.4 fish/ha during 1987–2004. Total lengths of burbot caught in the bottom trawls ranged from 320 to 860 mm.

Lake Huron

The variability of burbot density was similar across broad spatial areas in Lake Huron during 1970–2004. From 1970 to 1985, burbot density was low in the Michigan statistical districts MH-1 to MH-5, averaging 0.6 fish/km of gill net (Figure 4). After 1985, burbot density increased quickly in MH-2 and more slowly in other waters (MH-1 and MH-345) and peaked at 9.8 fish/km of gill net in 1989 before declining to an average of 1.9 fish/km in 2004. Density of burbot in the Ontario statistical districts OH-3, OH-5, and GB-4 declined almost annually from an average 8.4 fish/km in 1989 to only 0.7 fish/km in 2004. Burbot density averaged 11.5 fish/km in MH-2, 8.2 fish/km in OH-3, 5.7–5.8 fish/km in MH-1, GB-4, and MH-345, and 1.0 fish/km in OH-5 during 1989–2004.

Strong year-classes of burbot were pro-

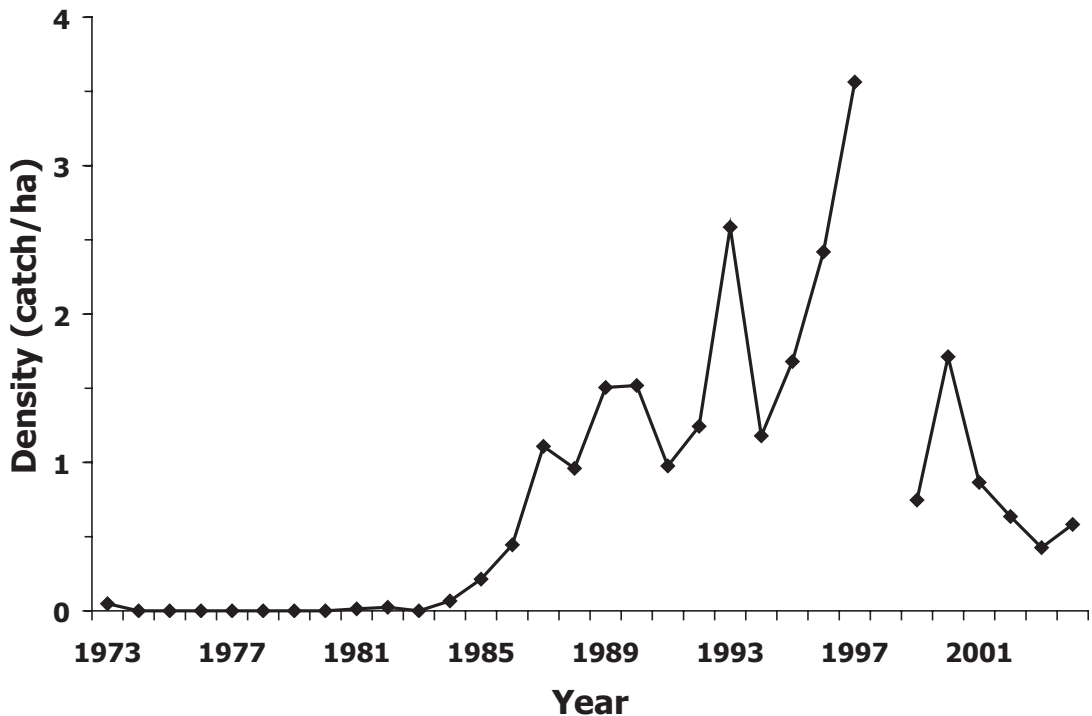


FIGURE 3. Density (catch/ha) of burbot caught in bottom trawl assessments in Lake Michigan. Data for 1998 were missing.

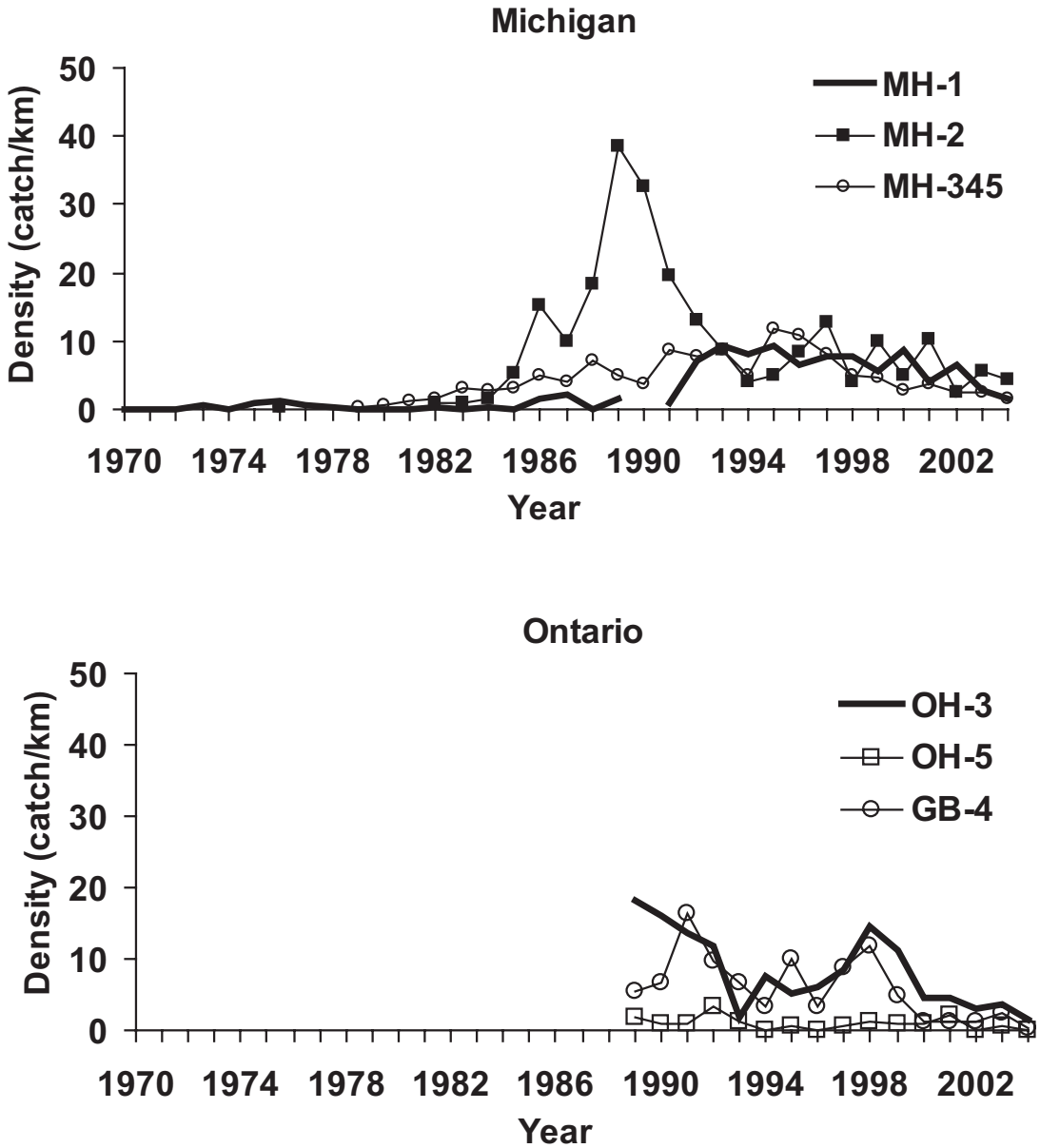


FIGURE 4. Catch per kilometer of gill-net lift of burbot in annual assessments in statistical districts of Michigan (USA) and Ontario (Canada) waters of Lake Huron.

duced in statistical district MH-1 during 1984–1987 that persisted in survey catches through 2002. The 1984 to 1987 year-classes were 2.4–3.6 times more abundant in gill net catches during 1995 and 1998–2004 than other year-classes produced during 1975–1999 in MH-

1. Densities of the 1984 to 1987 year classes ranged from 1.0 to 2.3 fish/km in 1995 to 0.3–0.6 fish/km in 2002. Year-classes produced after 1987 in MH-1 were of low to average abundances and their densities ranged from 0.0 to 1.3 fish/km during 1995 and 1998–2004.

Lake Erie

Burbot density increased significantly between 1985 and 2004, following lamprey treatment in fall 1986, in New York and in Ontario but not in Pennsylvania (Stapanian et al. 2006; Figure 5). During 1994–2004, burbot density increased by nearly 10 times in Ontario waters and by about 4 times in New York waters. During 2000–2004, burbot density averaged 53.4 fish/km of gill net in Ontario waters, 30.9 fish/km in New York waters, and 24.1 fish/km in Pennsylvania waters. Catch per kilometer of gill net of age-4 individuals declined dramatically after 2000 and low recruitment rates undoubtedly contributed to most of the decline in density in Ontario waters during 2001–2004 (Stapanian and Madenjian 2007).

Lake Ontario

Catches of burbot were relatively low, as 138 burbot were caught in annual gill net assess-

ments between 1983 and 2004 (Figure 6). Of these, 109 were measured for total length and weight. Burbot population density from gill net catches (Figure 6) was relatively low through the early 1990s (1983–1992 mean = 0.44 fish/km), began to rise in 1993, and reached a peak in 1998 (2.38 fish/km). Density dropped sharply between 1998 and 1999 and continued to decline through 2003. By 2002 population density had returned to the low levels seen in the early years and has remained low through 2004. Burbot density followed similar trends in Canadian waters of the eastern basin. Indices from index gill-net catches were relatively low from 1986 to 1992, increased between 1993 to 1997, fell off sharply after 1998, and remained low through 2002 (Hoyle and Schaner 2003). Nearly all of the fish from U.S. gill-net catches were 4 years of age and older. During the increase in burbot population density (1993–1998), age-4 and age-5 sized fish were common, but after 2001, all fish captured would likely have

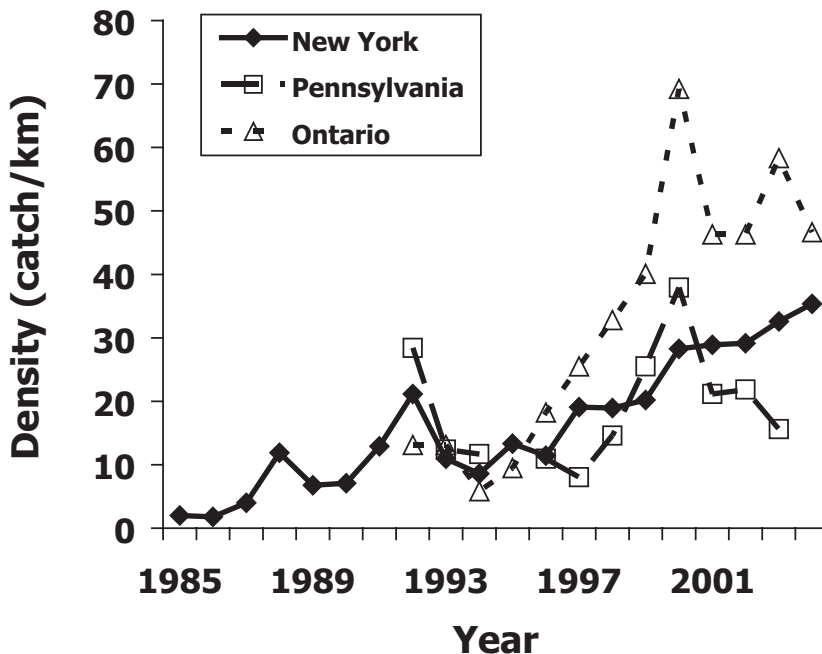


FIGURE 5. Catch per kilometer of gill-net lift of burbot in annual assessments in Lake Erie.

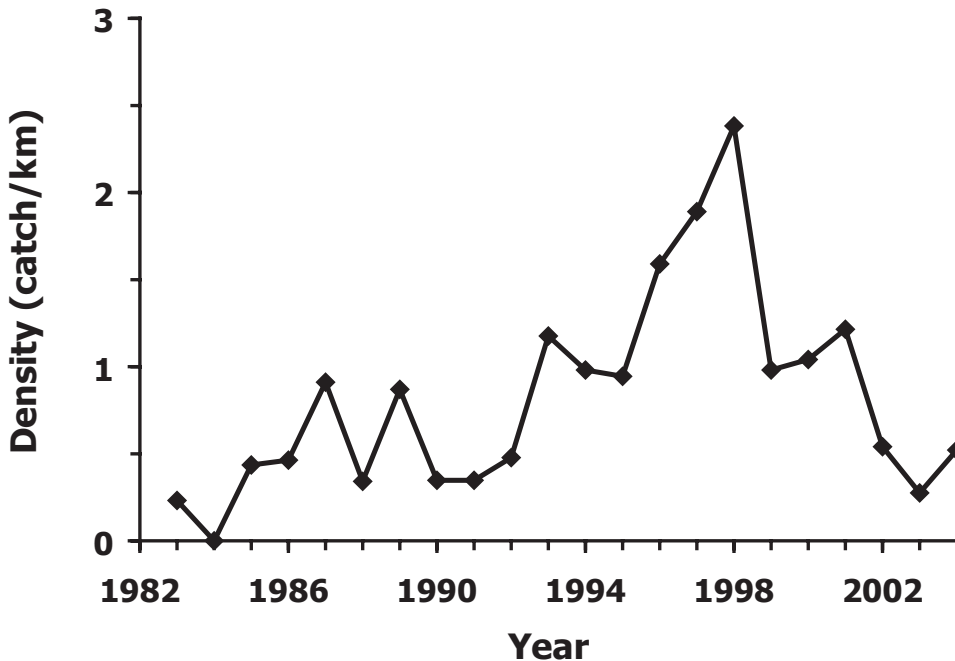


FIGURE 6. Catch per kilometer of gill-net lift of burbot in annual gill-net assessments in Lake Ontario.

been age 6 and older, with minimum size increasing in successive years.

Burbot population density from trawls in U.S. waters generally reflected the gill-net data except that density began to rise in 1987 and began declining in 1996. Trawl catches averaged 0.02 fish/ha during 1990–2004, peaked at greater than 0.04 fish/ha in 1992, and decreased to an average 0.01 fish/ha during 1998–2002 (Figure 7).

Discussion

Lake Superior

Populations of burbot remained relatively low throughout the time series. Although the decline of burbot in the last century in the other Great Lakes has been attributed to sea lamprey and alewife predation (Smith 1973), these factors likely have little to do with the low numbers of burbot in Lake Superior. Unlike Lakes Michigan, Huron, and Ontario,

alewives never became firmly established in Lake Superior due to unfavorable thermal conditions for overwintering fish and developing eggs (Bronte et al. 1991). Therefore, alewives were never a factor in controlling burbot populations in Lake Superior.

Unlike the other Great Lakes, Lake Superior did not lose its deepwater predator, the siscowet, a deepwater more robust morphotype of lake trout (Sweeny 1890) found mostly in waters beyond 80 m (Lawrie and Rahrer 1973; Moore and Bronte 2001; Bronte et al. 2003). Siscowet (or analogous forms) were present in the other Great Lakes but were extirpated by overfishing and sea lamprey predation (see Krueger and Ihssen 1995). Adult siscowet stocks in Lake Superior are currently much more abundant than lean lake trout stocks and have been increasing over the last 50 years (Bronte et al. 2003). We hypothesize that siscowet predation has kept Lake Superior burbot populations at low densities during

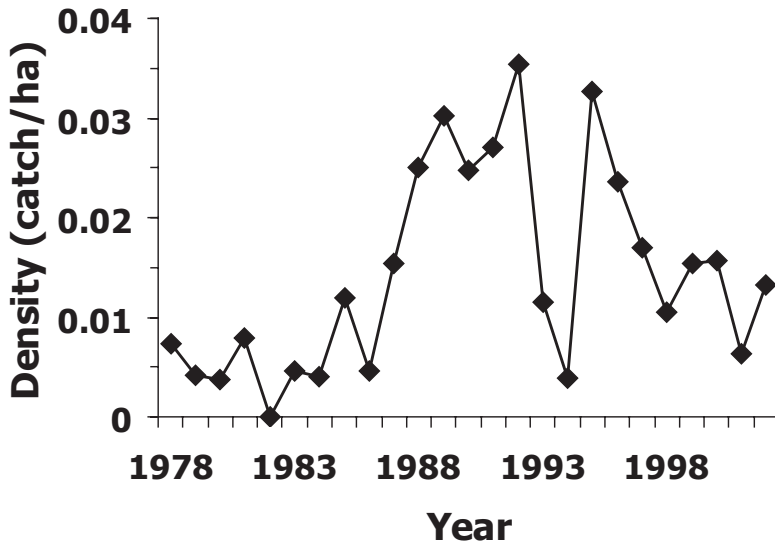


FIGURE 7. Density (catch/ha) of burbot caught in bottom trawl assessments in U.S. waters of Lake Ontario.

and prior to the 1990s. Recent studies supporting this hypothesis include diet analyses (Bronte et al. 2003; Ray 2004), stable isotope analysis (Harvey et al. 2003), and fish community modeling (Kitchell et al. 2000).

Lake Michigan

The burbot population in Lake Michigan exhibited a strong recovery during the 1980s and remained at relatively high levels during the 1990s. This recovery has been attributed, in part, to sea lamprey control (Madenjian et al. 2002). Sea lamprey control in Lake Michigan began in the late 1950s, and abundance of sea lamprey spawners was estimated to decrease by nearly 95% between 1956 and 1966 (Lavis et al. 2003). Sea lamprey abundance was sufficiently low and should have allowed for burbot recovery by the late 1960s (Madenjian et al. 2002). However, the recovery was delayed until the 1980s because a second requirement for burbot recovery was the lowering of alewife abundance (Eshen-

roder and Burnham-Curtis 1999; Madenjian et al. 2002). Alewives have been suspected of interfering with burbot reproduction in Lake Michigan by consuming the pelagic fry of burbot and possibly by outcompeting the burbot fry for food (Wells and McLain 1973; Eshenroder and Burnham-Curtis 1999). Alewife abundance in Lake Michigan decreased dramatically between 1966 and 1982 primarily due to predation by salmon and trout (Madenjian et al. 2005b). Alewife abundance during 1982–2004 was, on average, about six times lower than that observed in 1973.

Burbot population density declined in Lake Michigan during 1997–2004. This decline directly coincided with more than a doubling in abundance of spawning sea lampreys (Lavis et al. 2003). The recent increase in sea lamprey abundance has been attributed to a concomitant decrease in sea lamprey control measures (Madenjian et al. 2002). With sea lamprey control measures expected to intensify in the next few years (D. Lavis, U.S. Fish and Wildlife Service, Ludington, Michigan,

personal communication), we predict burbot abundance in Lake Michigan will increase within the next 5 years.

Lake Huron

Recovery of the Lake Huron burbot population was similar to that of Lake Michigan in that recovery was strongly associated with both sea lamprey control (Collins 1988) and low populations of alewife. In Lake Huron, sea lamprey numbers declined by 94% from 1949 to 1965, prior to initiation of chemical control, and remained low through 1978 (Smith and Tibbles 1980). Although sea lamprey abundance in Lake Huron increased from 70,600 in 1980 to a peak of 429,000 in 1993 and then declined to 130,000 in 2004 (Morse et al. 2003), these levels were still much lower than they were prior to sea lamprey control. However, the burbot population did not begin to recover until the early 1980s. Abundance of adult alewife in Lake Huron substantially declined during the 1970s and 1980s (Dobiesz et al. 2005). Alewife abundance in Lake Huron was very low in 1982 to 1986, when two of the four strong year-classes of burbot were produced. The slow decline in abundance of burbot in Lake Huron after the mid- to late-1990s was associated with a lack of recruitment. Future efforts shall include investigation into the factors influencing reduced recruitment of burbot in Lake Huron.

Changes in abundance of burbot in Lake Huron occurred nearly simultaneously throughout areas of the lake that were separated by hundreds of kilometers, suggesting that dynamics of the species in the lake was influenced by factors that operate at a lake-wide scale. Abundance of burbot increased, on average, ninefold in Lake Huron from 1970 to 1989 before declining to a lower level in 2004. This was threefold greater than it was in 1970 based on gill-net surveys in two of Lake Huron's three basins.

Lake Erie

Burbot in Lake Erie exhibited a strong recovery during 1985–2003, particularly in Ontario waters, and the main reason for this recovery was sea lamprey control (Stapanian et al. 2006). Stapanian et al. (2006) also tested alternative hypotheses for this recovery, including (1) reduced competition with lake trout, (2) increased prey abundance, and (3) reduced interference with burbot reproduction by alewife, but none of these were supported by the data. Environmental conditions that favored burbot during the study period apparently also favored lake trout because their abundances were positively correlated. Total available energy of the main prey species of burbot did not increase during the period. Adult alewife density in eastern Lake Erie was extremely low in nearly all years of the survey and exhibited no temporal trend. Ryan et al. (1999) attributed the low but variable abundance of alewife in eastern Lake Erie to their intolerance to the adverse water temperature regimes that exist under typical winter conditions in Lake Erie. Adult alewife density may always have been sufficiently low to allow for a burbot recovery in Lake Erie (Stapanian et al. 2006). Predation by sea lampreys on burbot is not expected to increase in the near future because lamprey control efforts have been maintained. The decline of burbot density during 2001–2004 in Ontario waters was associated with a decrease in recruitment (Stapanian and Madenjian 2007).

Burbot populations in Lake Erie were buffered from sea lamprey populations during the few years (1996–1999) when lamprey control was reduced (Stapanian and Madenjian 2007). Mortality of burbot was less during the period of reduced lamprey control than during the period of full control. Recruitment of burbot was relatively high during the period of reduced lamprey control. Burbot in Lake Erie achieve sexual maturity when they

are 3 or 4 years old and have a total length of about 500 mm (Stapanian et al. 2006; Stapanian and Madenjian 2007), which is smaller than the preferred prey size for sea lampreys (Swink and Fredericks 2000). The combined effects of the buffering effect of the lake trout population and the relatively early age and small total length at which burbot achieve sexual maturity enabled growth of the burbot population during the brief period when lamprey control was reduced (Stapanian and Madenjian 2007; and see Swink and Fredericks 2000).

Lake Ontario

Burbot abundance from both gill-net and bottom trawl catches showed similar trends, except that rises and declines were offset by 6 and 2 years respectively. The earlier rise in trawl catches (1987 versus 1993 for gill nets) appeared to also occur in the gill-net data, but the variability in the gill-net catch during the mid-1980s precluded us from making that determination. The decline in bottom trawls in 1996, 2 years prior to gill-net catches, was in part due to a gear change in 1997. In response to increasing abundance of dreissenid mussels, the 12-m trawl was abandoned in favor of an 18 m, 3-in-1 trawl that fished lighter on bottom and was less effective at catching benthic species like burbot (Owens et al. 2003).

Burbot recruitment in Lake Ontario was likely constrained by both larval predation by alewives and predation on adults by sea lampreys: reductions in predation potential of both species preceded the mid- to late-1990s peak in burbot abundance (Elrod et al. 1995; Mills et al. 2003, 2005; Owens et al. 2003). Numbers of large (>149 mm) alewife declined irregularly after 1983, dropping sharply in 1996 and remaining relatively low thereafter except for 2001 when the strong 1998 year-class recruited causing a brief surge in the population (Mills et al. 2003,

2005; O’Gorman et al. 2005). Estimated abundance of adult sea lampreys decreased about threefold, and sea lamprey-induced wounds on lake trout declined fourfold in the mid-1980s when several important lamprey-producing systems received larvacide treatment (Elrod et al. 1995; Larson et al. 2003; Lantry et al. 2005). In addition, burbot were further buffered from lamprey predation by a fourfold increase in the abundance of adult lake trout (age 5 and older) between 1984 and 1986 (Elrod et al. 1995).

The decline in the burbot population in the late 1990s was characterized by decreases in all ages commonly present in assessment catches. Age-4 and age-5 burbot were absent from catches after 2001, suggesting recruitment failure occurred in the mid-1990s. This period coincided with increased water clarity, movement of fishes to deeper water (O’Gorman et al. 2000), declines in the important benthic invertebrate *Diporeia* spp. (Lozano and Nalepa 2003; Mills et al. 2003), and recruitment declines in at least two other fish stocks, lake trout and lake whitefish *Coregonus clupeaformis* (Lantry et al. 2005; Hoyle et al. 2003). Greater predation by sea lampreys likely exacerbated the burbot decline. While total sea lamprey abundance had not changed greatly after 1993, the capacity of the lake trout population to buffer burbot from lamprey predation decreased substantially. Abundance of lake trout of the size preferred by lampreys (>432 mm) declined by 45% between 1996 and 1999 due to poor recruitment of stocked yearlings beginning in the early 1990s (B. F. Lantry, unpublished data). Coinciding with this decline in lake trout abundance, observed wounding rates increased on species preferred less by sea lampreys (e.g., Chinook salmon, Eckert 2005).

Burbot abundance will likely remain low in Lake Ontario as long as the predation potential of sea lamprey and alewife continue at 1998–2004 levels. Predation by sea lamprey

is not projected to decrease because most of the important spawning streams are already under managed control and the buffering capacity of the lake trout stock (e.g., Swink and Fredericks 2000; Stapanian and Madenjian 2007) should remain low. Low abundance of lake trout will likely continue because Lake Ontario stocking levels are fixed (S. LaPan, NYSDEC Cape Vincent Fisheries Station, personal communication) and recruitment has been low for over 10 years (Lantry et al. 2005). Despite declines in alewife abundance, densities in Lake Ontario have remained much higher than those observed in Lake Michigan since the 1970s (Madenjian et al. 2003) and are suspected to determine the upper limit of burbot larval survival. The predation potential of the alewife population appears to be continuing at mid-1990s levels as alewife abundance has remained near the current level since 1996. Moreover, the current fish community objectives for Lake Ontario indirectly protect alewife, the major prey for stocked salmonids, from further predation-induced declines in abundance (Stewart et al. 1999). In addition to these factors, the pace of ecosystem changes in Lake Ontario appears to have accelerated at the end of the 20th century (Mills et al. 2003, 2005; Owens et al. 2003).

Synthesis

Burbot populations in Lake Superior have remained low since at least 1978 but were not decimated. In Lakes Michigan (Madenjian et al. 2002) and Huron (Collins 1988), recovery of the burbot population required sea lamprey control and reduction of the alewife population. In Lake Erie, recovery of burbot appeared to be due to sea lamprey control (Stapanian et al. 2006). Alewife populations in Lake Erie were too low and variable to influence burbot recruitment in most years (Ryan et al. 1999; Stapanian et al. 2006). In Lake Ontario, recovery of the burbot popu-

lation has not occurred, due mainly to both larval predation by alewives and predation on adults by sea lamprey (Elrod et al. 1995; Mills et al. 2003, 2005; Owens et al. 2003). Recent declines in burbot population density in Lake Michigan were associated with a short-term increase in sea lamprey abundances, a result of reduced lamprey control. Recent declines in the burbot populations in Lakes Huron and Erie were associated with low recruitment.

During certain years in the Great Lakes, the relatively larger populations of adult lake trout, the preferred prey of sea lampreys, have been shown to serve as a buffer against sea lamprey predation and thus contribute to the recovery of other native species, including burbot. Swink and Fredericks (2000) suggested that the lake trout in Lake Huron acted as a buffer that reduced predation of burbot by sea lampreys. The slight increase in large lake trout in recent years (Woldt and He 2006) may offer some additional buffering potential in Lake Huron but at the expense of lake trout restoration. Wells and McLain (1973) suggested that the increase in abundance of large lake trout in Lake Michigan during the 1960s and 1970s served to lower the frequency of sea lamprey attacks on lake whitefish and therefore contributed to their recovery. Although lake trout may have buffered the burbot population in Lake Michigan from sea lamprey predation for nearly all years since the 1970s, high alewife abundance during the 1960s and early 1970s likely prevented successful recovery of the burbot population until the 1980s. Stapanian and Madenjian (2007) showed that relatively high populations of adult lake trout, compared to burbot, served as a buffer against sea lamprey predation on burbot in Lake Erie during the few years in which sea lamprey control was reduced. Burbot in Lake Ontario were likely buffered from sea lamprey predation by a fourfold increase in the abundance of adult lake trout between 1984 and 1986 (Elrod et al. 1995). However,

low populations of lake trout have undoubtedly reduced this buffering potential in recent years for Lake Ontario (Lantry et al. 2005) and Lake Michigan (Bronte et al. 2007).

Although the burbot population in Lake Superior was not decimated, we hypothesize that lake trout also served as a buffer against sea lamprey predation on burbot. Sea lamprey, a major factor in the demise of many nearshore lean lake trout stocks in Lake Superior (Lawrie and Rahrer 1973; Pycha and King 1975), probably had little impact on the burbot that were present in Lake Superior. Encounter probabilities between sea lamprey and low densities of burbot were likely extremely low and resulted in low predator/prey ratios. Additionally, residual standing stocks of siscowet lake trout likely served as adequate and more available forage for sea lamprey after nearshore stocks of lean lake trout were decimated. Contemporary lamprey wounding rates on siscowet indicated that sea lamprey continue to feed on siscowet as well as lean lake trout (Bronte et al. 2003) and supported our hypothesis that siscowet provided a buffer against sea lamprey impacts on burbot.

It is unclear what effects on burbot in the Great Lakes will occur from perturbations such as the loss of the important benthic prey resource *Diporeia* spp. and the rapid expansion of the nonnative round goby *Neogobius melanostomus* (M. Walsh, U.S. Geological Survey Great Lakes Science Center, unpublished data), an aggressive egg predator (Fitzsimons et al. 2006). Although burbot have been shown to feed on round gobies (Stapanian et al. 2006), some negative consequences for burbot (e.g., egg predation) are also possible. Catches of age-4 burbot in Lake Erie declined sharply during 2000–2004 (i.e., 1996–2000 year-classes) (Stapanian and Madenjian 2007), which corresponded with the large increases in round goby populations in the eastern basin of Lake Erie (Charlebois

et al. 1997). Future studies will investigate these potential impacts.

In conclusion, the Laurentian Great Lakes during the past 40 years have provided a clear example of burbot populations being able to recover from major ecological disturbances, given that appropriate management actions are taken. With sea lampreys under control by the mid-1960s, and allowing sufficient time for the stocking of salmon and trout to substantially reduce alewife abundance, burbot populations in Lakes Michigan and Huron exhibited strong recoveries beginning in the late 1970s or early 1980s. Similarly, with sea lampreys under control by the late 1980s, the burbot population in Lake Erie exhibited a strong recovery during 1987–2003. Although the sea lamprey population is sufficiently low, Lake Ontario's burbot population is not expected to recover until the alewife population is reduced. Considering the apparent need for conservation measures for many populations of burbot world-wide (Paragamian et al. 2005), the lessons learned from the Great Lakes may provide insights for recovery measures elsewhere.

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