Lake Superior Committee
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Status and Trends of Prey Fish Populations in Lake Superior, 2004[1]

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Abstract: The Great Lakes Science Center conducts an annual daytime bottom trawl survey of the Lake Superior fish community every spring to provide a long-term index of relative abundance and biomass. The survey began in 1978 for U.S. waters and was expanded in 1989 to include Canadian waters. Currently, 87 fixed stations are distributed around the perimeter of Lake Superior. In 2004, a total of 75 stations were sampled with 12-m bottom trawls between May 10 and June 19. Trawls were deployed cross-contour at median start and end depths of 15 and 65 m, respectively. Acoustic data were also collected concurrently at 70 of the 75 stations to test the assumption that fish are primarily demersal during the day and thus susceptible to bottom trawls. The mean lakewide biomass estimate for all species combined increased from 4.71 kg/ha in 2003 to 6.29 kg/ha in 2004, halting the downward trend that began in the early 1990s. Most of this increase was a result of recruitment of the 2003 lake herring year-class, which was the seventh highest during the 27-year survey. Bloater, burbot, and longnose suckers also made minor contributions to the increase in biomass. Lake whitefish made up the highest percent of the total mean biomass for any species (30%), followed by lake herring (29%), bloater (18%), longnose sucker (7%), and rainbow smelt (5%). Lake whitefish and rainbow smelt biomass remained at similar levels from 2003 to 2004, in spite of a moderate 2003 year-class of rainbow smelt. Biomass of lean lake trout and siscowets decreased in 2004, with siscowet biomass exceeding wild lake trout biomass for the first time and hatchery lake trout reaching their lowest biomass over the time series. The 2002 and 2003 lake herring year-classes were the largest consecutive cohorts since the 1988-1990 cohorts, though much smaller in magnitude. Bloater year-class strength increased for a second consecutive year, but still remains below the 1978-2004 average. Wisconsin waters continue to be the most productive (mean total biomass of 19.75 kg/ha), followed by western Ontario (5.33 kg/ha), Michigan (3.01 kg/ha), eastern Ontario (1.91 kg/ha), and Minnesota (0.75 kg/ha). Comparisons between acoustic techniques and bottom trawls indicate that, at a lakewide scale, mean fish biomass in the water column above the trawl path was 70% of the mean estimate derived from the bottom trawl data. Comparing estimates from both gears at western Lake Superior stations sampled concurrently in 2001, 2003, and 2004 shows high year-to-year and site-to-site variability in pelagic fish biomass during the day. The assumption that fish are primarily demersal during the day in the spring appears to be incorrect. These results suggest that fish behavior can have an impact on biomass estimates when daytime bottom trawling is the sole gear, and that relative differences in our spring survey indices may result from changes in fish behavior as well as actual changes in abundance. If absolute fish biomass estimates are a long-term goal for Lake Superior management agencies, consideration of a comprehensive lakewide survey that integrates multiple gears will be necessary.

[1]Presented at: Great Lakes Fishery Commission, Lake Superior Committee Meeting, Ypsilanti, Michigan 24 March 2005

Introduction

The Great Lakes Science Center's Lake Superior Biological Station conducts an annual daytime bottom trawl survey every spring in Lake Superior. The survey began in 1978 for U.S. waters and was expanded in 1989 to include Canadian waters. The survey is intended to provide a long-term index of relative abundance and biomass of Lake Superior's fish community in nearshore waters. In this report, we update the time series of relative abundance and biomass densities with data collected in 2004. Additionally, we present preliminary data that test the assumption that fish are primarily demersal during the day in the spring, making them susceptible to bottom trawling.

Methods

Currently, 87 fixed sampling stations are distributed around the perimeter of Lake Superior. In 2004, a total of 75 stations were sampled with 12-m bottom trawls between May 10 and June 19 during daylight hours (Fig. 1). Trawls were deployed cross-contour. Eighty percent of the trawls 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 trawl duration was 25 minutes (range 6-60 minutes). One trawl tow was made at each station.

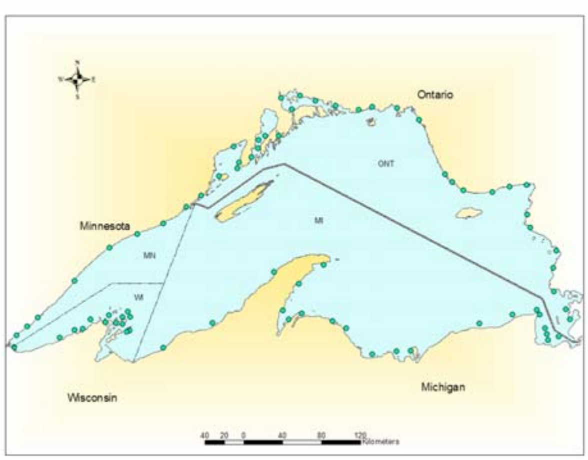


Figure 1. *Locations of 75 stations sampled during the 2004 annual spring bottom trawl survey in Lake Superior.*

For each trawl, fish were sorted and counted by species and weighed in total (for each species) to the nearest gram. Counts and biomass were standardized to the number of hectares swept to estimate abundance (fish/ha) and biomass (kg/ha) densities. The arithmetic mean was used to measure species-specific biomass densities and year-class strength of important prey species. Year-class strength is estimated as abundance density (fish/ha) of age-1 fish (the first age-class that recruits to our bottom trawl in the spring). To be consistent with past reports and to more easily identify the year in which a cohort was produced, year-class strength is plotted against the year in which the cohort was produced (year sampled minus 1) and not the year the age-1 fish were caught. Standard errors (SE) were calculated as $SD/\sqrt{n}$, where SD = the sample standard deviation and n = number observations. The SE was standardized by the relative standard error (RSE): RSE = SE/mean*100. An RSE = 100% indicates the standard error was equal to the estimated mean.

Lake herring were aged using otoliths or scales, depending on total fish length. Scales were used for fish < 300 mm and otoliths were used for fish ≥ 300 mm. Past experience indicates that this is the length at which scale aging becomes less reliable. Lake Superior was divided into nine regions, and ten lake herring per 10-mm length bin were aged for each region by a single experienced reader. Length-frequency distributions were used to determine age-1 fish for rainbow smelt (< 100 mm), lake whitefish (< 150 mm), and bloater (< 140 mm). These length cutoffs have been used since 2002 but can change from year-to-year based on inter-annual variability in growth rates.

To test the inherent assumption that fish are primarily demersal during the day and thus susceptible to bottom trawls, acoustic data were collected concurrently with bottom trawls at 70 of the 75 stations sampled in 2004. Total biomass estimates from the bottom trawl were compared with total biomass estimates in the water column above the trawl path measured with acoustic techniques. Similar data from the western arm of Lake Superior in 2001 and 2003 were also examined to determine how much biomass the bottom trawl may be missing, and if this amount varies from year-to-year and from site-to-site. Unpublished data (GLSC-LSBS, Ashland, WI) from Lake Superior indicate acoustic techniques provide a comparable estimate of pelagic biomass when compared to concurrent midwater trawling (Trawl Biomass = 0.71*Acoustic Biomass + 2.10, $n = 11$, $r^2 = 0.73$).

Results

Lake Herring

Year-class strength for the 2003 lake herring cohort, at 25 fish/ha, was the seventh highest recorded over the survey period and was a slight decrease from year-class strength of the 2002 cohort (35 fish /ha) (Fig. 2A). The 2002 and 2003 cohorts were the largest consecutive year-classes since the 1988-1990 year-classes, though much smaller in magnitude (Fig. 2A). Relative standard error (RSE) fluctuated between 20 and 100% over the survey period, with the 2004 estimate having the best precision (Fig. 2B). Year-class strength in 2003 was similar between U.S. and Canadian waters (24 and 26 fish/ha, respectively).

Lake herring mean biomass increased from 0.64 kg/ha in 2003 to 1.80 kg/ha in 2004 (Fig. 3A), although current standing stock is still below the 1978-2004 average of 3.17 kg/ha. RSE fluctuated between 25 and 90% over the survey period and does not appear to be related to mean biomass (Fig. 3).

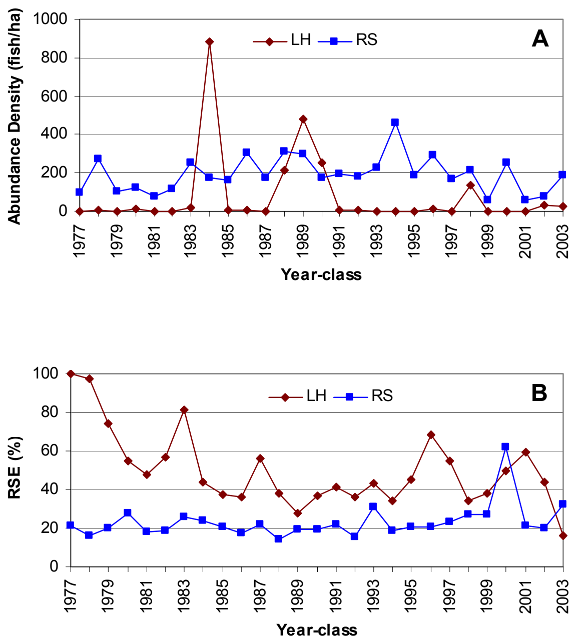


Figure 2. ***(A)*** *Year-class strengths (number of age-1 fish/ha) for lake herring (LH) and rainbow smelt (RS) for all sampling stations in Lake Superior for cohorts produced from 1977 to 2003. Note only U.S. waters were sampled for the 1977-1988 year-classes. Also note that X-axis reflects the year the cohort was produced, not the year the year-class strength was estimated (year-class+1).* ***(B)*** *RSE (relative standard error) of year-class strengths in (A). RSE is calculated as SE/mean*100.*

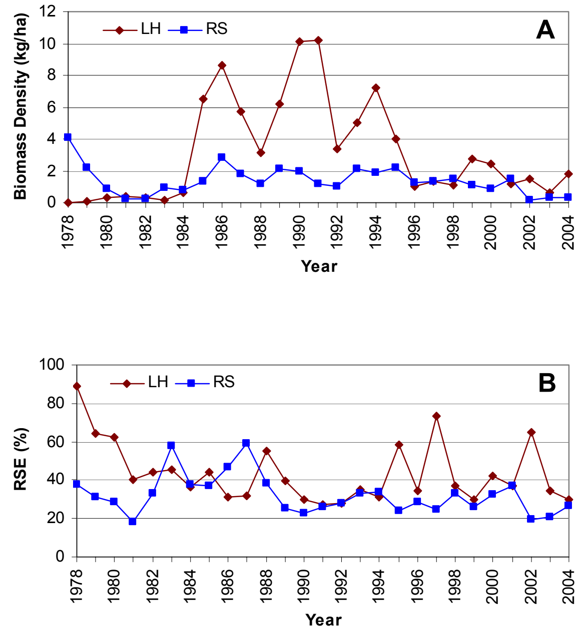


Figure 3. ***(A)*** *Mean biomass density (kg/ha) of age-1 and older lake herring (LH) and rainbow smelt (RS) for all sampling stations in Lake Superior, 1978-2004. Note Canadian waters were not sampled until 1989.* ***(B)*** *RSE (relative standard error) of mean biomass in (A). RSE is calculated as SE/mean*100.*

Increases in mean lake herring biomass were seen in each political jurisdiction (Figs. 4 and 5). Wisconsin waters showed the largest absolute increase from 2003 to 2004 (2.16 to 6.41 kg/ha), followed by Ontario (0.31 to 0.99 kg/ha), Minnesota (0 to 0.16 kg/ha), and Michigan (0.44 to 0.60 kg/ha). Only Minnesota is above its 1978-2004 average of 0.14 kg/ha, although Wisconsin is close (1978-2004 average = 6.9 kg/ha).

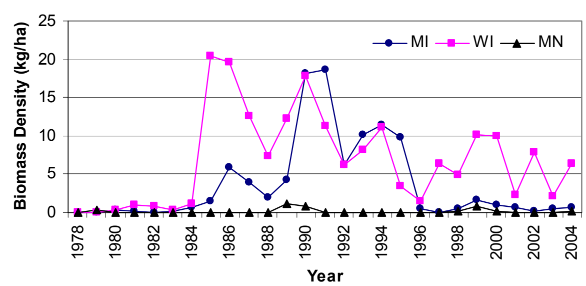


Figure 4. *Mean biomass density (kg/ha) of lake herring (age-1 and older) in Michigan, Wisconsin, and Minnesota waters of Lake Superior, 1978-2004.*

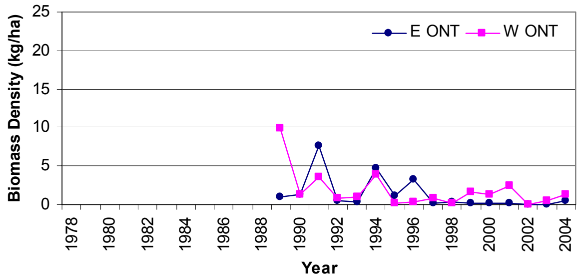
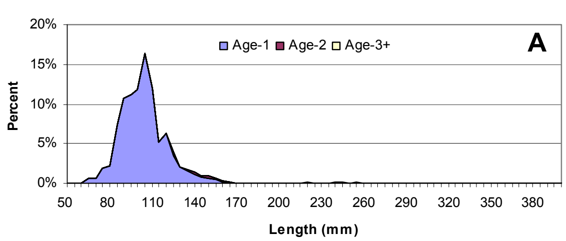


Figure 5. *Mean biomass density (kg/ha) of lake herring (age-1 and older) in eastern and western Ontario waters of Lake Superior, 1978-2004. Eastern and western Ontario waters are divided in the northeast corner of Lake Superior, near Marathon, Ontario. Axes are similar to Figure 4 to facilitate comparisons across jurisdictions.*

The 2003 year-class dominated the catch of lake herring in 2004, accounting for 97% of all lake herring caught (Fig. 6A). The 2002 year-class represented 2% of the 2004 catch, while all older year-classes represented 1% of the catch (Fig. 6A). The 1999 and 1998 year-classes represented 37 and 36%, respectively, of all captured lake herring age-5 and older (Fig. 6B). The 1997 and 1996 year-classes represented 12 and 6%, respectively, of all captured lake herring age-5 and older (Fig. 6B). These results do not match expectations from year-class strength (Fig. 2A). We are currently evaluating our aging methods, and will be working with Wisconsin DNR and Ontario MNR in a comparison study.



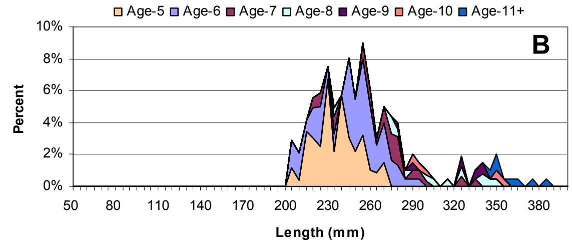


Figure 6. ***(A)*** *Cumulative area plot of age-length distribution of lake herring caught in all waters of Lake Superior in 2004. A total of 339 fish were aged, and an age-length key was applied to total catch.* ***(B)*** *Same as (A) but for all lake herring ≥ age-5, with Y-axis standardized to total catch of lake herring ≥ age-5. Total number of lake herring aged ≥ age-5 was 188.*

Rainbow Smelt

Year-class strength increased from 78 fish/ha for the 2002 cohort to 186 fish/ha for the 2003 cohort of rainbow smelt (Fig. 2A). Year-class strength for the 2003 cohort is slightly less than the average over the entire survey period (193 fish/ha), and follows two of the weakest year-classes since 1978 (Fig. 2A). RSE has remained fairly constant over the entire survey period, at roughly 20%, with the 2000 year-class the only exception at 60% (Fig. 2B).

The lakewide mean biomass for rainbow smelt remained at about the same level in 2004 (0.31 kg/ha) as in 2003 (0.30 kg/ha) (Fig. 3A), despite the recruitment of a moderate 2003 year-class to the bottom trawl (Fig. 2A). This continues a three-year low in biomass estimates, similar to the low estimates in 1981 and 1982 (Fig. 3A). RSE has fluctuated between 20 and 60% over the survey period (Fig. 3B).

Decreasing trends in rainbow smelt biomass are evident at the jurisdiction level, as Wisconsin, Michigan, Minnesota, and eastern Ontario continue slow, steady declines since the mid-1990s (Figs. 7 and 8). Mean biomass of rainbow smelt in western Ontario waters remains at very low levels for the third year in a row, after relatively high biomass estimates from 1989-2001 (Fig. 8).

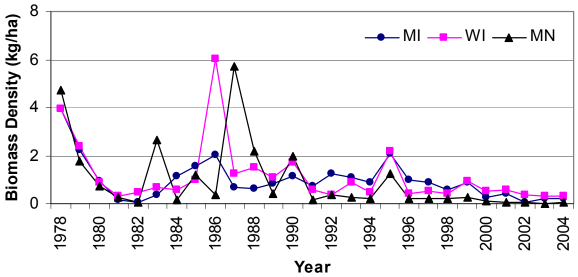


Figure 7. *Mean biomass density (kg/ha) of rainbow smelt (age-1 and older) in Michigan, Wisconsin, and Minnesota waters of Lake Superior, 1978-2004.*

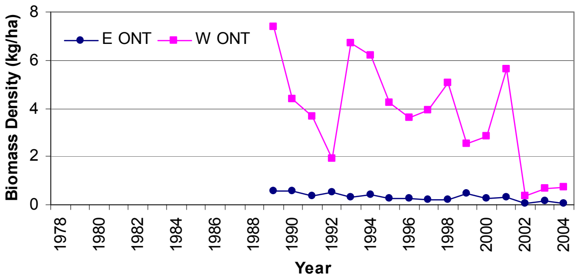


Figure 8. *Mean biomass density (kg/ha) of rainbow smelt (age-1 and older) in eastern and western Ontario waters of Lake Superior, 1978-2004. Axes are similar to Figure 7 to facilitate comparisons across jurisdictions.*

The length-frequency distribution of rainbow smelt in 2004 was characterized by two modes – one at 60 mm and the other at 105 mm (Fig. 9). Comparison of 2004 length-frequency data to similar data collected in 1978, a time when rainbow smelt biomass was much greater (Fig. 3A), demonstrates a dramatic shift in rainbow smelt size structure (Fig. 9). The modes of the 1978 length-frequency distribution were at 45-60 mm and 165 mm (Fig. 9). At present, far fewer rainbow smelt reach larger sizes.

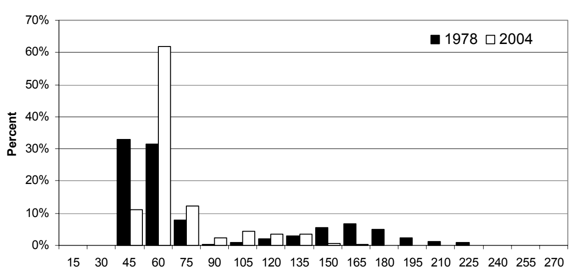
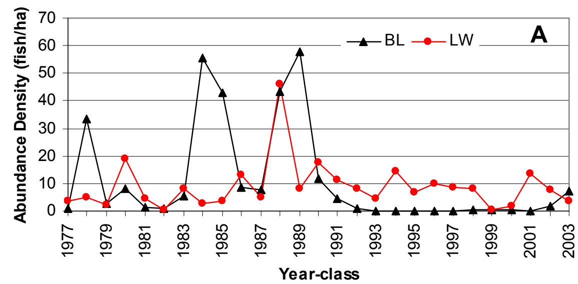


Figure 9. *Length-frequency distributions of rainbow smelt from the Apostle Islands region of Lake Superior in 1978 and 2004. Lakewide mean biomass density for each time period was 4.07 kg/ha in 1978 and 0.32 kg/ha in 2004.*

Bloater

The 2003 year-class strength for bloater was 7 fish/ha, up from 2 fish/ha for the 2002 year-class (Fig. 10A). The 2003 year-class represents the highest abundance of age-1 bloaters since 1990 (12 fish/ha) and represents a second straight year of increase (Fig. 10A). The increase in year-class strength from the 2002 to the 2003 cohorts was evident in both U.S. (2 to 9 fish/ha) and Canadian (2 to 5 fish/ha) waters. RSE fluctuated between 20 and 60% over the survey period (Fig. 10B).



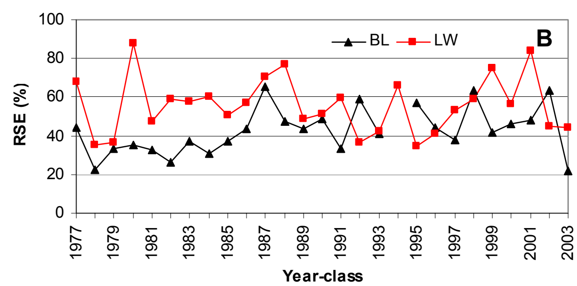


Figure 10. ***(A)*** *Year-class strengths (number of age-1 fish/ha) for bloater (BL) and lake whitefish (LW) for all sampling stations in Lake Superior for cohorts produced from 1977 to 2003. Note only U.S. waters were sampled for the 1977-1988 year-classes. Also note that X-axis reflects the year the cohort was produced, not the year the year-class strength was estimated (year-class+1).* ***(B)*** *RSE (relative standard error) of year-class strengths in (A). RSE is calculated as SE/mean*100.*

Bloater mean biomass increased slightly from 0.88 kg/ha in 2003 to 1.14 kg/ha in 2004 (Fig. 11A). This is a second straight year of increase, but the 2004 mean biomass still remains well below the 1978-2004 average of 2.08 kg/ha. Similar increases from 2003 to 2004 were evident in Michigan (0.33 to 0.90 kg/ha), Wisconsin (4.04 to 4.44 kg/ha), Minnesota (0 to 0.06 kg/ha), and western Ontario (0.14 to 0.18 kg/ha) waters (Figs. 12 and 13). Mean biomass in eastern Ontario decreased from 0.25 kg/ha in 2003 to 0.08 kg/ha in 2004 (Fig. 13). Bloater mean biomass estimates in each jurisdiction remain below their respective 1978-2004 averages.

Positive identification of age-1 coregonids has been problematic, as evident by lack of apparent bloater year-classes between 1992 and 2001 (Fig. 10A) in spite of biomass increases in 1996 and 1998 (Fig. 11A). These discrepancies are a result of general difficulties in identifying age-1 coregonids to species, and simultaneous application of different species classification models in different regions of Lake Superior during most of the 1990s (C. Bronte, USFWS, pers. comm.). We are currently working with a variety of metrics to sort out species assignments to historical age-1 coregonid data. We are also developing a study plan for the 2006 field season to evaluate our ability to identify age-1 coregonids to species (kiyi, lake herring, and bloater) consistently (comparison among sorters) and accurately (comparison of field identifications to genetic profiles).

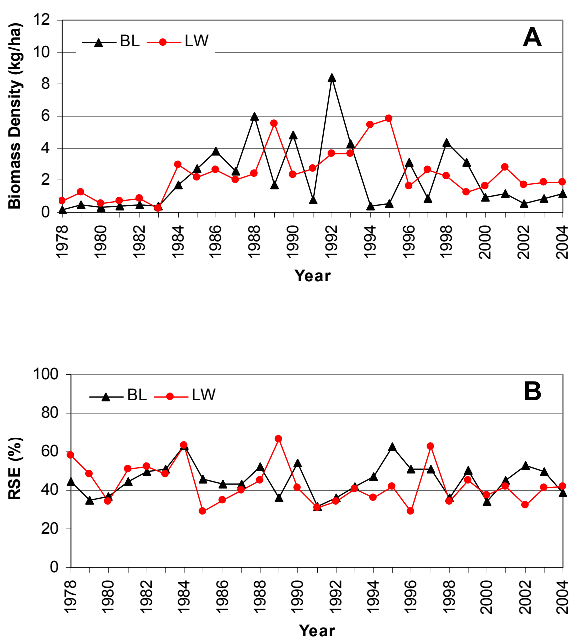


Figure 11. ***(A)*** *Mean biomass density (kg/ha) of age-1 and older bloater (BL) and lake whitefish (LW) for all sampling stations in Lake Superior, 1978-2004. Note Canadian waters were not sampled until 1989.* ***(B)*** *RSE (relative standard error) of mean biomass in (A). RSE is calculated asSE/ mean*100. Y-axis is similar to Figure 3 to facilitate comparisons across major prey species.*

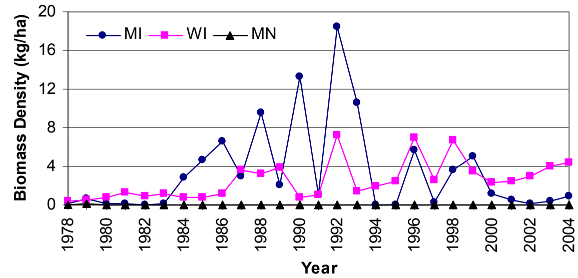


Figure 12. *Mean biomass density (kg/ha) of bloater (age-1 and older) in Michigan, Wisconsin, and Minnesota waters of Lake Superior, 1978-2004.*

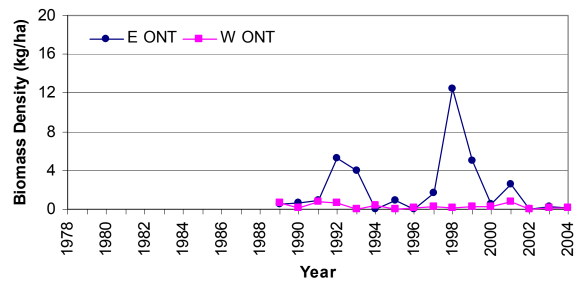


Figure 13. *Mean biomass density (kg/ha) of bloater (age-1 and older) in eastern and western Ontario waters of Lake Superior, 1978-2004. Axes are similar to Figure 11 to facilitate comparisons across jurisdictions.*

Lake Whitefish

Lake whitefish year-class strength for the 2003 cohort (4 fish/ha) was half that for the 2002 cohort (8 fish/ha), and represents a second straight year of decrease (Fig. 10A). RSE for lake whitefish year-class strength has fluctuated between 40 and 80% over the survey period (Fig. 10B). The 2003 year-class was much stronger in U.S. waters (6 fish/ha) compared to Canadian waters (1 fish/ha). Average year-class strength for lake whitefish over the survey period is 9 fish/ha.

Despite the decreased recruitment of age-1 fish to the bottom trawl, the mean lake whitefish biomass estimate for all waters did not change from 2003 (1.84 kg/ha) to 2004 (1.88 kg/ha) (Fig. 11A). Mean biomass has remained steady since 1996, averaging 1.96 kg/ha over this period. RSE for lake whitefish biomass has remained fairly constant, fluctuating between 25 and 60% (Fig. 11A). At the jurisdiction level, lake whitefish have only been caught once (1995) in Minnesota waters over the entire time series (Fig. 14). Most lake whitefish biomass comes from Wisconsin waters (Fig. 14), which showed a decrease from 8.65 kg/ha in 2003 to 7.20 kg/ha in 2004. All other jurisdictions showed slight (Michigan, 0.64 to 0.76 kg/ha; eastern Ontario, 0.27 to 0.31 kg/ha) to modest (western Ontario, 0.35 to 1.05 kg/ha) increases (Figs. 14 and 15).

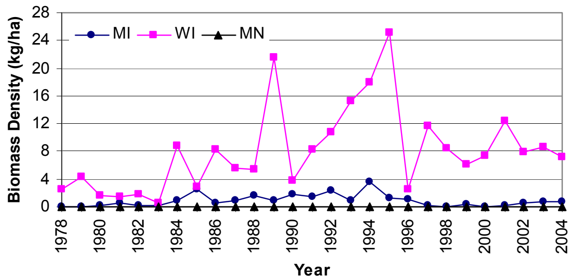


Figure 14. *Mean biomass density (kg/ha) of lake whitefish (age-1 and older) in Michigan, Wisconsin, and Minnesota waters of Lake Superior, 1978-2004.*

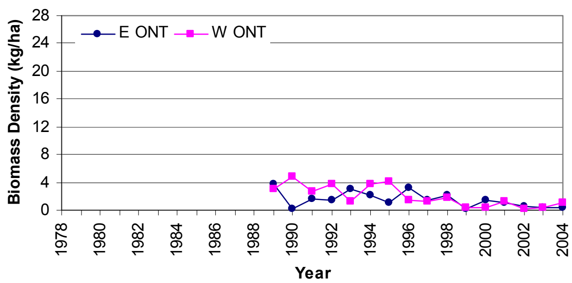


Figure 15. *Mean biomass density (kg/ha) of lake whitefish (age-1 and older) in eastern and western Ontario waters of Lake Superior, 1978-2004. Axes are similar to Figure 14 to facilitate comparisons across jurisdictions.*

Other Species

Ninespine stickleback – Lakewide mean biomass for ninespine sticklebacks indicated a rebound from persistently low and decreasing estimates since 1993 (Fig. 16). Mean biomass for all waters in 2004 was 0.08 kg/ha compared to 0.01 kg/ha in 2003.

Sculpins – Mean biomass for all three sculpin species combined (spoonhead, deepwater, and slimy) has followed the same trajectory as ninespine sticklebacks since 1993 (Fig. 16). There was a 50% increase from 2003 to 2004 (0.02 to 0.03 kg/ha, respectively). Slimy sculpins averaged 66% of the total sculpin biomass across all years, but represented a higher percentage in the earlier years (81% from 1978 to 1983 compared to 62% from 1984 to 2004).

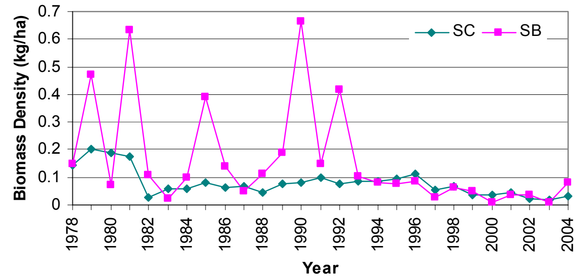


Figure 16. *Mean biomass density (kg/ha) of age-1 and older sculpins (slimy, spoonhead, and deepwate combined; SC) and ninespine stickleback (SB) for all sampling stations in Lake Superior, 1978-2004. Note Canadian waters were not sampled until 1989.*

Lake Trout – Siscowet biomass (0.15 kg/ha) exceeded wild lake trout biomass (0.11 kg/ha) in 2004 for the first time ever in the spring survey (Fig. 17). Wild lean lake trout biomass decreased from 0.33 kg/ha in 2003 to 0.11 kg/ha in 2004, while siscowet biomass decreased from 0.24 to 0.15 kg/ha (Fig. 17). Wild lean lake trout biomass has shown a consistent decreasing trend since 1995 (Fig. 17). Hatchery lake trout biomass was the lowest ever recorded for the spring survey at 0.007 kg/ha (Fig. 17).

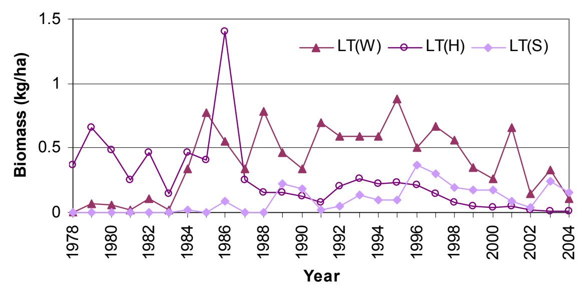


Figure 17. *Mean biomass density (kg/ha) of age-1 and older wild lake trout (LT(W)), hatchery lake trout (LT(H)), and siscowet (LT(S)) for all sampling stations in Lake Superior, 1978-2004. Note Canadian waters were not sampled until 1989.*

Fish Community

Mean biomass of all fish species caught by our bottom trawl survey increased from 4.71 kg/ha in 2003 to 6.29 kg/ha, halting the downward trend since the early 1990s (Fig. 18). Increased biomass in 2004 is a result of increases in lake herring (increase of 1.16 kg/ha from 2003), bloater (0.26 kg/ha increase), burbot (0.19 kg/ha increase), and longnose sucker (0.17 kg/ha increase) (Fig. 18). Lake whitefish, lake herring, rainbow smelt, and bloater represented 82% of the average biomass for all waters of Lake Superior in 2004. Lake whitefish made up the highest percentage of biomass for any species (30%), followed by lake herring (29%), bloater (18%), longnose sucker (7%), and rainbow smelt (5%). In 2003, lake whitefish represented 39% of the average lakewide biomass, followed by bloater at 19% and lake herring at 14%.

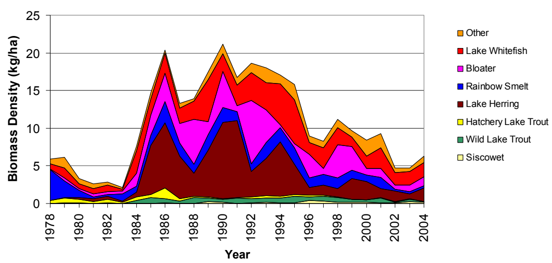


Figure 18. *Cumulative area plot of mean biomass density (kg/ha) of fish community for all sampling stations in Lake Superior, 1978-2004. Note Canadian waters were not sampled until 1989. Other category consists of: kiyi, round whitefish, pygmy whitefish, spoonhead sculpin, slimy sculpin, deepwater sculpin, longnose sucker, burbot, ninespine stickleback, and trout-perch.*

Assumption of Demersal Distribution

Acoustics were deployed concurrently with daytime bottom trawls at 70 of the 75 bottom trawl stations sampled. Mean biomass for these 70 stations was 6.50 kg/ha using the bottom trawl and 4.52 kg/ha using the acoustics (water column above the trawl path).

Comparing mean biomass estimates from the same general region of western Lake Superior in 2001 (n=11 stations), 2003 (n=8 stations), and a subset of 2004 data (n=10 stations) indicates substantial fish biomass in the water column above the trawl path and variability in the average distribution of biomass in the water column across years (Fig. 19A). In 2001, the acoustic biomass estimate in the water column was greater than the bottom trawl estimate by 50% (4.52 versus 3.02 kg/ha, respectively; Fig. 19A). RSEs for each gear in 2001 were similar at approximately 58%. (Fig. 19B). Acoustic biomass in the water column also exceeded the bottom trawl biomass estimate in 2003, but only by 11% (7.63 versus 6.90 kg/ha, respectively; Fig. 19A). RSE was higher for the bottom trawl estimate (71%) compared to the acoustic estimate (44%; Fig. 19B). In 2004, acoustic biomass was 85% of bottom trawl biomass in the western arm of Lake Superior (9.07 versus 10.56 kg/ha, respectively; Fig. 19A), and had a much higher RSE (98% versus 43%, respectively, Fig. 19B). Both gears demonstrate a similar pattern in fish biomass across years: 2004 > 2003 > 2001.

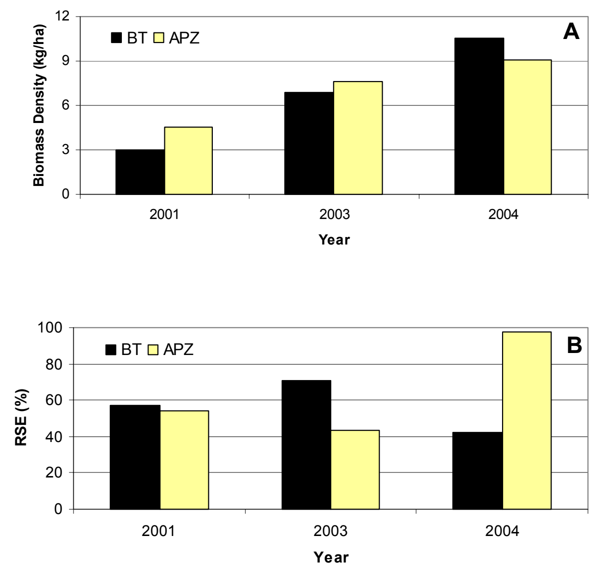


Figure 19. ***(A)*** *Mean fish biomass density (kg/ha) from the western arm of Lake Superior based on bottom trawls (BT) and acoustic techniques (water column above the trawl path; APZ) deployed concurrently during the day in 2001, 2003, and 2004.* ***(B)*** *RSE (relative standard error) of mean biomass in (A). RSE is calculated as SE/mean*100.*

At the station level, only 1 of the 11 stations with multiple years of observations showed consistently higher biomass estimates from the bottom trawl compared to acoustic estimates in the water column zone (Station 151; Fig. 20). Three stations (190, 65, and 36) showed no differences or just slightly higher bottom trawl estimates, three stations (186, 187, and 210) showed greater acoustic estimates in one or more years, and four stations (139, 205, 76, and 206) showed differences that flip-flopped between gears across years (Fig. 20).

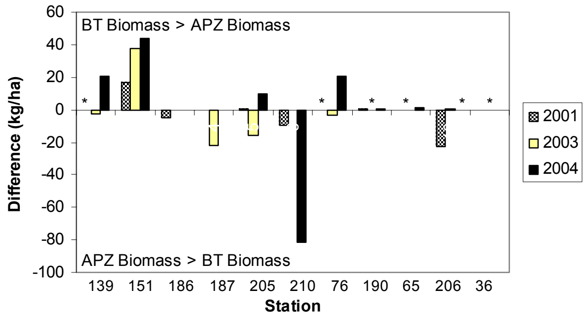


Figure 20. *Difference between bottom trawl (BT) and acoustic pelagic (APZ) biomass density estimates from stations where concurrent sampling was done for multiple years. Values greater than zero indicate higher bottom trawl estimates, and values less than zero indicate higher acoustic pelagic estimates. Asterisks denote years not sampled.*

Discussion

The spring bottom trawl survey indicated that total fish biomass increased by 34% in 2004, and that most of this increase was a result of recruitment of the 2003 lake herring year-class to the bottom trawls. Lake whitefish and rainbow smelt biomass remained at similar levels from 2003 to 2004, in spite of a moderate 2003 year-class of rainbow smelt recruiting to the bottom trawl. Lake trout biomass decreased from 2003 to 2004, with siscowet biomass exceeding wild lean lake trout biomass for the first time and hatchery lean lake trout reaching their lowest biomass over the time series. Total mean biomass for all species (6.29 kg/ha) was below the 1978-2004 average (10.71 kg/ha) but has increased each of the past two years.

With the exception of the earliest years of the spring survey when rainbow smelt dominated the fish community biomass, lake herring (and to a certain extent bloater) have been driving the fish community biomass dynamics. Large lake herring year-classes in 1984 and 1988-1990 supported the largest peaks in total biomass, although the dip in 1992 lake herring biomass and subsequent buildup to a peak in 1994 (Fig. 3A) is not explained by production of year-classes after 1990 (Fig. 2A). The 1998 year-class produced a smaller peak in lake herring biomass in 1999, but this peak subsequently diminished in the following years until the increase in 2004 (Fig. 3A).

The recovery of lake trout populations in Lake Superior (Hansen 1999) appears to be driving the decline in rainbow smelt populations (Bronte et al. 2003). Over the period of the spring survey, Lake Superior lake trout have preferentially consumed rainbow smelt (Conner et al. 1993, Ray 2004). Comparisons between abundance and size structure of rainbow smelt populations in 1978, when lake trout recovery was underway, and 2004, after recovery of lake trout, indicates a prey population that is under intense predation pressure. Conner et al. (1993) and Ray (2004) both indicate rainbow smelt were a dominant forage item for lake trout in spite of greater availability of coregonids, although predation on coregonids may be on an upward trend (Ray 2004). Bronte et al. (2003) suggest increased broadening of rainbow smelt size structure in the future is unlikely if predation remains high. The apparent decline in lake trout biomass, as measured by our spring survey (Fig. 17), presents a future test of this hypothesis if lake trout declines are real and continue in the coming years.

The assumption that fish are primarily demersal during the day in the spring and thus susceptible to day bottom trawling appears to be incorrect. On a lakewide basis in 2004, average biomass in the water column was 70% of the bottom trawl estimate. The range in biomass estimates across stations using daytime acoustics was similar to the range in estimates from bottom trawls. Acoustic biomass estimates exceeded bottom trawl estimates during day sampling in over 33% of transects concurrently sampled. Across-site differences in biomass estimates from the two gears illustrate high spatial variability in the proportions of fish occupying open water above the trawl path (e.g., Station 151 versus 210 in 2004; Fig. 20), as well as temporal differences within a site (e.g., Station 205 across years; Fig. 20). These results suggest that fish behavior can have an impact on biomass estimates when daytime bottom trawling is the sole gear, and that relative differences in our spring survey indices may result from changes in fish behavior as well as actual changes in abundance. How one apportions the variability associated with fish behavior versus real population change is unclear at this time. However, given that the spring bottom trawl survey appears to capture general long-term trends in major fish species (e.g., decline of rainbow smelt, strong year-classes of lake herring, and recovery of lake trout), the more important question may be how much better (i.e., closer to absolute) do management agencies require biomass estimates to be to improve their ability to manage fish populations?

Results from the acoustic data at least partly explain estimated differences between predator demand and prey supply in Lake Superior (Negus 1995, Ebener 1995). In these analyses, prey supply estimates were taken from the USGS spring survey. Negus (1995) suggested that these prey fish estimates, from day bottom trawls, were the most likely explanation for the discrepancy. This is not surprising, as the spring survey provides only a relative index, and we have demonstrated a substantial amount of biomass in the water column during the day that is not susceptible to bottom trawls. Mason et al. (submitted) also found that biomass estimates based on acoustics at night (in summer) could account for the apparent predator:prey paradox reported by Negus (1995) and Ebener (1995).

Preliminary results from a pilot study in the Apostle Islands region of Lake Superior in 2004 indicate that biomass estimates for lake herring may be 26 times greater using acoustics and midwater trawls at night compared to estimates from bottom trawls during the day. All other species, with the exception of deepwater sculpin, exhibit at least a doubling of biomass estimates when sampled at night (compared to day) regardless of gear type. Additionally, species vary in their susceptibility to each gear, with sculpin species and lake whitefish primarily susceptible to bottom trawls. This indicates that each gear's strength is the other's weakness. Additionally, preliminary results from the ongoing lakewide acoustic monitoring program indicate similar amounts of lake herring biomass in offshore waters (> 150 m bathymetric depth) as in nearshore waters as measured by acoustic techniques at night (T. Hrabik, Univ. MN-Duluth, pers. comm.). If generating prey fish biomass estimates in absolute terms is a long-term goal for the Lake Superior management community, consideration of a comprehensive lakewide survey design that integrates and draws upon the strengths of multiple gears will be necessary.

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