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Temporal trends in the numbers and characteristics of Lake Huron fish schools between 2000 and 2004

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ABSTRACT

We used hydroacoustics to characterize temporal dynamics of fish schools in Georgian Bay and the North Channel of Lake Huron from 2000 to 2004. Dramatic changes in fish school numbers and characteristics were observed over the 5-year period. In 2000, fish schools had an average trace length of 18.2 m and an average height of 2.7 m. Between 2000 and 2004, there was then an increase in the distance of schools from bottom and a drop in the number of schools per kilometer of transect, in the number and proportion of benthic schools, and in the depth, length, height, area, and volume of schools. Netting data confirm that there was a reduction in alewife (*Alosa pseudoharengus*) that could explain the declines in the number of schools and the changes in fish school characteristics. There was also evidence that the alewife schools were replaced, to a degree, by lake herring schools in Georgian Bay and rainbow smelt schools in the North Channel. Our work provides an example of how fisheries acoustics can be used to study the spatial and behavioural dynamics of fish schools in the Great Lakes.

Introduction

Schooling fish form an important component of the pelagic food web in the Great Lakes. In Lake Huron, the predominant pelagic schooling fishes are alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*), lake herring (*Coregonus artedi*), and more recently, emerald shiner (*Notropis atheronoides*). The abundances of these species are dynamic, showing both episodic fluctuations and long-term trends driven by factors such as predation, climate, and the invasion of exotic species. Alewife are an exotic species that was first observed in Lake Huron in 1933 (Madenjian et al., 2008), reaching large numbers in the 1960s and 1970s, but since then declining in abundance (Dobiesz et al., 2005). Large fluctuations in alewife recruitment are commonly observed in the Great Lakes, with large die offs being attributed to cold temperatures (Ridgway et al., 1990; O'Gorman et al., 2004; Madenjian et al., 2005). Other factors, most notably predation, are also thought to impair the recruitment of alewife and could be contributing to the observed declines (Ridgway et al., 1990; O'Gorman et al., 2004). Rainbow smelt are also exotic and together with alewife can make up over half of the forage fish caught in Lake Huron bottom trawls (Argyle 1982). Stocked piscivores including lake trout (*Salvelinus namaycush*), rainbow trout (*Oncorhynchus mykiss*), and Chinook salmon (*Oncorhynchus tshawytscha*) now feed primarily on alewife and rainbow smelt (Dobiesz 2003; Madenjian et al., 2006). Lake herring were once the dominant prey of lake trout, but by 1970 had collapsed in all of the Great Lakes including Lake Huron (Henderson and Payne 1988; Dobiesz et al., 2005; Madenjian et al., 2008). In recent years, however, there are signs that lake herring are increasing in numbers (Henderson and Payne 1988; Dobiesz et al., 2005; Warner et al., 2009).

The full extent of the interaction between alewife, lake herring, and rainbow smelt is unknown. Given that they are all schooling forage fish that occupy pelagic habitats, there is some expectation that they could negatively influence one another. For example, rainbow smelt are thought to negatively impact lake herring through competition and predation on young lake herring (Krueger and Hrabik 2005, Gorman 2007), but the importance of these effects is debated (Selgeby et al., 1978; Henderson and Fry 1987; Dobiesz et al., 2005). Also, although alewife are thought to have a negative impact on many species (Eck and Wells 1987; Brown et al., 2005; Lantry et al., 2007; Madenjian et al., 2008), Madenjian et al. (2008) recently presented evidence that rainbow smelt and lake herring are only minimally affected by alewife; this is because the time window for alewife to predate on larval herring and smelt is small as a result of limited overlap in habitat. The

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conclusions by Madenjian et al. (2008) provide helpful generalizations for the Great Lakes as a whole, but the extent that these species interact with one another on a finer scale also needs to be considered, especially when noting the spatial heterogeneity in available habitat that exists in lakes as diverse as Lake Huron.

The episodic crashes in recruitment and abundance of alewife provide an opportunity to observe any ensuing dynamics in the other pelagic forage fish. Between 2000 and 2003, the abundance of alewife underwent a dramatic decline in Lake Huron (Fielder et al., 2007; Riley et al., 2008; Warner et al., 2009). This decline is thought to have contributed to strong year classes of walleye *Sander vitreus* (Fielder et al., 2007) and emerald shiner *Notropis atheronoides* (Schaeffer et al., 2008) but there could have been other impacts, for example on the other schooling species. In this article, we focus on the possible spatial and behavioural dynamics of the alewife decline, examined by considering changes in the characteristics of fish schools in Lake Huron.

The quantification of fish schools requires sampling and statistical techniques that have yet to be rigorously applied to freshwater systems. These techniques involve the use of hydroacoustic technology which has already been successfully employed to study fish schools in marine environments (Gerlotto and Paramo 2003; Petitgas 2003; Soria et al., 2003; Gerlotto et al., 2004; Weber et al., 2009). In lakes, hydroacoustics (or more specifically, fisheries acoustics) have been used primarily to monitor and assess patterns in fish and zooplankton population biomass (Argyle 1992; Mason et al., 2005; Holbrook et al., 2006; Stockwell et al., 2007; Warner et al., 2009). It is also possible to use fisheries acoustics to extract fish school parameters including school numbers, distribution, and morphology from split-beam or multibeam echo-sounders. Information on school morphology can also be used in some cases to identify the species composition of a school (Rose and Leggett 1988; Cabreira et al., 2009; Fernandes 2009). As the total biomass of fish in schools can be substantial, this information could be of profound importance to understanding population and spatial dynamics of entire communities, including the pelagic fish community of Lake Huron.

The purpose of this article is threefold. First, we document temporal trends in the characteristics of fish schools in the North Channel and Georgian Bay during the presumed decline in alewife that took place in other parts of Lake Huron. We focus our analysis on the years 2000 to 2004 and use hydroacoustics to extract biological metrics including the number, position, morphology, and acoustic backscattering intensity of fish schools. Second, we use concurrent netting data to provide clues as to how species composition contributes to any observed changes in school numbers and characteristics. Third, we highlight the usefulness of hydroacoustics for studying schooling behaviour of fishes in freshwaters. Schools represent a significant component of the spatial distribution and availability of pelagic prey for predators, something that the more commonly used nighttime acoustic surveys (e.g., Mason et al., 2005) do not provide. To our knowledge, this represents the first published account of the use of hydroacoustics for studying fish school characteristics in the Great Lakes and we highlight the applicability of this approach for examining the spatial and temporal dynamics of patchily distributed pelagic fishes in freshwaters. In a more general context, the patterns of change in fish schools we show in Georgian Bay and the North Channel contribute to growing evidence (e.g., Fielder et al., 2007; Riley et al., 2008; Schaeffer et al., 2008; Warner et al., 2009) of a recent regime shift in Lake Huron.

Methods

Annual hydroacoustic surveys of pelagic fish were conducted in seven sampling areas, termed frames, within the North Channel and Eastern Georgian Bay of Lake Huron during September of 2000 and July–August of 2001 to 2004. Each sampling frame was approximately 12,000 ha and was situated within the vicinity of double-crested

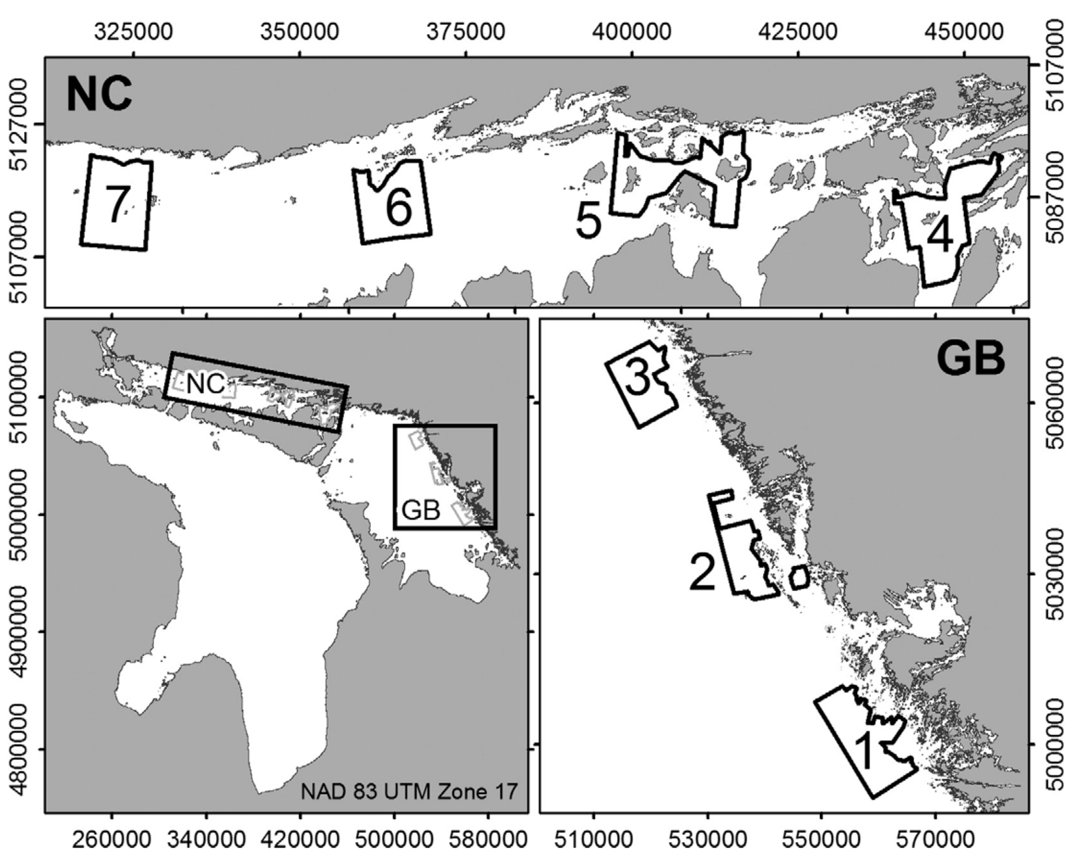

Fig. 1. Survey frames on Georgian Bay (GB) and the North Channel (NC) of Lake Huron. Annual hydroacoustic transects were conducted within each frame in 2000–2004.

cormorant breeding colonies (Fig. 1). Frames 1 through 3 were located in Georgian Bay and frames 4 through 7 were located in the North Channel. The total area within the boundaries of the seven survey frames was approximately 84,000 ha and represents approximately 4.7% of the total surface area of the North Channel and Georgian Bay basins. The frames were created for a large-scale experiment used to study the impact of cormorants on fish biomass.

All surveys were completed using small-craft vessels (<8 m) with average survey vessel speeds ranging from 3.0 to 5.4 m s^{-1}. Within each sampling frame, parallel transects perpendicular to shore and spaced at approximately 1 km apart, were surveyed during the day and night between 12:00–04:00 h local time. The length (mean 5.3 km ± 2.7 km standard deviation) and total number (range 11–26) of transects within each frame varied and was dependent on the coastline complexity and the proximity of the double-crested cormorant colonies to the acoustic sampling area. In order to maximize diel coverage over the sampling frame, daytime surveys were completed on every other transect (i.e., 2 km spacing between daytime surveys) starting at one side of the sampling frame and concluding at the opposite side. All remaining transects were then surveyed during the nighttime period.

Hydroacoustic data in 2000–2002 were collected using a Simrad EY500, 120 kHz split-beam echo-sounder using a 0.3 ms pulse duration and an acoustic ping interval of 0.2 to 0.25 s. An acoustic transducer, with a half power beam width of 7.1°, was mounted on an aluminum pole affixed to the midship of the survey vessel at a depth of ~1.0 m. Calibration of the Simrad EY500 system was completed using a standard 23.0 mm diameter copper sphere following the procedures provided by the manufacturer (Simrad Subsea LOBE, 17.1.1995).

Hydroacoustic data were collected in 2003–2004 using a BioSonics DT-6000 and DT-X 123 kHz split beam echo-sounder system. We sampled using a 0.3 ms pulse duration and a ping interval of 0.2 to 0.3 s. The digital transducer had a half power beam width of 7.4° and was deployed within a 1.3-m long tow fish (BioSonics BioFin) suspended alongside the survey vessel at a depth of ~0.75 m below the surface. Calibration verification was completed using a standard 33.0 mm diameter tungsten carbide calibration sphere just prior to and following the surveys using the methods provided by the manufacturer (Biosonics Inc. Operation Manual: DT/DE Series).

Acoustic processing

Echo integration, single target analysis, and school detection was completed using Echoview® (Myriax Software Pty. Ltd., version 3.20.87) processing software. For echo integration analyses, we applied a minimum volume backscattering (S_v) threshold of −65.0 dB. Single targets were created using Echoview's® single target detection variable using angular and uncompensated target strength (TS) data following closely the methods of Soule et al. (1997). We applied a minimum TS threshold of −54.9 dB to all single target data. Single target detection parameters are given in Appendix 1. All echograms were scrutinized to eliminate occurrences of electronic noise, cavitation, and bottom intrusion within the analysis layers before processing. All data samples less than ~4.0 m below the transducer and within ~0.3 m from the acoustic defined bottom were excluded.

Schools were detected and measured using Echoview's® 2D School Detection Module which defines a school by including only acoustic samples that are (i) contiguous and (ii) have a volume backscattering strength S_v that exceeds a minimum value of −65 dB (−70 dB for 2002). In Echoview® and for the purposes of this paper, the schools we are detecting are acoustic schools and we do not differentiate between true schools and shoals as defined by Pitcher and Parrish (1993). A plot of the frequency distribution of the mean integrated S_v showed a bimodal pattern. The distribution centered on smaller S_v values was assumed to represent invertebrate patches, with the trough between the two distributions centered at −55 dB. Therefore, only school regions with an echo integrated mean S_v greater than −55 dB were included in the analysis. The school detection parameters used in Echoview® to define a school are as follows: minimum total school length = 3.5 m, minimum total school height = 1.25 m, minimum candidate length = 0.15 m, minimum candidate height = 3.1 m, maximum vertical linking distance = 0.2 m, maximum horizontal linking distance = 2.5 m, and distance mode is GPS.

School measurements

There are generally five different categories of parameters describing fish schools that can be extracted from hydroacoustics data: numerical, positional, morphometric, energetic, and environmental (adapted from Reid et al., 2000). The data extracted in this study are described in detail below.

Numerical parameters:

(i) *Number of schools per kilometer of transect*. The number of schools per kilometer of transect was calculated for each year and frame.
(ii) *Number of benthic schools per kilometer of transect*. Benthic schools were defined as those schools whose maximum region depth was within 5 m of the acoustic detected bottom. The maximum region depth is the bottom of the school and is defined by the deepest acoustic sample of the school.
(iii) Number of suspended schools per kilometer of transect. Suspended schools were defined as those schools whose maximum region depth was greater than 5 m from the acoustic detected bottom.

Positional parameters:

(i) *School depth*. This was the depth of the center of the school.
(ii) *Distance of school from bottom*. This was the distance of the center of the school to the acoustic detected lake bottom.

Morphometric parameters:

(i) *School trace length*. This represents the observed length of the school in the horizontal dimension (also referred to as the school width). The trace length of the school was computed by using the Pythagorean theorem to subtract the global positioning system coordinates of the first pixel encountered in the defined region from the last one encountered. Echoview® can correct for errors caused by school depth and position relative to the acoustic beam, but we did not do this because survey depths were shallow enough that beam angles were narrow, pulse lengths were short, and errors were consequently small (Diner 1998; Milne et al., 2005).
(ii) *School height*. This was an observed measurement of the school in the vertical dimension. The height of a school was calculated at the point of encounter by subtracting the depth of the shallowest pixel in the defined region from the depth of the deepest pixel.
(iii) *Corrected school length*. The trace length only provides the horizontal measurement across the school at the point of encounter along the survey track (i.e., sequential acoustic beams make one or more slices through the school and do not necessarily encounter the full length of the school). The actual length of the school is usually much larger and the trace length must be corrected to estimate the true length of the school (Simmonds and MacLennan 2005). We estimated the true length of a school (herein referred to as the “corrected length”) by assuming the school was circular in planar cross section and by making inferences about the range of values the true length

fell within. The minimum possible school length was equal to the observed trace length. We set the maximum to the observed 97.5% trace length value within the survey frame and year (frames 6 and 7 were pooled because sample size was <30) because the largest schools observed were likely those that were bisected along their entire length. The 97.5 percentile was chosen so that the very largest schools were excluded and could not bias the results as outliers. The corrected school length was then randomly drawn from a uniform distribution between the minimum and maximum values. We assumed a uniform random distribution because the boat intersected the schools at a random location. Our assumption that schools are circular in cross section is only an approximation as schools can be more rough and uneven along the edges. Corrected school length contains error and should therefore be considered as an approximation of the true school length; however, this approximation likely does not bias relative trends in corrected school length over time.

(iv) *School area*. This was the two-dimensional surface area of the school, calculated from the corrected school length using the formula for the area of a circle (πr_h^2) where r_h is half of the school height.

(v) *School volume*. We assumed that schools had an elliptical shape and calculated volume as $\frac{4}{3}\pi r_l^2 r_h$, where r_l is half of the corrected school length and r_h is half of the school height.

Energetic parameters:

(i) *Acoustic backscattering strength*. We used the nautical area scattering coefficient (NASC; $m^2/n\ mi^2$) as a measure of acoustic backscatter strength returned from a school, which is a scaled measure of the area backscattering coefficient (Simmonds and MacLennan 2005). This measure was taken from the echo integration of acoustic backscatter through the defined school region only and did not include the surrounding empty water.

(ii) *Number of fish per school per kilometer*. Estimates of fish density ρ_a (numbers per square meter) within each school (i.e., not including surrounding empty water) were calculated from the echo-integrator equation $\rho_a = E/\sigma$, where E is the mean echo integral and σ is the expected value of the backscattering cross section of a schooling fish (Simmonds and MacLennan 2005). We estimated σ from the observed mean target strength of nighttime single target detections within each frame and year between −50.5 dB and −37.12 dB. This target strength range was chosen to represent a schooling fish in the size range of 5 to 25 cm and was estimated from Love's (1971) general relationship (Hartman et al., 2000): $TS = 19.1 \times \log(L_m) + 0.9 \times \log((c/f)/1000) - 23.9$ where L_m is the total length (m), c is the speed of sound in water ($m\ s^{-1}$) and f is the transmitted frequency (kHz). The mean echo integral was measured as the area backscatter coefficient (ABC) and is equivalent to the total acoustic backscattering scaled to 1 m^2 at the surface (Simmonds and MacLennan 2005). A minimum size of 5 cm was chosen for our target strength–length relationship because we wanted to exclude young-of-year fish and instead wanted to focus on schooling species that are yearlings and older; also, the nets used to verify species identity (described in more detail below) were not small enough to capture fish below 5 cm.

The number of schools per kilometer of transect was calculated for each frame and year and then averaged across all frames in each basin to provide an annual mean. The other parameters were calculated for each individual school and then averaged for each basin and year. A calibration problem occurred in 2002 which affected the TS gain calibration parameter and potentially biased estimates of acoustic backscattering strength and number of fish per school. The calibration problem had no discernable effect on the school morphometric or numerical measurements because these are directly observable measurements that do not rely on backscattering strength values. Nonetheless, to compensate for this possible bias, we reduced the S_v threshold for 2002 (to −70 dB) and we do not present the affected estimates for 2002.

Statistical analysis of school data

To determine if year was a significant driver of school numbers and characteristics, multiple linear regressions were performed for several response variables and categorical predictors (with the categorical predictors transformed into dummy variables). There were two types of response variables: the first was the number of schools per kilometer and the second was the various school characteristics such as size and shape. The number of schools per kilometer was an aggregated number, calculated for each frame, year, and school type (benthic or suspended). The school characteristics were calculated for each school and the multiple regressions for this type of response variable were performed on a matrix which contained information on each school. The categorical predictors considered were year, frame, basin, and school type (benthic or suspended). All combinations of response and predictor variables were considered except for the following, which had obvious a priori correlations: (i) models with frame and basin included together as predictors, (ii) models with numbers of benthic or suspended schools as responses and school type as predictors, or (iii) models with distance from bottom as a response with school type as a predictor. A P-value of 0.05 was used to test the significance of all statistical tests. SPlus was used to perform the linear regressions.

Netting

We utilized two types of netting data available from the Ontario Ministry of Natural Resources (OMNR): (i) time series netting data collected in the Clapperton Island region (in frame 5 of the North Channel) in 2002–2004 and (ii) netting data available for all frames in 2004. Netting provided an indication of the species composition of schools observed with the acoustics but note that the smallest mesh sizes used will not likely catch young-of-year fish as well as certain small species such as emerald shiner. For the purposes of this paper, we only focus on the three primary schooling species that were captured in all nets: lake herring, rainbow smelt, and alewife.

Time series for Clapperton Island

An annual standardized gill netting survey was conducted by the OMNR in the Clapperton Island region, which is located inside of frame 5 of the North Channel. Although netting data were available for 2000 and 2001, we focused on 2002–2004 because these years included a small mesh panel (31.8 mm) that was added to the gear which enabled the capture of smaller fish such as alewife and smelt. In July of 2002–2004, overnight bottom-set gill nets composed of monofilament graded meshes ("small mesh" = 12 m of 31.8 mm; "standard mesh" = 25 m of 38 mm, and 50 m each of 51 mm, 63.5 mm, 76.2 mm, 89 mm, 101.6 mm, 114.3 mm, and 127 mm; all net sizes given in stretch mesh) were randomly set within selected 5° latitude × 5° longitude management grids. Nets were 1.8 m in height and set parallel to the bottom contour at depths between 5 and 32 m. Each year, netting occurred for 6 to 7 days in July with a total of 7 nets set in 2002, 14 nets set in 2003, and 18 nets set in 2004. The average soak time per net for all years was 22 h.

Netting in each frame in 2004

Standard index and small mesh gill netting was completed in each frame in 2004. Standard graded monofilament gill nets ("small mesh" = 15 m panel of 19 mm, 2 × 15 m panels of 25 mm and 15 m panel of 32 mm; "standard mesh" = 25 m of 38 mm, and 50 m each of 51 mm, 63.5 mm, 76.2 mm, 89 mm, 101.6 mm, 114.3 mm, and 127 mm; all mesh sizes given as stretch mesh) of 1.8 m in height were set overnight on the bottom or suspended below surface floats. To choose netting locations, a numbered grid of 1 km^2 cells was applied over the 2003 hydroacoustic transect lines. For each segment of the acoustic transects that fell within a grid, the average estimated fish biomass was estimated from the 2003 acoustic survey. The biomass estimate of the transect segment was assumed to be indicative of the fish density within the entire 1 km^2 grid cell in 2003. It was also assumed that the spatial distribution of fish observed in 2003 did not change in 2004 at the 1 km^2 scale. The 2004 netting sites were then randomly selected from only those grids where the expected biomass would be greater than 50 kg ha^{-1}. This site selection method was chosen as an attempt to maximize net catches. At each netting site, one gill net of each graded mesh type (small mesh and standard mesh) and configuration (bottom and suspended) were set. At least one net of each gear type and configuration was set concurrently within 24 h of the hydroacoustic survey in all frames, with the exception of frame 6. Additional netting effort in frames 6 and 7 was completed 27 to 39 days prior to the hydroacoustic surveys in these frames.

Results

For all years, there was a positive relationship between observed school height and length (Fig. 2). In general, almost all schools had dimensions that fell below the 1:1 relationship indicating that they were longer than they were tall (Fig. 2). Only school sizes less than 10 m in diameter approached spherical shapes in 2000 while in subsequent years this pattern was nearly absent for smaller schools. Although retaining their shape, the dimensions of schools did change over time. Moving from 2000 through to 2004, the height of schools tended to decrease and the slope of the relationship between observed height and length became increasingly shallow (Fig. 2). At least part of this slope change was due to the disappearance of very large schools (Fig. 2).

Temporal patterns were detected in fish school numbers and location in the water column. Fig. 3 shows a visual representation (for an example frame) of the decline in school numbers and in the reduction of benthic schools that occurred between 2000 and 2004. Analyzing means by basin, the total number of schools per kilometer, regardless of position in the water column, decreased sharply from 2000 to 2002 and then remained low in 2003 and 2004 with the loss of fish schools being greatest in Georgian Bay (Fig. 4a). This pattern was reflected by the significance (at $P<0.05$) of regression models including year as a factor in explaining the decline of fish schools per kilometer (Table 1). To examine this pattern further, we focused on the regression model with the highest amount of variance explained (Table 2). Coefficients for 2001 and especially 2002 were larger in magnitude and negative illustrating the importance of the early decline in fish schools relative to 2003 and 2004 (Table 2). Most frames in the North Channel (frames 4, 6, and 7) had significant negative coefficients (or nearly so; Table 2).

The proportion of fish schools near bottom was initially very high but did not show a clear decline until 2004 (Fig. 4b), 2 years after the decline in the number of schools per kilometer (Fig. 4a). The overall decline in fish schools can be attributed to the loss of benthic schools (Fig. 4c). This loss was significant with respect to combined year and basin effects but not by frame or basin alone (Table 1). The significant effects of year and basin/frame indicate that losses of benthic oriented fish schools were occurring at different rates in different localities over time, a conclusion reflected by the patterns of loss in Fig. 4c. Suspended schools showed a slight increase towards the end of the time series (Fig. 4d), but regression models with year, frame or basin were not significant (Table 1).

The general pattern of loss in the number of schools and in the proportion of benthic-oriented schools was reflected in the water column position and shape of fish schools. Schools were located at depths exceeding 20 m in 2000 but then underwent a consistent decrease in depth until 2004 when fish schools in both Georgian Bay and the North Channel were located on average at about 12 m (Fig. 5a). This increasingly shallow depth of schools in both regions stemmed from a shift from benthic oriented schools to more suspended schools with the sharpest change in this orientation occurring from 2003 to 2004 (Fig. 5b). Because the mean depth of schools showed a relatively consistent trend to shallower depths each year (Fig. 5a), while distance from bottom showed relatively small changes until the 2003–2004 period (Fig. 5b), it appears that the shift to suspended schools in 2004 was preceded by an initial shift to shallower depths by benthic-oriented schools. The mean height of schools dropped below 2 m in 2004 while school trace length dropped from a range of approximately 15–25 m in 2000 to 10–15 m by 2004 (Figs. 5c and d).

After adjusting the trace (or observed) length to an estimated true (or corrected) school length, the mean corrected length of schools was estimated as 24.7 m in Georgian Bay and 34.8 m in the North Channel in 2004 (Fig. 5e), with corresponding surface areas in each region of less than 2000 m^2 (Fig. 5f). The mean volume of schools in

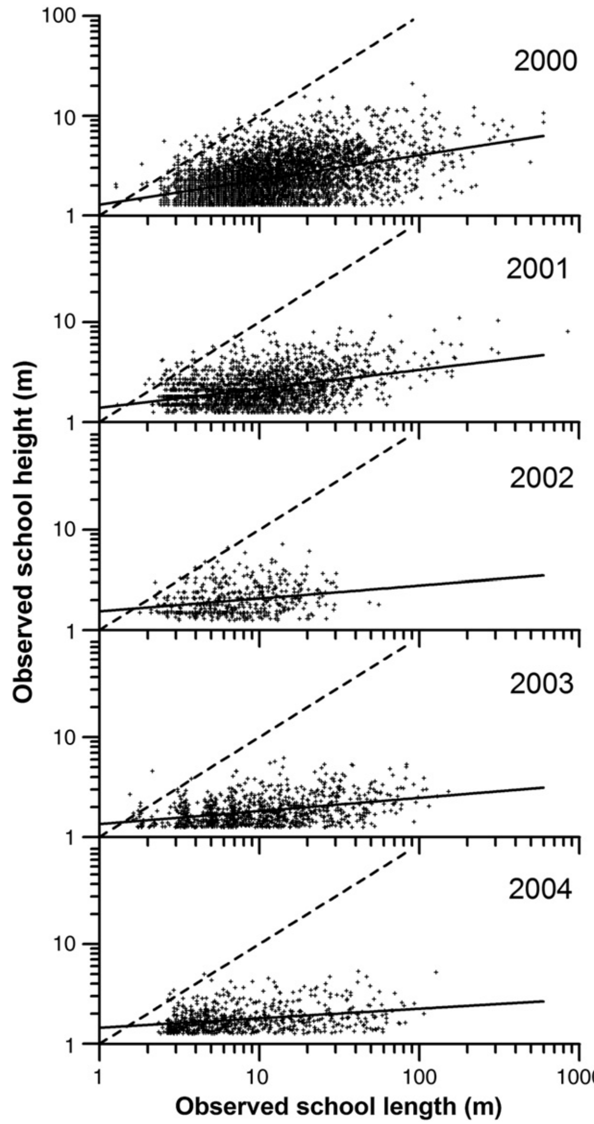

Fig. 2. The relationship between observed (trace) length and height of schools for 2000–2004. The dashed line is the 1:1 relationship and the solid line is a least squares linear regression of the data.

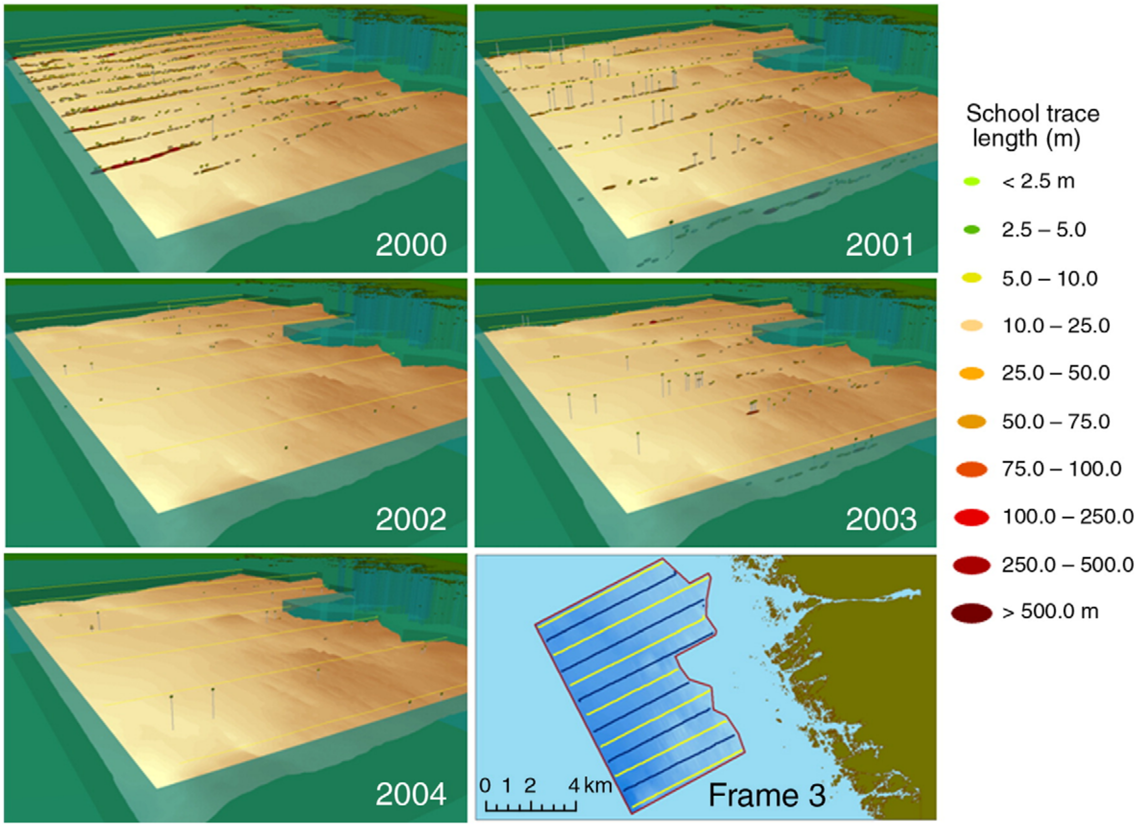

Fig. 3. Fish school density in Frame 3, Georgian Bay. Legend depicts the observed (trace) length of schools. Suspended schools are those >5 m from bottom and are shown with a vertical line. All other schools are benthic schools located within 5 m of the bottom.

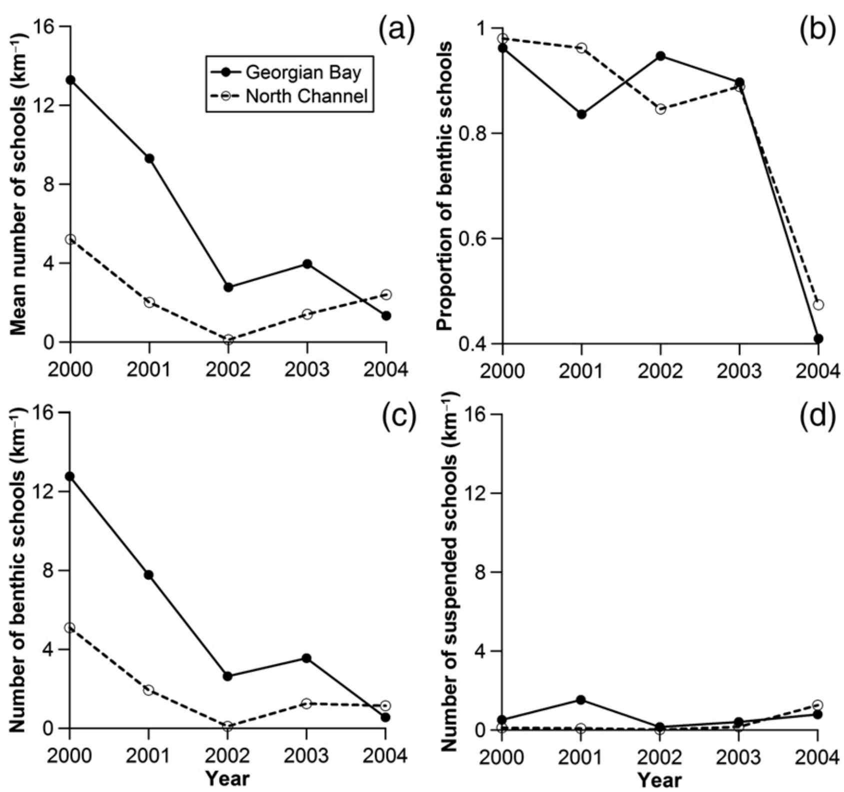

Fig. 4. Temporal trends in school numbers. (a) Number of schools, (b) the proportion of schools that are benthic, (c) the number of benthic schools, and (d) the number of suspended schools. Benthic schools are those within 5 m of the acoustic detected bottom and suspended schools are >5 m from the acoustic detected bottom. The number of observed schools was divided by transect length to give the number of schools per kilometer.

Table 1
Regression models for fish school numbers and characteristics where year, frame, and basin are included as predictors. The Δ Akaike information criterion (ΔAIC) shows the relative performance of each model for a given response variable compared against the best model for each response variable. All models include an intercept.

Response variable	Predictors	Sample size	F statistic	*P* value	Variance explained (%)	ΔAIC
Number of schools (km^{-1})	Year + frame	32	5.294	0.0006	71.6	0
Number of schools (km^{-1})	Year + basin	32	5.107	0.0022	49.6	8
Number of schools (km^{-1})	Year	32	3.633	0.0171	35.0	14
Number of schools (km^{-1})	Frame	58	1.946	0.0889	17.0	76
Number of schools (km^{-1})	Basin	64	3.993	0.0501	6.1	82
Number of benthic schools (km^{-1})	Year + frame	32	5.722	0.0004	73.2	0
Number of benthic schools (km^{-1})	Year + basin	32	5.619	0.0012	51.9	9
Number of benthic schools (km^{-1})	Year	32	4.418	0.0071	39.6	14
Number of benthic schools (km^{-1})	Frame	32	2.411	0.0562	36.7	20
Number of benthic schools (km^{-1})	Basin	32	4.286	0.0471	12.5	20
Number of suspended schools (km^{-1})	Basin	32	1.162	0.2897	3.7	0
Number of suspended schools (km^{-1})	Year	32	1.019	0.4153	13.1	3
Number of suspended schools (km^{-1})	Year + basin	32	1.156	0.3570	18.2	3
Number of suspended schools (km^{-1})	Year + frame	32	1.031	0.4520	32.9	7
Number of suspended schools (km^{-1})	Frame	32	1.046	0.4201	20.1	98
Depth of school (m)	Year + frame	8223	561.1	0.0000	40.6	0
Depth of school (m)	Frame	8223	575.4	0.0000	29.6	1390
Depth of school (m)	Year + basin	8223	361.2	0.0000	18.0	2639
Depth of school (m)	Year	8223	303	0.0000	12.9	3139
Depth of school (m)	Basin	8223	247.5	0.0000	2.9	4020
Distance from bottom (m)	Year + frame	8223	282.3	0.0000	25.6	0
Distance from bottom (m)	Frame	8223	236.7	0.0000	14.7	1111
Distance from bottom (m)	Year + basin	8223	270.3	0.0000	14.1	1168
Distance from bottom (m)	Year	8223	327.6	0.0000	13.8	1201
Distance from bottom (m)	Basin	8223	2.318	0.1280	0.0	2410
Observed school height (m)	Year + frame	8223	91.06	0.0000	10.0	0
Observed school height (m)	Year + basin	8223	91.68	0.0000	5.3	408
Observed school height (m)	Year	8223	111.8	0.0000	5.2	417
Observed school height (m)	Frame	8223	55.82	0.0000	3.9	528
Observed school height (m)	Suspended	8223	61.17	0.0000	0.7	786
Observed school height (m)	Basin	8223	23.7	0.0000	0.3	823
Trace length (m)	Year + frame	8222	66.39	0.0000	7.5	0
Trace length (m)	Frame	8222	101	0.0000	6.9	46
Trace length (m)	Year + basin	8222	44.81	0.0000	2.7	408
Trace length (m)	Basin	8222	131.3	0.0000	1.6	491
Trace length (m)	Year	8222	20.72	0.0000	1.0	545
Corrected school length (m)	Year + frame	8223	429.1	0.0000	34.3	0
Corrected school length (m)	Frame	8223	608.8	0.0000	30.8	424
Corrected school length (m)	Year + basin	8223	179.3	0.0000	9.8	2596
Corrected school length (m)	Basin	8223	432.9	0.0000	5.0	3017
Corrected school length (m)	Year	8223	98.34	0.0000	4.6	3061
Horizontal area (m^2)	Year + frame	8223	111.8	0.0000	12.0	0
Horizontal area (m^2)	Frame	8223	173.3	0.0000	11.2	62
Horizontal area (m^2)	Year + basin	8223	44.59	0.0000	2.6	820
Horizontal area (m^2)	Basin	8223	129.1	0.0000	1.5	904
Horizontal area (m^2)	Year	8223	19.21	0.0000	0.9	961
School volume (m^3)	Year + frame	8223	28.56	0.0000	3.4	0
School volume (m^3)	Frame	8223	43.13	0.0000	3.1	18
School volume (m^3)	Year + basin	8223	11.98	0.0000	0.7	212
School volume (m^3)	Basin	8223	27.65	0.0000	0.3	236
School volume (m^3)	Year	8223	6.833	0.0000	0.3	242
NASC (m^2nmi^{-2})	Year + frame	7739	19.49	0.0000	2.2	0
NASC (m^2nmi^{-2})	Frame	7739	21.73	0.0000	1.7	38
NASC (m^2nmi^{-2})	Year + basin	7739	10.93	0.0000	0.6	120
NASC (m^2nmi^{-2})	Year	7739	10.88	0.0000	0.4	129
NASC (m^2nmi^{-2})	Basin	7739	13.59	0.0002	0.2	144
Number of fish per school (km^{-1})	Year + frame	7739	18.48	0.0000	2.1	0
Number of fish per school (km^{-1})	Frame	7739	16.78	0.0000	1.3	59
Number of fish per school (km^{-1})	Year + basin	7739	14.27	0.0000	0.7	98
Number of fish per school (km^{-1})	Year	7739	16.13	0.0000	0.6	104
Number of fish per school (km^{-1})	Basin	7739	4.831	0.0280	0.1	144

Table 2
Multiple regression model of the number of schools with year and frame included as explanatory variables. Years are compared against 2000 and frames are compared against frame 1. The sample size was 32.

Response variable	Term	Coefficient	*t* value	*P* value	Variance explained (%)	Model F statistic	Model *P* value
Number of schools (km^{-1})	Intercept	3.98	7.15	0.0000	71.6	5.29	0.0006
	2001	−1.75	−2.04	0.0545			
	2002	−1.87	−3.43	0.0025			
	2003	−0.63	−1.84	0.0795			
	2004	−0.49	−1.86	0.0771			
	Frame2	2.92	3.03	0.0064			
	Frame3	0.15	0.26	0.7947			
	Frame4	−1.03	−2.08	0.0496			
	Frame5	0.18	0.54	0.5950			
	Frame6	−0.52	−2.07	0.0513			
	Frame7	−0.58	−2.72	0.0129			

Georgian Bay (4423 m^3) and the North Channel (19,633 m^3) were clearly different in 2000, decreased over the course of this survey while maintaining some difference in volume, and by 2004 were very similar in volume (1362 m^3 for Georgian Bay and 1521 m^3 for the North Channel) (Fig. 5g). Owing to a change in transducers between 2002 and 2003, there was a change in beam width that could alter school length estimates. However, the beam width changed by only a small amount, making the effect on length minimal (e.g., a school

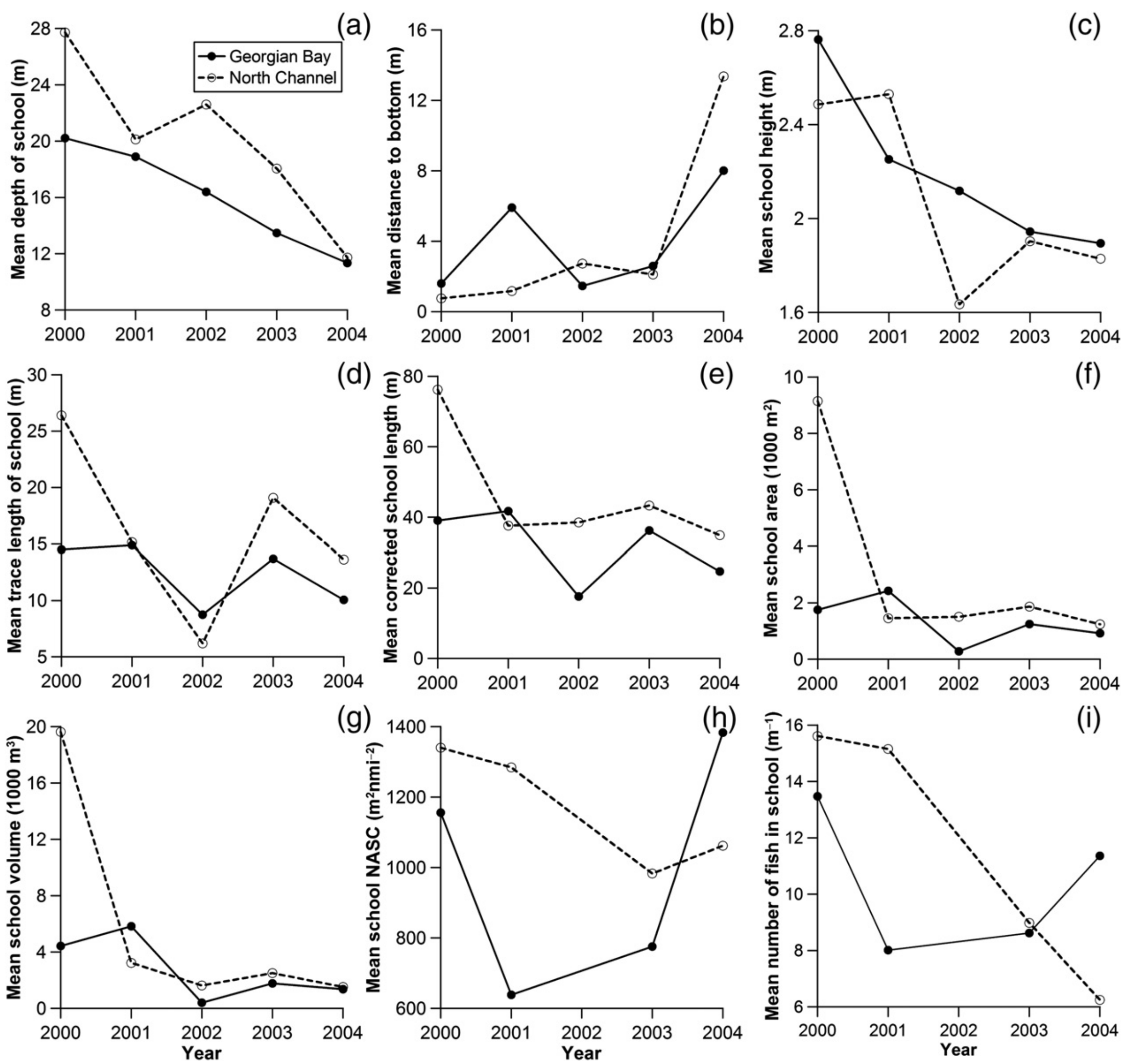

Fig. 5. Temporal trends in school characteristics. (a) Depth, (b) distance to bottom, (c) observed (trace) length, (d) height, (e) corrected length, (f) area (calculated using corrected length), (g) volume (calculated using corrected length), (h) backscattering energy (NASC), (i) number of fish per school. School length was corrected from observed values because schools were not always intersected along congruent lines. Data for (h) and (i) were unavailable for 2002.

observed in 2000–02 at 20.8 m, the mean depth of all schools observed, would be estimated to be only 11 cm larger in 2003–04), and the direction of change was in the opposite direction of the trends observed.

In contrast to similarities in the shift to suspended schools of similar volume in Georgian Bay and the North Channel, backscattering strength (NASC) and density of schools showed visible differences between the regions by 2004 (Figs. 5h and i). Loss of backscattering energy by fish schools occurred between 2000 and 2001 (Fig. 5h), especially in Georgian Bay relative to the North Channel, well before the loss of most benthic-oriented fish schools (Fig. 4b). By 2004 in Georgian Bay, backscattering energy recovered to 2000 levels (Fig. 5h), but with less fish per school than in 2000 (Fig. 5i). In the North Channel, the recovery of backscattering energy in 2004 was not of the same magnitude as in Georgian Bay (Fig. 5h), with less fish per school than any previous year (Fig. 5i).

When considered together, a number of features of fish schools in the North Channel and Georgian Bay point to a shift in species composition of fish schools. The decline and recovery of backscattering energy of fish schools in both regions (Fig. 5h), the shift from bottom-oriented to suspended schools (Figs. 4, 5b), and the differences in the number of fish per school (Fig. 5i) suggest a species change in school composition.

Although year was a significant predictor of school numbers and characteristics, other predictors were also important (Tables 1 and 2). Most notable was the importance of frame. We observed frame to frame differences in the number of schools. Frames 3 (in Georgian Bay) and 5 (in the North Channel) show different patterns compared to the other frames: they both have positive coefficients (like frame 2 but unlike the others) and they do not have a large effect compared against frame 1 (Table 2). The effects of individual years, on the other hand, were consistently strong and the coefficients were all negative (Table 2). In other words, compared to 2000, there was a significant drop in the number of schools for all years.

Netting

Time series for Clapperton Island

Changes detected in school position, shape and backscattering energy point to a change in species composition of fish schools in Georgian Bay and the North Channel. Netting data can help ascertain the extent of this possible species compositional change. Analysis of netting data indicates that the fish community of Clapperton Island (in frame 5 of the North Channel) underwent changes between 2002 and 2004. Alewife were prevalent in the catch in 2002 but almost entirely disappeared in 2003 and 2004 (Fig. 6; the mean catch of alewife per netting night was 12.34 in 2002, 0.21 in 2003, and 0.06 in 2004). Lake herring did not show a noticeable change in the length–frequency histogram (Fig. 6) but they did increase in mean catch per netting night from 5.14 in 2002, to 5.79 in 2003, and then 6.89 in 2004. The mean catch per netting night of rainbow smelt first increased from 1.43 in 2002 to 1.86 in 2003 but then decreased to 0.94 in 2004.

Netting in each frame in 2004

Netting in each frame in 2004 also showed the relative scarcity of alewife and the presence of lake herring and rainbow smelt as the predominant schooling fish in the surveys. Alewives were not caught in Georgian Bay and relatively few were detected in the North Channel (predominantly in frame 7) in 2004. Although there were similar lake herring CPUE levels in suspended standard nets in both regions (Fig. 7a), in Georgian Bay, lake herring had higher catches than rainbow smelt in both mesh sizes whether on the bottom or suspended (Figs. 7a and c). Rainbow smelt had higher CPUE in both suspended and bottom small mesh nets in the North Channel relative to Georgian Bay (Figs. 7b and d). Although smelt and lake herring were present in both regions, based on the netting comparisons, rainbow smelt may represent a higher proportion of schooling fish in the North Channel than Georgian Bay while lake herring represent a relatively greater proportion of schooling fish in Georgian Bay than in the North Channel.

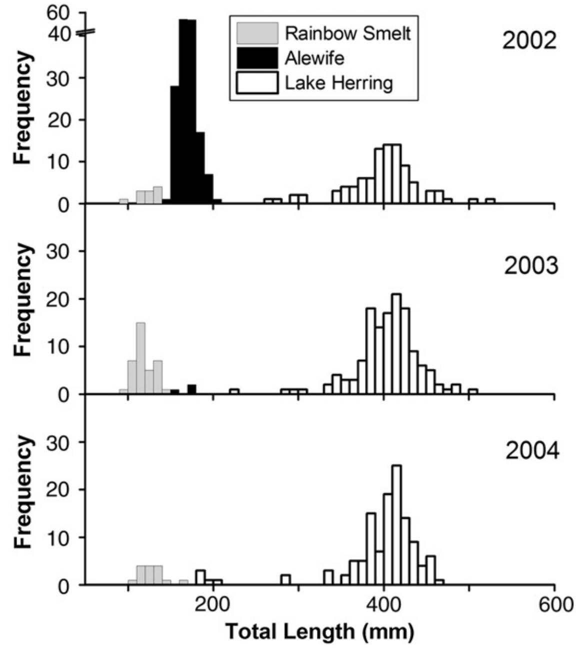

Fig. 6. Length distribution of the three main schooling species caught in the offshore index gill nets in the Clapperton Island region (in frame 5 of the North Channel).

Discussion

We conclude that changes in fish school characteristics, along with patterns in species composition of the netting surveys, reflects the loss of alewife and a shift to rainbow smelt and lake herring within Georgian Bay and the North Channel of Lake Huron. We found dramatic temporal shifts in school numbers and characteristics that coincided with a reduction in alewife abundance detected in other parts of Lake Huron (Fielder et al., 2007; Riley et al., 2008; Warner et al., 2009) and observed in our netting data. Between 2000 and 2004 there was a sharp decrease in the number of schools and in particular, in the number and proportion of benthic schools. Schools also became shallower and were located further from the bottom. At the same time, the number and proportion of suspended schools rose slightly, although not significantly. The dimensions of schools also changed as schools narrowed in height relative to length between 2000 and 2004. This suggests that there have been substantial changes in the Lake Huron fish community that are reflected in the abundance and morphology of pelagic fish schools. When considering the implications of this change in terms of planktivory and production for top predators, the patterns detected in this study could be regarded as a regime shift in Lake Huron. Recent papers on the shift to yellow perch and walleye in Saginaw Bay (Fielder et al., 2007), a shift to emerald shiner in the pelagic zone of the main basin of Lake Huron (Schaeffer et al., 2008), the collapse of the deepwater demersal fish community (Riley et al., 2008), and the decline of non-native pelagic species (Warner et al., 2009) all point to a basic broad-scale change occurring in the fish assemblage of this large lake.

There is some indication that the decline in alewife promoted an increase in lake herring and smelt populations. The available small mesh netting data for the Clapperton Island region only began in 2002 but trends in school numbers suggest that the decline in alewife began

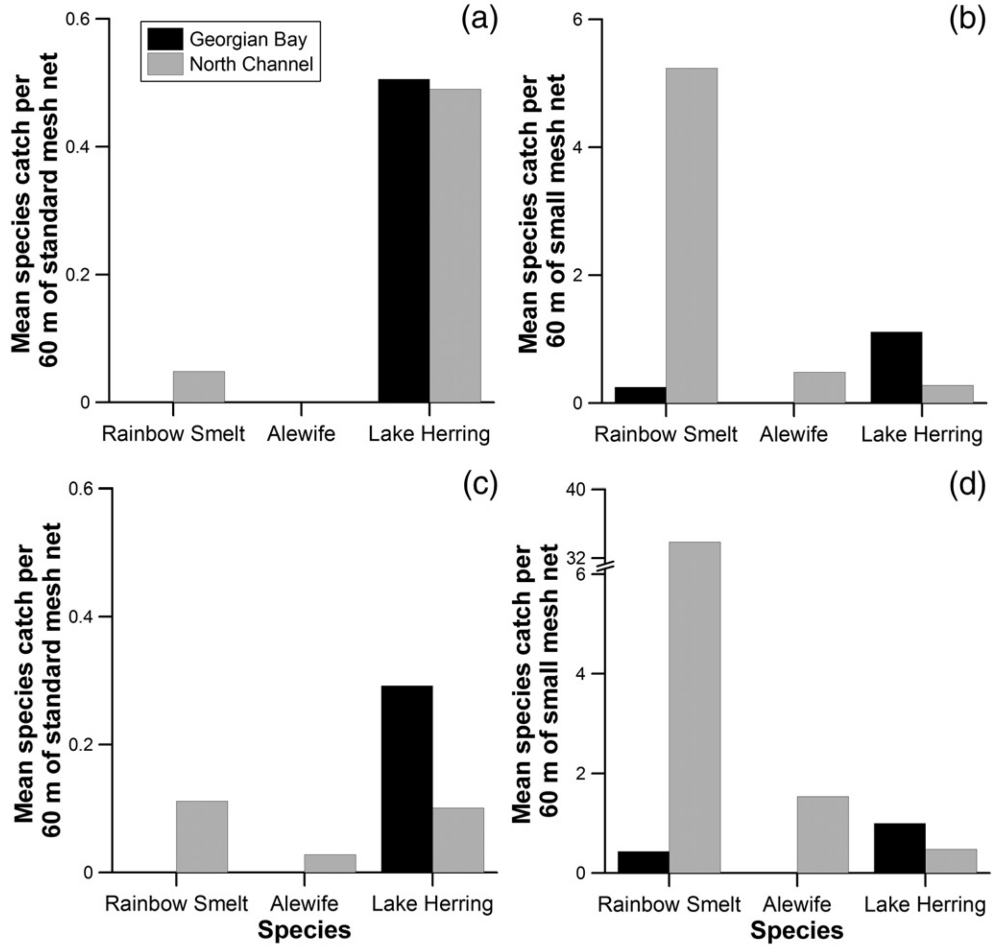

Fig. 7. Catch per unit effort by basin from the 2004 offshore index gill netting conducted in each frame. Nets were suspended (panels a and b) or set on the bottom (panels c and d) and were either small or standard meshes (see text for details). Effort is one net lift.

as early as 2001. Interestingly, changes in the speed or direction of change in school attributes were noted in 2003–2004 that could be explained by a delayed or phased response in the other two schooling species. Most notably, the energy density of schools and the number of fish per school first decreased between 2000 and 2001, but then increased again (for Georgian Bay) towards the end of the 5-year period. Such a pattern could be explained by an initial decrease in alewife and a subsequent shift to different species with different body sizes, school characteristics, behaviour, and acoustic attributes. Our results suggest that lake herring and smelt perhaps form more suspended schools than alewife. There is little previous information on the relative depth distribution of schools of these species, except for reports that both alewife and smelt shifted to a deeper distribution in Lake Ontario following the invasion of dreissenid mussels (O'Gorman et al., 2000) and that lake herring are generally thought of as occupying waters closer to the surface as our netting data also suggests (Fig. 7). There was a shift towards schools that were more narrow in height, suggesting that the morphological characteristics of lake herring and smelt schools could also be different than alewife schools. In marine systems, the morphological characteristics of a school can be used to identify its species composition (Rose and Leggett 1988); a similar approach might be possible in Lake Huron and the other Great Lakes but would require more research.

Following the initial declines in alewife, there appeared to be differences in the species composition of schools between Georgian Bay and Lake Huron. In Lake Huron's North Channel, smelt were more common in 2004 nets than lake herring (note that the netting conducted in the Clapperton Island region between 2002 and 2004 did not detect this trend because the mesh sizes were not as small as those used in the 2004 multiframe netting survey). In contrast, 2004 netting in Georgian Bay suggests that lake herring were more dominant than smelt. These are interesting findings because they suggest a stronger influence of alewife on smelt and herring than has been previously concluded. For example, after analyzing Great Lakes time series data, Madenjian et al. (2008) hypothesized that alewife were less likely to impact smelt because smelt larvae move quickly to offshore areas after hatching when alewife have already migrated inshore to spawn. Interestingly, our findings of a possible increase in smelt with the decline in alewife in the North Channel could have occurred because this region of the lake is on average shallower, with less traditional offshore areas than either Georgian Bay or the main basin of Lake Huron (Schertzer et al., 2008); this would increase the overlap between smelt and alewife, making the potential interaction more significant.

Acoustic surveys and bottom trawling was also conducted in 1997, 2004–05, and 2007 in Lake Huron's main basin, North Channel and Georgian Bay by the United States Geological Survey (USGS) Great Lakes Science Center (GLSC) (Warner et al., 2009). There are some similarities between that study and ours that are worth pointing out. The GLSC surveys found a decline in alewife biomass between the earlier surveys in 1997 and the surveys in more recent years (2004–07) in all basins, a pattern consistent with what we observed in the North Channel and Georgian Bay. Three periods of change were noted by the GLSC surveys: (1) a high biomass community dominated by non-native species, (2) a low biomass community dominated by non-native species, and (3) a low biomass community dominated by native species. These findings support our general conclusion of a species composition change. However, the GLSC surveys found a decline in smelt and an increase in bloater; we found some evidence suggesting an increase in smelt in the North Channel and we did not capture bloater in our nets. The likely reasons for these discrepancies are that (1) the GLSC surveys were conducted further offshore than our surveys and (2) the post-alewife GLSC surveys were conducted between 2004 and 07 whereas our surveys captured the years when the alewife crash was actually occurring (2001–04). Nevertheless, both studies found a large shift in the biomass and species composition of the pelagic fish community, pointing to the occurrence of a large-scale ecosystem change in this important component of Lake Huron's food web.

There could be several reasons for the decline of alewife noted in this and other (e.g., Fielder et al., 2007; Riley et al., 2008; Warner et al., 2009) studies. Recruitment failure and declines in alewife abundance in the past have been attributed to cold winter temperatures, but predation can also cause declines or lead to impaired recovery (Ridgway et al., 1990; O'Gorman et al., 2004; Madenjian et al., 2005). Behavioural changes of schooling species could also alter the positional, morphological, or energetic properties of schools. Predation by the highly abundant double-crested cormorant is one factor that could have impacted the species composition and behaviour of fish schools in Lake Huron. However, alewife also declined in the main basin of Lake Huron (Warner et al., 2009) where there were few, if any, cormorants. The extent to which predators are causing changes in the Lake Huron fish schools cannot be ascertained in the present study but future research could lead to increased understanding of the forces driving variability in the spatial patterns of the schooling component of the fish community.

The analysis of fish schools in this study would not have been possible without hydroacoustics. Fish schools living in marine environments have been researched extensively using echo-sounder data (Reid and Simmonds 1993; Reid et al., 2000; Gerlotto and Paramo 2003; Gerlotto et al., 2004; Paramo et al., 2007). In freshwaters, hydroacoustics has been used to assess pelagic species abundance (Argyle 1992; Warner et al., 2009) and vertical distribution (Hrabik et al., 2006; Stockwell et al., 2007), but it is only recently that the technology has been applied to the study of schooling behaviour (Guillard et al., 2006; Milne et al., 2005). To our knowledge, this study represents the first published hydroacoustic analysis of fish schools in the Great Lakes and we believe the technology holds great potential for future research on schooling fishes in this and other lake systems. Nevertheless, there are several caveats that need highlighting. For instance, our characterization of each school was based on two-dimensional slices through schools and we needed to estimate the true school length and make assumptions about the school shape (i.e., assuming a two-dimensional school area and an elliptical shape in three dimensions). These assumptions were necessary because we were relying on a split-beam echo sounder. The use of multibeam technology would have enabled us to capture details of the 3-dimensional characteristics of fish schools and we would not have had to make the assumptions we did (e.g., Gerlotto et al., 1999; Gerlotto and Paramo 2003; Gerlotto et al., 2004; Paramo et al., 2007). However, split-beam technology is more accessible given the often smaller budgets afforded in studies of freshwater lakes and we wanted to highlight that interesting information can be extracted even by analyzing schools in two dimensions. We also feel confident that our assumptions of school shape did not bias the results of this study. First, schools did appear to have an elliptical shape in this study (e.g., Fig. 2). This was also the case in another study focusing on the Northwest Atlantic where a herring school was observed to have a flattened ellipsoid shape in three dimensions (Weber et al., 2009). Second, the large-scale relative trends are unlikely to be influenced by assumptions of school shape. Third, the dramatic decline in school height (Fig. 2) was observed independent of the assumptions and would have translated directly into reductions in school volume. The notable trends of decreasing school numbers, decreasing school depth, increasing distance from bottom, and the patterns in backscattered energy and number of fish per school (Figs. 2, 3, and 5) were also observed independently of our assumptions of school shape.

Any acoustic analysis of schools raises the question of what defines a school. Schools defined by acoustics represent aggregations of fish and the classification of what constitutes a school depends on the threshold values used. Therefore, what is observed is an acoustic school, which is not necessarily a true school but is a representation of what is observed on the echo sounder (Reid et al., 2000). Most notably, our analysis of schools in this study did not differentiate between true schools and shoals. Although the aggregations of fish we classified as schools in Lake Huron were observed to be defined structures and were clearly distinct from looser groups of fish, invertebrates, and single targets, the fundamental questions governing what defines a school and what mechanisms drive formation of a school should be considered.

In conclusion, fish schools in Lake Huron underwent a significant change over the 5 years of this study that coincided with a reduction in alewife. The fish schools in Lake Huron should therefore be considered as dynamic entities that respond to fish community structure and environmental factors such as temperature. Understanding how fish aggregations change in relation to population abundance, exploitation pattern, predators, food availability, and the environment are important if we wish to further comprehend what impact these changes have on food webs, commercial and recreational fishing, stock assessment, and management. The results of this study provide a constructive example of the tools that can used to gain this understanding.

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Appendix 1

Summary of the echo-sounder parameters and single target detection criteria used within the acoustic processing software to analyze the 2000–04 hydroacoustic survey data.

Single target detections	2000–2001	2003–2004	Units
Echo-sounder system	Simrad EY500	BioSonics DT6000/DTX	
Nominal frequency	119	123	kHz
Transmitted pulse duration	300	300	ms
Equivalent 2-way beam angle	-20.6	-20.97	dB re 1 sr
Source level		221.2	dB re 1 μPa at 1 m
Receiver sensitivity		−52.5	dB
y-Axis 3dB one-way beam width	7.1	7.4	°
x-Axis 3dB one-way beam width	7.1	7.4	°
Estimated speed of sound	1447.27	1447.27	$m \cdot s^{-1}$
Estimated absorption coefficient	0.003800	0.004698	$dB \cdot m^{-1}$
Wavelength of medium	0.012162	0.011766	m
Echoview® single target detection operator	Split beam (method 1)	Split beam (method 2)	
Minimum threshold (40Log*R*)	−61	−61	dB
Single target strength threshold	−55	−55	dB re 1 m^2
Pulse length determination level (PLDL)	6	6	dB re 1 m^2
Minimum normalized pulse length	0.6	0.6	–
Maximum normalized pulse length	1.8	1.8	–
Maximum beam compensation	6	6	dB
Maximum standard deviation of minor-axis angles	0.536	0.536	°
Maximum standard deviation of major-axis angles	0.536	0.536	°

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