Acoustic fish stock assessment in the Laurentian Great Lakes

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1. History of fisheries acoustics in the Laurentian Great Lakes

1.1. Early years: 1960s and 1970s

Applications of underwater acoustics in the Great Lakes can be traced back to the 1960s. These early studies focussed on fish distributions at power plant thermal plumes (Spigarelli *et al.*, 1973; Stuntz, 1973), and on estimating zooplankton distribution and biomass (McNaught, 1968). During these early years, data assimilation consisted of a paper chart recorder and an analog recording of output voltages on magnetic tape. Even with limited technology, McNaught (1969) was one of the first researchers, in marine or freshwater environments, to propose and develop a multi-frequency sonar system for size–class discrimination of zooplankton. Due to data storage and analysis limitations, these early studies were completed on a localised scale. With technological improvements in electronic and computer technology, larger scale surveys were conducted on Lakes Michigan (Brandt, 1975, 1978, 1980; Brandt *et al.*, 1980; Janssen and Brandt, 1980), Huron (Argyle, 1982), and Superior (Heist and Swenson, 1983) and provided the first quantitative estimates of fish abundance, density, and spatial distribution. Using a 50 kHz single beam scientific echosounder and deconvolution techniques (Peterson *et al.*, 1976), Brandt (1980) studied the diel ver-

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tical migration, thermal ecology, and spatial segregation of various life stages of alewives in Lake Michigan. He found that alewife migrate to the thermocline at night and disperse, and that adult and young–of–the year (YOY) alewives thermally segregate. This information was the foundation for nighttime assessment of alewives in the Great Lakes. Heist and Swenson (1983) estimated rainbow smelt abundance in the western basin of Lake Superior during 1978–1980 to provide prey fish numbers used in re–establishing the native piscivore community and for assessing the impact of an expanding commercial fisheries. Their acoustics application was one of the first in the Great Lakes that focussed on direct management applications.

1.2. Momentum building years: 1980s

Throughout the 1980s, acoustic hardware and data analysis techniques continued to progress and the use of underwater acoustics for fisheries assessment gained wider acceptance. Multiple–beam transducers (Burczynski and Johnson, 1986; Foote *et al.*, 1986) allowed for direct, *in situ* measures of fish target strength and gave scientists better estimates of fish sizes. The first application of a multiple–beam acoustic system to a lakewide acoustic survey was conducted on Lake Michigan in the spring and summer of 1987 (Brandt *et. al.*, 1991, Argyle, 1992). In response to a declining alewife population, Brandt *et al.* (1991) initiated a lakewide, multi–agency acoustic assessment of the pelagic prey fish community (alewife, rainbow smelt, and bloater). This first lakewide acoustic assessment demonstrated the need for Great Lakes fisheries management to change from a program of stocking determined by hatchery production limitations to management based on food web and carrying capacity of the lake.

1.3. Recent years: 1990s

Following the work by Brandt *et al.* (1991) and Argyle (1992) in the late 1980s, fisheries acoustics has become a component of assessment programs throughout most of the Great Lakes. Assessment efforts are directed on pelagic prey species: alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*), as well as other species such as bloater (*Coregonus hoyi*) and lake herring (*Coregonus artedii*). On Lakes Erie and Ontario, the Ontario Ministry of Natural Resources (OMNR) and New York Department of Environmental Conservation (NYDEC) have combined trawling and acoustic efforts to assess population abundance of rainbow smelt and alewife (Schneider and Schaner, 1995; Schaner and Lantry, 1997; Rudstam *et al.*, 1996). In an era of shrinking management budgets, an echosounder was purchased through a cooperative effort between the United States and Canada for common use by all fisheries agencies on Lake Erie (Witzel *et al.*, 1995). The United States Geological Survey–Biological Research Division (USGS–BRD) now assesses populations of alewife, rainbow smelt, and bloater in Lakes Michigan and Huron using fisheries acoustics. There is also recent pressure to integrate acoustic assessment into the prey fish assessment program in Lake Superior.

Fisheries managers have recognised that abundance estimates alone are not sufficient for successful management of fish populations. An understanding of the spatial and temporal distribution and ecology of both predator and prey species is needed.

New areas of ecological research have developed in response to high spatial resolution data made available through advances in fisheries acoustics technology. One such area is the concept of spatially explicit growth rate potential of pelagic predators (Brandt *et al.*, 1992). This concept integrates spatial information of prey fish using fisheries acoustics, the thermal environment, bioenergetics theory, and foraging theory to quantify complex spatial habitat features of the pelagic environment. Thus, spatially explicit growth rate potential quantifies an individual fish's growth response to non–uniform spatial distributions of prey resources and physical conditions. Applications of this technique have included a functional definition of habitat quality based on a species' physiological reqnirements (Mason *et al.*, 1995), examination of spatial patterns of planktivory in the Chesapeake Bay (Luo and Brandt, 1993), a map of seasonal patterns of predator growth rate potential in the Chesapeake Bay (Brandt and Kirsch, 1993), and an examination of the importance of predator and prey spatial overlap with respect to the thermal environments in Lake Ontario (Goyke and Brandt, 1993).

In this chapter, we present a general introduction to fisheries acoustics, a case study of Lake Ontario, and compare prey fish population estimates from two Laurentian Great Lakes, Lake Michigan and Lake Ontario, to gain insight into the carrying capacity of these lakes for supporting salmonine stocking rates.

2. Fish abundance estimates

A primary goal for fisheries managers is to obtain abundance estimates for a given fish population or community within a particular region or lake. The accuracy and precision of these estimates depends, to a degree, on the spatial and temporal distributions of the fish and the ability to survey these distributions. Thus, a critical component to obtaining abundance estimates from acoustic methods is a biological understanding of the species of interest. The biology of the species dictates the survey design. Survey design deals with the aspects of when, where, number of transects, type of transects (zig–zag, parallel, randomly located), and the spatial coverage required to sample the population. For example, if population estimates of rainbow smelt are desired, the optimal time for an acoustic survey is late summer/early fall, when the greatest proportion of smelt are pelagic. MacLennan and Simmonds (1992) and Misund (1997) provide excellent overviews on abundance estimation and survey design. The process of 'scaling–up' from local measurements to regional estimates requires quantifying variability in acoustic measurements and fish distribution. Variability in acoustic measurements is primarily dependent on the behaviour (e.g. migration, schooling/dispersion, orientation, activity, and vessel avoidance) of the fish (Love, 1977; Nakken and Olsen, 1977; Foote and Nakken, 1978; Foote, 1980; Clay and Heist, 1984; Medwin and Clay, 1998) and the insonifying frequency (Clay and Horne, 1994; Jech *et al.*, 1996). A number of statistical techniques have been developed and/or adapted to quantify the variance in estimates due to sampling inadequacies of fish distributions. These statistical methods range from conventional statistics, to time series and geostatistics (Misund, 1997; Petitgas, 1993). These methods quantify precision, not accuracy. As of yet, there is no uniform method to obtain abundance estimates in all environments, nor a veritable method to check their accuracy. Confidence in abundance estimates (i.e. lower variance) increases with experience, fundamental acoustic measurements of backscatter, and knowledge of the spatial and temporal fish distributions.

2.1. Sonar equation

The key for successful estimates of pelagic fish abundance resides in the application of the SONAR equation. The SONAR equation is the fundamental starting point for fisheries acoustics and can be written in linear form to describe scattering for individual targets as

$$P_e^2 = D^4\,\sigma_{bs}\left[\frac{\langle po\rangle^2\,G_E}{R^4\,10^{\frac{4aR}{20}}}\right] \qquad (1)$$

where p_e is echo pressure at the transducer, $\langle p_o\rangle$ is source pressure at the transducer, D is the directional response of the transducer (discussed in the 'Echosouuders' section), α is the attenuation coefficient [dB m^{-1}], R is range [m] from the transducer to the target, and G_E is a generic term encompassing echosounder gains. The acoustic backscattering cross–section, $\sigma_{bs,}$ [m^2] is the 'acoustic' size of the target. Acoustic size is the ability of the target to scatter sound back to the transducer and is the primary variable used throughout all subsequent calculations and conversions to numeric density, fish length, and biomass. A common form of the acoustic size given in fisheries acoustics literature is the logarithmic form of target strength (TS) = 10 $\log_{10}(\sigma_{bs})$ [dB]. Echo pressure, p_e, is directly proportional to σ_{bs} as all the other variables are constants and are either echosounder/transducer dependent (known through calibrations) or based on the physics of sound propagation. For more detailed descriptions and derivations of the SONAR equation see Forbes and Nakken (1972), Urick (1975), Clay and Medwin (1977), MacLennan and Simmonds (1992), Misund (1997), and Medwin and Clay (1998).

2.2. Population abundance

To estimate volumetric density (ρ) [# m^{-3}] for a fish population, we use volume reverberation (s_v), or the total backscattered energy from acoustic targets in a sampled volume. Assuming incoherent addition of backscatter and linearity (Foote, 1983) we obtain s_v by integrating equation (1) over the volume sampled (i.e. Echo Squared Integration) and simplify to the form (Clay and Medwin, 1977):

$$s_v = \sum_i N(i)\,\sigma_{bs}(i) \qquad (2)$$

where N is the number of targets of type i (e.g. zooplankton, fish with swimbladders, and/or fish without swimbladders) adjusted for echosounder variables, gains and corrections. For detailed information on echo–squared integration see Thorne (1983), Powell and Stanton (1983), and Medwin and Clay (1998). Contribution to the total volume scattering for different types of targets is proportional to their abundance, and the *exact* solution requires a known $\sigma_{bs}(i)$ for each type of target (Foote, 1983). A less diverse distribution of target types increases confidence in estimates. Equation (2) can be simplified to solve for numeric density (modified from eqn. 7.3.13 in Clay and Medwin, 1977):

$$\hat{\rho} = \frac{s_v}{\hat{\sigma}_{bs}} \tag{3}$$

where $\hat{\rho}$ [# m^{-3}] is the density estimate, and $\hat{\sigma}_{bs}$ is the best estimate of acoustic size. To calculate density, we must have an estimate of the acoustic size for all targets and $\hat{\sigma}_{bs}$ should be representative of all types of scatterers.

2.3. Acoustical size

Acoustic size, $\hat{\sigma}_{bs}$, can be obtained from a) individual *in situ* targets, b) previous knowledge, or c) derived using concurrent catch data. Derivations from catch data require a regression equation that relates σ_{bs} to individual targets [i.e. a TS-Length equation (Love ,1971a, 1971b; Foote, 1980, 1991), s_v-to-density (Gerlotto *et al.*, 1994; Massé and Retiere, 1995), or s_v-to-biomass (Fleischer *et al.*, 1997)]. TS-Length equations are often based on laboratory experiments where a series of individual fish are tethered, σ_{bs} is measured, and a regression equation is fit to σ_{bs} vs. length data. If one knows the length distribution from catch data, these lengths can be converted to $\hat{\sigma}_{bs}$ and then used in equation (3). A disadvantage to using catch data is that nets are size selective, whereas sonars detect all sizes of fish. When comparing catch data to acoustically derived size data, care must be taken to compensate for gear selectivity. *In situ* target data require targets detectable as individuals. An advantage to *in situ* targets is that the distribution of acoustic sizes should be representative of the distribution of fish lengths. However, data must be collected when fish are not schooling or densely aggregated. In the Laurentian Great Lakes, TS has been converted to fish length using the empirical relationships developed by Love (1971a, 1971b, 1977) and/or Foote *et al.* (1987). Love's (1977) equation has been used to describe fish length vs. fish target strength relationship for pelagic fishes of the Great Lakes (Brandt *et al.*, 1991). However, this relationship has recently been found to be less accurate for Great Lakes species (Fleischer *et al.*, 1997). Fleischer *et al.* (1997) provides TS-length and TS-mass relationships explicitly developed for pelagic planktivores of the Great Lakes.

2.4. Hardware

2.4.1. Echosounders

Three primary types of echosounders are currently used for fisheries assessment in the Great Lakes: single beam, dual-beam, and split-beam. The primary difference between these echosounders is in the technique used to estimate acoustic size. From the SONAR equation, the transducer directional response (*D*) is a measure of target location relative to the acoustic axis and must be known to calculate acoustic size. Essentially, a fish will have a larger acoustic size in the middle of the beam (on-axis) than it will on the edges (this is analogous to a flashlight where objects appear brighter in the beam than on the fringe). This effect must be corrected to accurately determine the acoustic size. Single beam transducers require the statistical techniques of 'Echo Amplitude Probability Density Function (PDF)' and 'deconvolution' (Craig and Forbes, 1969; Clay, 1983; Lindem, 1983; Stanton and Clay, 1986; Rudstam *et al.*, 1988) to correct for the beam pattern effect. These methods require a large number of targets, and hence require integration over large volumes. Dual-beam and split-beam echosounders correct echoes from individual targets for the beam pattern by using multiple beams housed in a single transducer. Dual-beam echosounders use the ratio of the intensities from a narrow and a wide beam to determine the off-axis position (Ehrenberg *et al.*, 1976; Traynor and Ehrenberg, 1979). Split-beam echosounders divide the beam into four quadrants and use a phase relationship to determine the off-axis position (Foote *et al.*, 1986). Split-beam echosounders have the advantage of being able to measure 3-dimensional movement (horizontal and range to transducer) of a target (Ehrenberg and Torkelson, 1996), while dual and single beams only detect one-dimensional movement (range from transducer). Split-beam systems also provide improved target strengths estimates compared to single and dual beam systems (Ehrenberg and Torkelson, 1996).

2.4.2. Transducer

Transducers are the link between echosounder/data collection and organisms in the water. The transducer converts a voltage to a pressure wave (ping), listens for sound scattered from objects (echoes), and converts these back to a voltage. The ideal transducer mount minimises the amount of roll, pitch, and yaw. Hull mounted transducers are generally found on larger research vessels and are often quite stable as they are only subject to vessel motion. The disadvantage to hull mounted transducers is that they can't be used on other vessels. Transducers mounted on towbodies are portable, but are more susceptible to sea state, bow wake, or propeller noise. A dead weight towbody designed and built at the Center for Limnology, University of Wisconsin-Madison in 1985, has proven to be robust and inexpensive (Figure 1).

3. Case study: Lake Ontario

3.1. Project objectives and goals

Classical predator-prey dynamics highlight the numerical response of a predator population to changes in the prey population (Lotka, 1925, Volterra,1926). In the Laurentian Great Lakes, however, predator populations are artificially controlled by hatchery production rather than by density-dependent feedback mechanisms. These artificially controlled piscivore populations support a recreational sport fishery valued in the billions of dollars (Talhelm, 1988). In such a system, hatchery production is maximised in response to public demand at the risk of exceeding the ecosystem's capacity to support stocking rates. More recently, management practices consider the status of prey fish populations when making stocking decisions. Stocking rates require accurate estimates of the abundance and production of open-water planktivorous fishes for the sustainability and wise management of the salmonine fishery (Rudstam *et al.*, 1996).

In Lake Ontario, the capacity of the lake to support the put-grow-take salmonine

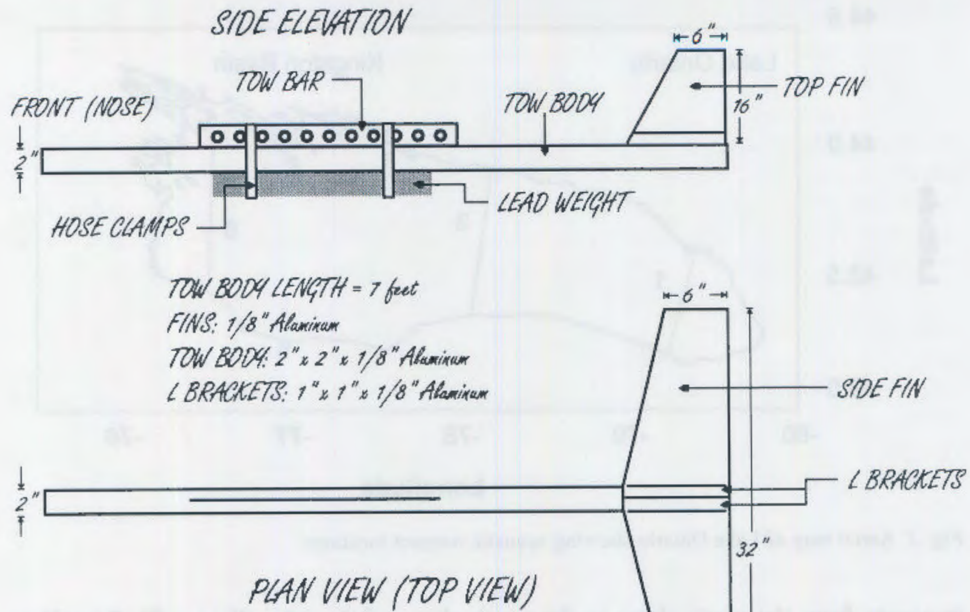

Fig. 1. Technical drawing of a 7 foot dead–weight towable platform (towbody). The towbody should be balanced by manipulation of the tow–point and lead weight position, in the fore–aft direction, for proper towing. Transducers are typically mounted forward of the lead weight, but can be attached anywhere along the main body. The size of the towbody can be lengthened or shortened, and the fins scaled appropriately, to accommodate multiple transducers or more weight depending on the vessel and towing speeds. This basic design was first built at the Center for Limnology, University of Wisconsin–Madison in 1985 (by J. M. Jech, G. Lee and C. S. Clay) and has been used in a variety of aquatic environments (*e.g.* Atlantic Ocean, Laurentian Great Lakes, coastal estuaries, and small freshwater lakes).

sport fishery is unknown. Recent evidence suggests that Lake Ontario may have exceeded its capacity to support stocked salmonines. To fully understand and to estimate the carrying capacity of Lake Ontario for stocked salmonine populations, we must have knowledge of the abundance of prey and how these prey species are distributed across space (Mason *et al.*, 1995; Mason and Brandt, 1996). This study was designed to address these two fundamental issues for Lake Ontario: prey abundance and prey distribution. Here, we provide estimates of the lakewide abundance, size, and spatial distribution of pelagic planktivores in Lake Ontario for several seasons between 1990 and 1992.

3.2. General methodology

Lakewide acoustic surveys were conducted during the fall of 1990 (Oct 29–Nov 9) and during the spring of 1992 (Apr 28–29). Additional acoustic transects where conducted during the summer of 1990 (Jul 30–Aug 3) and 1991 (Jul 8–9) and during the fall of 1991 (Oct 31–Nov 1). Acoustic data were collected continuously along three

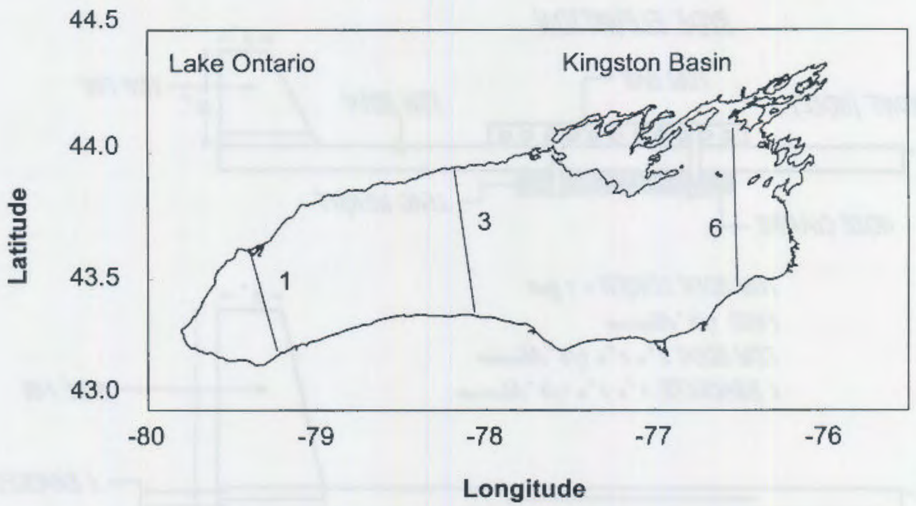

Fig. 2. Aerial map of Lake Ontario showing acoustic transect locations.

transects from the north shore to the south shore of the lake (Figure 2). Sampling commenced about 1 h after dark and ceased just before dawn. Acoustic transducers were housed in a stable platform (Figure 1) and towed alongside the ship at a speed of about 2.5 m s^{-1}. Vertical temperature profiles were recorded using an electronic bathythermograph at fixed locations along transects. Bottom trawls and midwater trawls were used to identify acoustic echoes to species. Detailed descriptions of the general acoustic sampling protocol can be found in Goyke and Brandt (1993) and are only briefly summarised below.

We used a 120 kHz dual-beam (10°, 25°) echosounder (Biosonics model 102). Equipment performance was monitored in the field using a chart recorder and an oscilloscope. Signals were adjusted using a $40\log_{10}R$ time varied gain (TVG), digitised, and recorded on VHS videocassette tapes for later analyses in the laboratory. Reference voltages were recorded on each video cassette tape to calibrate signals before analysis. Overall system performance of the acoustic equipment was determined during each survey using a tungsten carbide reference sphere of known target strength (Foote *et al.*, 1987; Foote, 1991).

Acoustic data were processed using both echo-squared integration and dual-beam analyses (see above). Echo-squared integration (Powell and Stanton, 1983; Thorne, 1983) was performed on the narrow (10°) beam using an echo integrator (Biosonics model 221) to place the data into a two-dimensional spatial array. The water column was divided into 1-m vertical strata beginning 2.5 m from the transducer. The echo integrator averaged 30 s intervals, corresponding to a horizontal resolution of about 75 m at a boat speed of 2.5 m·s^{-1}. Echo-squared integration values were corrected for signal spreading by adjusting the $40\log_{10}R$ TVG to a $20\log_{10}R$ TVG in our software before applying the mean backscattering coefficient (see below).

Dual-beam analyses (Traynor and Ehrenberg, 1979; Burczynski and Johnson, 1986), were used to determine the depth distribution of fish backscattering coefficients and fish target strengths. Only individual targets from 0.5° to 5.0° off-axis were used in the analysis. Mean backscattering coefficients ($\bar{\sigma}_{bs}$) were calculated for each cell in the array using three times the horizontal resolution of the echo integration data (225 m) because many cells containing echo-squared integration data did not have individual echoes due to high concentrations fish in those cells. Target strength values were converted to estimates of fish length using an empirical relationship developed by Love (1977). Lowest target strength included for the abundance calculation was –63.8 dB, which corresponds to a 10-mm fish. We used Love's equation to allow comparisons between Lake Ontario and Lake Michigan (see below). Length was converted to mass using the expression Mass (9) = 1.94×10^{-6} TL(mm)$^{3.24}$ (Goyke and Brandt,1993).

We used horizontal and vertical spatial stratification procedures to estimate lakewide planktivore abundance and biomass (as per Brandt *et al.*, 1991). Horizontal stratification was based on bathymetric contours, which included nine intervals (0–9 m, 10–18 m, 19–27 m, 28–37 m, 38–46 m, 47–55 m, 56–64 m, 65–73 m, and 74–100 m). Vertical stratification was based on mid water strata depth and was also divided into the same nine strata. Water depths less than 3 m were not sampled effectively due to the near-field effect and were assumed to have the same fish densities as depths of 4–9 m. Average density and biomass (fish m^{-3} and g m^{-3}) were calculated for each depth stratum for each transect.

We estimated total fish density and biomass by multiplying the interval average (across the entire transect) by the area or volume of the interval in the region represented by each transect (Figure 2). Summing totals of all strata produced regional density and biomass estimates; summing regional density and biomass produced lakewide estimates of abundance.

3.3. Pelagic fish abundance and spatial distribution

3.3.1. Spatial distribution and size

Fish size varied with location and depth. Smallest fish were found in the Kingston Basin during fall and along transect 6 during spring (Figure 3). Within each transect, the smallest fish were generally shallower, and size increased with depth. Acoustic sizes indicated that young-of-year (YOY) fish were found above the thermocline, and larger fish found around and beneath the thermocline (40–50m).

3.3.2. Patterns in density within and between seasons

Fish biomass and numerical densities per unit area varied with region. Highest densities occurred in the Kingston Basin region with an average biomass of 31.4 g m^{-2} and average density of 15.3 fish m^{-2} (Table 1). Fish biomass and numeric densities ranged from 10.2 to 34.0 g m^{-2} and 8.2 to 20.5 fish m^{-2} (Tables 2 and 3). Within Lake Ontario proper (excluding the Kingston Basin), mean biomass and density were 26.1 g m^{-2} and 7.0 fish m^{-2} during fall 1990, and 9.1 g m^{-2} and 2.4 fish m^{-2} during spring 1992 (Table 1). Biomass and numeric density ranged from 2.8 to 30.8 g m^{-2} and 1.25 to 16.5 fish m^{-2} in fall 1990, and 2.3 to 17.5 g m^{-2} and 0.76 to 17.1 fish m^{-2} in spring 1992 (Tables 2 and 3).

Fish biomass and numeric densities per unit volume also varied with region. Fish biomass and densities ranged from 0.002 g m^{-3} to 1.5 g m^{-3} and 0.0004 to 1.2 fish

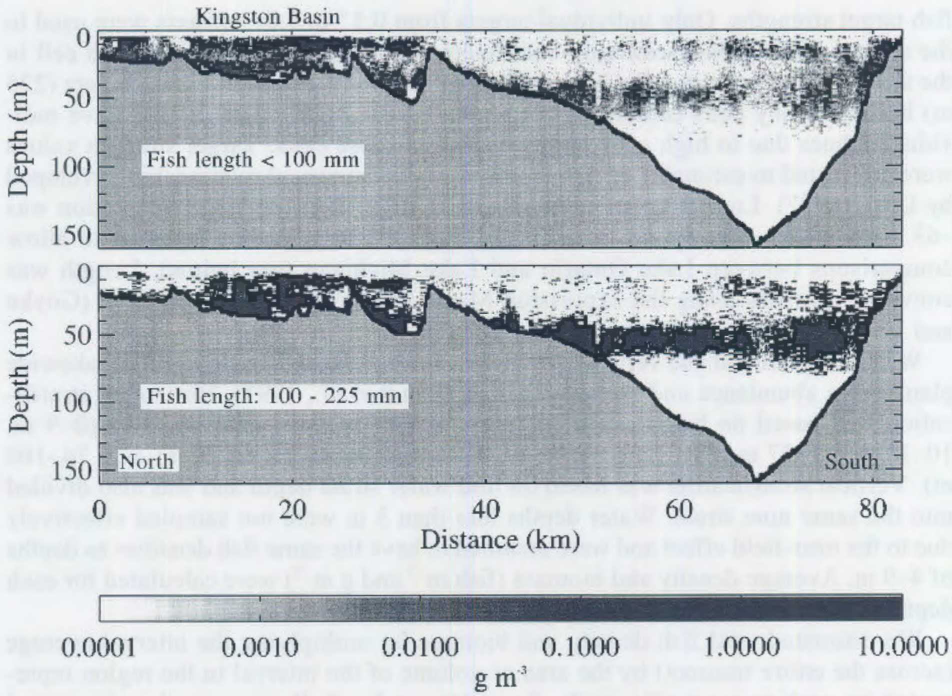

Fig. 3. Echograms showing the biomass density (logarithmic gray scale) of pelagic fish less than 100 mm (top) and from 100–225 mm (bottom) along transect 6. Acoustic data were collected along the transect beginning 1 hr after sunset to 1 hr before sunrise from October 29 to November 9, 1990. Note the high biomass of fish in the Kingston Basin region.

Table 1. Mean biomass (g m^{-2}), density (fish m^{-2}), total biomass, and number of fish for each complete cross–lake transect (KB–Kingston Basin).

Transect	Average Biomass (g m^{-2})	Average Density (fish m^{-2})	Average Weight (g)	Average Length (mm)	Total Biomass (ktonnes)	Total Fish (billions)
			Fall 1990			
1	11.37	5.62	2.02	72	43.08	21.30
3	26.14	6.97	3.75	87	231.61	61.75
6	11.31	3.95	2.87	80	44.72	15.61
KB	31.42	15.29	2.06	73	49.84	24.25
			Summer 1991			
3	10.84	13.91	0.78	54	96.01	123.23
			Fall 1991			
3	20.75	9.48	2.19	74	183.86	83.98
			Spring 1992			
1	5.69	1.40	4.07	90	21.57	5.30
3	9.14	2.36	3.87	88	80.96	20.90
6	7.19	1.52	4.72	94	28.41	6.03

Table 2. Mean fish biomass (g m^{-2}) for various bottom contours ≤ 100 m (KB– Kingston Basin).

Transect	Bottom Contour (m)								
	0–9	**10–18**	**19–27**	**28–37**	**38–46**	**47–55**	**56–64**	**65–73**	**74–100**
					Summer 1990				
1	—	—	6.41	5.28	4.69	4.34	2.53	8.00	6.08
					Fall 1990				
1	—	2.76	9.09	8.43	3.66	24.25	26.27	15.97	13.41
3	—	7.66	5.51	9.79	8.28	21.54	29.20	30.76	22.08
6	3.28	9.74	4.98	4.14	8.34	11.76	5.48	6.56	8.47
KB	10.24	18.06	34.00	23.76	23.17	—	—	—	—
					Summer 1991				
3	—	9.19	2.80	0.81	1.69	1.32	1.40	1.38	1.43
					Fall 1991				
3	—	6.55	6.54	6.55	4.52	1.89	9.43	6.53	10.84
					Spring 1992				
1	—	9.38	9.25	16.07	15.94	19.22	17.11	5.17	2.77
2	—	2.25	9.91	14.69	13.27	15.46	11.40	6.05	7.61
3	—	17.47	6.96	9.24	3.12	6.12	9.54	3.53	3.75

Table 3. Mean fish density (fish m^{-2}) for various bottom contours ≤ 100 m (KB– Kingston Basin).

Transect	Bottom Contour (m)								
	0–9	**10–18**	**19–27**	**28–37**	**38–46**	**47–55**	**56–64**	**65–73**	**74–100**
					Summer 1990				
1	—	—	6.41	5.28	10.03	9.01	5.87	17.60	13.12
					Fall 1990				
1	—	1.79	1.49	1.59	2.57	3.81	7.54	5.17	3.79
3	—	1.25	7.86	2.50	9.26	9.26	12.83	16.54	11.02
6	2.55	11.78	4.99	3.28	3.52	4.23	3.13	2.85	4.35
KB	8.22	15.67	14.93	12.28	20.51	—	—	—	—
					Summer 1991				
3	—	20.56	43.45	14.68	24.49	33.67	20.65	23.68	12.33
					Fall 1991				
3	—	5.13	1.71	1.59	1.33	0.68	1.86	0.39	0.23
					Spring 1992				
1	—	12.68	7.98	14.77	8.05	17.09	11.97	7.78	8.69
3	—	7.28	4.69	7.76	3.87	3.25	1.59	0.76	1.11
6	—	3.40	4.47	9.25	12.69	11.71	2.45	1.22	1.61

Table 4. Mean fish biomass (g × 10^3 m^{-3}) for various depth strata averaged across the entire transect for depth strata ≤ 100 m (KB– Kingston Basin).

Transect	Vertical Depth Strata (m)								
	0–9	10–18	19–27	28–37	38–46	47–55	56–64	65–73	74–100
					Summer 1990				
1	—	—	—	1.3	1.0	0.4	0.1	<0.1	<0.1
					Fall 1990				
1	421.3	269.6	67.5	70.4	17.5	7.0	6.6	2.4	1.6
3	1,225.1	614.0	89.7	56.2	157.8	56.5	7.8	2.2	3.3
6	281.6	322.9	42.7	52.9	170.5	161.6	38.1	4.4	9.4
KB	1,510.1	890.7	403.3	277.1	143.0	—	—	—	—
					Summer 1991				
3	1,070.7	107.1	14.8	11.2	6.8	2.8	1.1	0.4	0.2
					Fall 1991				
3	1,345.5	512.9	170.5	159.2	132.6	67.8	18.6	3.9	2.3
					Spring 1992				
1	321.6	124.9	58.4	47.9	51.3	49.0	29.4	11.7	5.9
3	473.0	142.7	97.5	100.9	115.5	103.1	49.7	17.7	6.0
6	249.9	139.1	145.0	301.3	63.4	18.8	7.3	7.5	6.9

Table 5. Mean fish density (fish × 10^3 m^{-3}) for various depth strata averaged across the entire transect for depth strata ≤ 100 m (KB– Kingston Basin).

Transect	Vertical Depth Strata (m)								
	0–9	10–18	19–27	28–37	38–46	47–55	56–64	65–73	74–100
					Summer 1990				
1	—	—	10.0	7.5	4.7	2.3	1.3	0.9	0.6
					Fall 1990				
1	299.1	167.6	97.6	43.2	18.3	8.6	5.5	1.4	0.4
3	277.4	253.4	98.6	46.9	24.5	7.5	3.4	1.4	0.3
6	186.6	146.5	31.0	44.5	45.3	12.1	3.0	2.4	1.1
KB	1,176.2	522.3	126.8	87.2	20.7	—	—	—	—
					Summer 1991				
3	1,220.0	264.7	30.0	32.6	14.0	6.6	1.9	0.1	3.0
					Fall 1991				
3	766.7	207.0	62.7	24.0	8.4	3.4	2.1	2.5	0.8
					Spring 1992				
1	93.9	40.6	13.9	3.3	6.4	3.3	1.3	0.5	1.7
3	146.3	38.1	25.1	19.2	13.5	14.6	14.6	5.9	3.9
6	41.1	50.1	15.8	28.5	37.6	21.1	8.4	3.9	2.1

Table 6. Mean biomass (g m^{-2}), mean density (fish m^{-2}), total biomass, and total number of pelagic planktivores in Lake Ontario during the fall of 1990 and spring of 1992 (KB– Kingston Basin).

Season, Year	Coverage	Average Biomass ($g\ m^{-2}$)	Average Density (fish m^{-2})	Average Weight (g)	Average Length (mm)	Total Biomass (ktonnes)	Total Fish (billions)
Fall, 1990	Lake	17.97	5.67	3.24	83	312.8 ± 43.8	98.6 ± 20.7
Fall, 1990	Lake + KB	20.30	6.76	3.00	82	362.2 ± 51.3	122.9 ± 24.0
Spring, 1992	Lake	10.95	2.70	4.06	90	181.9 ± 27.9	44.8 ± 11.7

m^{-3} in fall 1990, and 0.006 g m^{-3} to 0.4 g m^{-3} and 0.0005 fish m^{-3} to 0.1 fish m^{-3} in spring 1992. In general, highest densities of fish were found in the uppermost stratum (0–9m) for all seasons and at all locations, while lowest fish densities were below the thermocline. Greatest density of fishes occurred in the Kingston basin region with 1.5 g m^{-3} and 1.2 fish m^{-3} in fall 1990 (Tables 4 and 5).

Acoustic estimates for transect 3 in summer 1991, fall 1991, and spring 1992 allowed us to evaluate changes in fish abundance and size across seasons. Density was highest during summer, with an average of 13.9 fish m^{-2} (Table 1) and decreased into the fall to 9.5 fish m^{-2}. Biomass increased from summer to fall, 10.8 to 20.8 g m^{-2}, and was highest during fall (Table 1). Total biomass in the region of the lake represented by transect 3 was 96.0 kt in summer, 183.9 kt in fall, and 81.0 kt in the following spring. Average size of fishes derived from acoustic data increased from summer (0.74 g, 54 mm) through fall (2.19 g, 74 mm) and into spring (3.87 g, 88 mm). Small average size of fish during the summer of 1991 suggests that these fish were YOY. This is consistent with the observed trend of decreasing size and age of alewives and rainbow smelt as noted by O'Gorman *et al.* (1987). Fish numerical abundance was 123.2 billion in summer, 84.0 billion in fall, and 20.9 billion in spring 1992. During the winter of 1991–92, biomass of pelagic planktivores declined by 56%, and abundance declined by 76%. This decrease corresponded to lower numbers of age 1 alewife during early spring of 1992 (C.P. Schneider, N.Y. Department of Environmental Conservation, Personal Communication) suggesting a high mortality of YOY fishes over the winter.

3.3.3. Lakewide population estimates

Fish biomass estimates for Lake Ontario during fall 1990 were 312 ± 43.8 kt for the lake proper and 362.2 ± 51.3 kt for the lake and Kingston Basin combined (Table 6). YOY fishes accounted for over half of Kingston Basin biomass and about 20% of the biomass from the other transects (Figure 4). Estimates of total abundance were 98.6 ± 20.7 billion fish for the lake proper and 122.9 ± 24.0 billion fish for the lake and Kingston Basin combined. Kingston Basin region accounted for 14% and 20% of the total summer lakewide biomass and numerical abundance, respectively, while making up only ~8% of the total lake surface area and ~4% of the total lake volume. For spring 1992, estimates of total biomass and numerical abundance for Lake Ontario proper only were 181.9 ± 27.9 kt and 44.8 ± 11.7 billion fish.

Errors may have occurred in our acoustical abundance estimates from the use of the TS-length relationship derived by Love (1977) and from the choice of a lower TS threshold (–63.8 dB) to include in our calculations of mean TS. Errors in the TS-

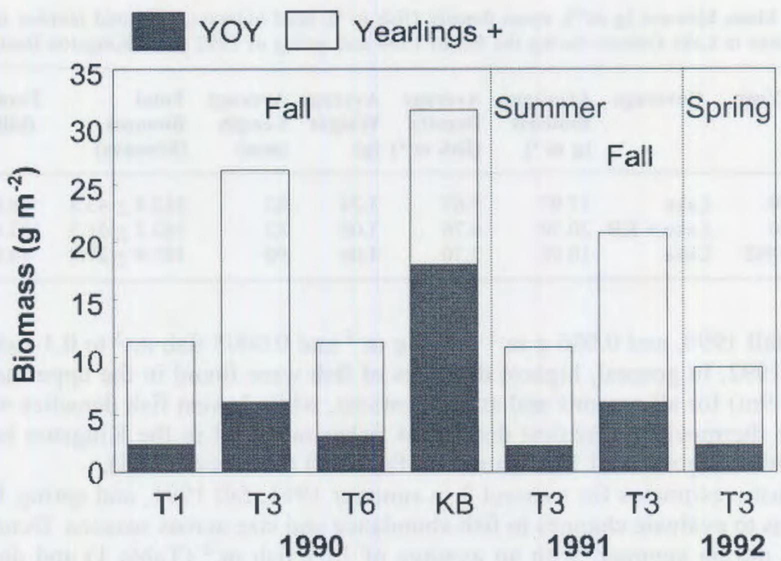

Fig. 4. Biomass density of young–of–year and yearling and older fish measured acoustically in Lake Ontario for transects 1–3 (T1, T3, T6) and Kingston Basin (KB) during fall in 1990, transect 3 (T3) during summer and fall in 1991 and transect 3 (T3) during spring in 1992.

length relationship can account for large biases in population estimates (e.g., Bjerkeng *et al.*, 1991). Recently, Fleischer *et al.* (1997) demonstrated that Love's TS-length relationship is not appropriate for Great Lakes pelagic planktivores and that it estimates shorter fish lengths for fish less than ~120 mm and longer fish lengths for fish greater than ~120 mm. A low TS threshold may include non-fish targets and a mean TS calculated from the often numerous small targets will bias our mean towards smaller sizes. Using a mean TS that is biased towards smaller sizes will increase our overall estimates of abundance. Thus, our estimates of abundance may be biased high, but these estimates are still useful for comparison with previous population assessments on Lake Michigan, which used the equation developed by Love (1977) and a similar lower value for the TS threshold.

4. Laurentian Great Lakes comparison: Lake Michigan and Lake Ontario

4.1. Great Lakes fishery: fishery at risk

A contrast between Lake Michigan and Lake Ontario provides an historical example of the risk of hatchery over-production and stocking. Alewives are the preferred prey of salmonines in Lake Michigan (Jude *et al.*, 1987) and Lake Ontario (Brandt, 1986). Angler harvests, return of salmonines to hatchery streams, average weight of angler-caught chinook salmon, and survival rates of Pacific salmon all declined in Lake Michigan during the mid to late 1980's (Stewart and Ibarra, 1991). Stocking rates continued to be high through the late 1980's and early 1990's despite warnings of

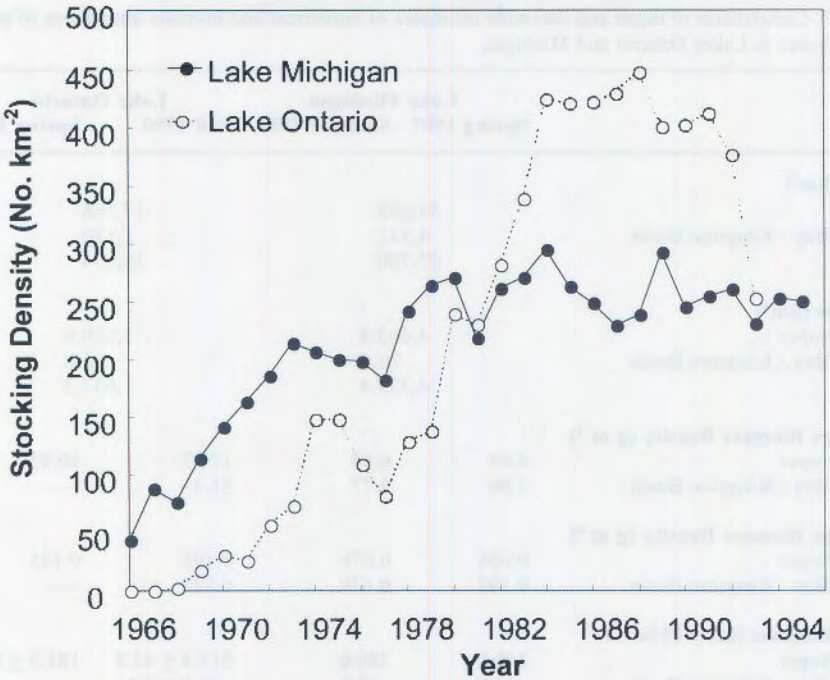

Fig. 5. Stocking density (number stocked/surface area of the lake) for Lakes Michigan and Ontario from 1966 to 1995.

salmonine over-stocking (Stewart *et al.*, 1981) (Figure 5). Lake Ontario has experienced higher stocking densities than Lake Michigan (Figure 5) and has also shown signs of stress. Following an increase in the stocking rates in 1982, brown trout and coho salmon experienced a negative response in growth rates (size at age) (O'Gorman *et al.*, 1987; Rand and Stewart, 1998). Signs of declining alewife abundance in Lake Ontario have prompted studies on the current status and future prospects of alewife, and re-evaluation of stocking plans for salmonids (see above).

Our previous work on Lake Michigan emphasised the use of acoustics and bioenergetic models for estimating the magnitude of predator demand placed on the system. Here, we will compare estimates of prey fish abundance for Lake Ontario to our earlier estimates from Lake Michigan (Brandt *et al.*, 1991). Ultimately, we want to answer the question: can natural levels of prey fish abundance sustain the level of exploitation inferred from present stocking rates?

4.1.1. How similar are Lakes Michigan and Ontario?

We compared estimates of prey fish abundance measured during fall 1990 for Lake Ontario to our earlier estimates of prey fish abundance during late summer 1987 for Lake Michigan (Brandt *et al.*, 1991). The purpose of our comparison was to evaluate the relative status of prey fish in Lake Ontario to a period of time in Lake Michigan when salmonine populations were stressed and prey fish were known to be limiting salmonine growth and survival.

Table 7. Comparison of mean and lakewide estimates of numerical and biomass abundance of pelagic planktivores in Lakes Ontario and Michigan.

	Lake Michigan		Lake Ontario	
	Spring 1987	Summer 1987	Fall 1990	Spring 1992
Area (km^2)				
Lake		53,268		17,388
Green Bay / Kingston Basin		4,512		1,586
Total		57,780		18,974
Volume (km^3)				
Lake Proper		4,663.4		1,580.6
Green Bay / Kingston Basin		70.0		56.8
Total		4,733.4		1,637.3
Average Biomass Density (g m^{-2})				
Lake Proper	4.89	6.88	17.97	10.95
Green Bay / Kingston Basin	3.06	9.77	31.4	—
Average Biomass Density (g m^{-3})				
Lake Proper	0.056	0.078	0.198	0.115
Green Bay / Kingston Basin	0.197	0.630	0.878	—
Total Biomass (kt) ± 95% CI				
Lake Proper	260.8	380.0	312.4 ± 43.8	181.9 ± 27.9
Green Bay / Kingston Basin	13.8	42.8	49.8 ± 7.5	
Total	274.6 ± 67.1	410.8 ± 97.5	362.2 ± 51.3	*181.9 ± 27.9
Average Number Density (# m^{-2})				
Lake Proper	0.86	2.19	5.67	2.70
Green Bay / Kingston Basin	1.00	5.95	15.29	
Average Number Density (# m^{-3})				
Lake Proper	0.010	0.025	0.064	0.028
Green Bay / Kingston Basin	0.064	0.384	0.428	—
Total Numbers (billions) ± 95% CI				
Lake Proper	45.8	117.5	98.6 ± 20.7	44.8 ± 11.7
Green Bay / Kingston Basin	4.5	26.2	24.3 ± 4.7	
Total	**50.2 ± 11.7**	**143.6 ± 22.7**	**122.9 ± 24.0**	***44.8 ± 11.7**

* Kingston Basin not included in estimate.

Overall, fish abundance and biomass were similar between Lake Michigan during 1987 and Lake Ontario in 1990. Despite Lake Michigan having approximately 1.2 times as many pelagic fishes based on a mean number and mean biomass, differences in abundance between lakes were not significant (Table 7). However, when abundance was scaled to the size of each lake (area and volume), pelagic fish numbers were greater in Lake Ontario. Numbers and biomass of fish per unit surface area and per unit volume were nearly 2.6 times higher in Lake Ontario proper than in Lake Michigan proper. In addition, Kingston Basin contained more fish and more fish biomass on a per unit size than did Green Bay (Table 7). When fish biomass was scaled to number of salmonine predators in each lake, Lake Michigan had an estimated 21.9 kg prey fish per predator and Lake Ontario had 29.3 kg prey fish per predator [Lake Michigan: 16,716,000 predators (Stewart and Ibarra, 1991), Lake Ontario: 10,667,000 predators (Rand and Stewart, 1998)].

4.2. Fish size

Fish sizes, as measured acoustically, were larger in Lake Michigan during late summer than Lake Ontario during fall. Mean fish sizes across Lake Ontario ranged from 2.02 to 3.75 g and from 72 to 87 mm, whereas mean sizes in Lake Michigan ranged from 2.15 to 4.78 g and from 74 to 94 mm (Brandt *et. al.*, 1991). Green Bay had the smallest average fish size of either lake, where average sizes for the two Green Bay transects were 1.26 and 2.01 g, and 62 and 72 mm. Larger fish at deeper depths in Lake Michigan correspond to the larger bloater.

4.3. Species composition and distribution

Approximately 78% of the lakewide prey fish biomass (i.e., bloater) in Lake Michigan was unavailable to salmonines without foraging in suboptimal thermal habitats and low light environments. In contrast, vertical and thermal distributions of pelagic prey fish in Lake Ontario were more favourable for foraging and growth of salmonines. Figure 6 demonstrates the differences in pelagic fish distribution between Lakes Ontario and Michigan. Note that all of the prey fish biomass for Lake Ontario is located in the upper part of the water column corresponding to the epilimnion and metalimnion. However for Lake Michigan, most of the biomass is locked up in the hypolimnion on a volume basis.

Despite the similar overall potential prey fish biomass between lakes, Lake Ontario may support a pelagic prey fish community most beneficial to stocked salmonines. If we assume that approximately 78% of the total pelagic fishes in Lake Michigan are unavailable to salmonines as forage (Brandt *et al.*, 1991), then Lake Ontario (362.2 kt) had 4 times the lakewide biomass of available prey fish than Lake Michigan (90.4 kt). Consideration of prey availability also increased the difference in prey biomass to predator ratio between lakes. Lake Michigan had an estimated 4.8 kg of prey per predator, where as Lake Ontario had 6 times the prey biomass to predator than Lake Michigan.

Bioenergetics analysis using estimates of alewife abundance for Lake Michigan suggests that alewife were being exploited at a high rate. We found that up to 43% of alewife production was removed by chinook salmon, coho salmon and lake trout, with a total of 60% of the alewives removed by all predators and the commercial fishery combined (Brandt *et al.*, 1991). The high exploitation rate of alewives coupled with poor growth and survival of stocked salmonines suggest that the artificially enhanced predator population exceeded the carrying capacity of the lake. Rand and Stewart (1998) performed a similar bioenergetics exercise for Lake Ontario. They found that chinook salmon, coho salmon, and lake trout combined to remove 12.7% of the available prey fish production. However, Rand and Stewart (1998) also estimated that greater than 100% of the adult alewife production was being consumed by these predators. Despite the apparent imbalance between salmonine demand and availability of adult alewife in Lake Ontario, the salmonine populations did not ex-

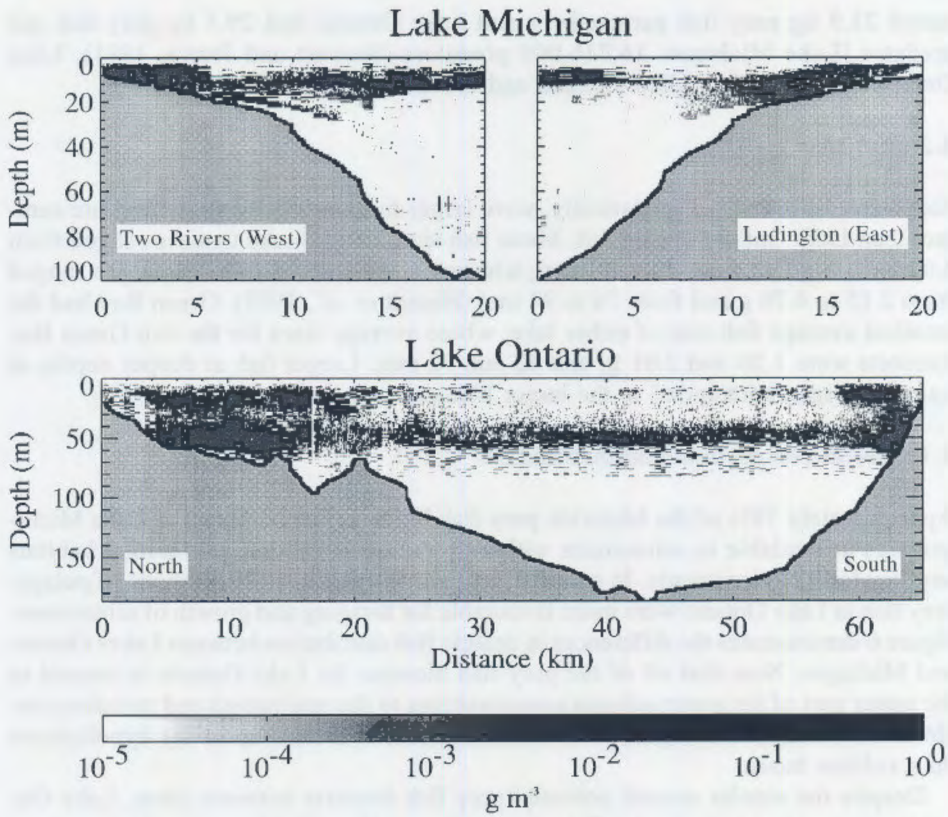

Fig. 6. Echograms showing biomass density (logarithmic gray scale) for two transects in Lake Michigan and for transect 3 in Lake Ontario. Acoustic data were collected along the transect beginning 1 hr after sunset to 1 hr before sunrise for Lake Ontario (from Oct. 29 to Nov. 9, 1990) and from 1 hr after sunset to approximately midnight for Lake Michigan (from Aug. 26 to Sept. 10, 1987). Note the presence of fish (bloater, *Coregonus hoyi*) in the hypolimnion of Lake Michigan and the lack of fish in the hypolimnion of Lake Ontario.

perience the same high levels of mortality and stress as observed for salmonines in Lake Michigan. Based on these bioenergetics analyses and the biomass of prey available to each predator, Lake Ontario did not appear to exceed the capacity to support salmonines to the degree of Lake Michigan and may have been near or slightly below the capacity of the system to support continued salmonine production.

4.4. Comparison of basins as a source of prey fish

Green Bay and the Kingston Basin region contained the highest densities of fish and contributed greater numbers to the total fish abundance of each lake than would be expected based on surface area or volume alone. It is not known whether fish migrate into these basins from the lakes to spawn or whether recruitment is more successful in these more productive waters. As this pattern exists for both lakes, it is interesting to speculate as to whether these large basins act as a source for pelagic fishes in the lake proper. Further research is needed to evaluate the contribution of such embayments to overall prey fish production within the Great Lakes.

4.5. Implications for the salmonine fishery

Accurate estimates of the number, biomass, and distribution of pelagic planktivores is important for a sustainable salmonine fishery. Fisheries acoustic data meet many of the needs identified by the International Symposium on Stocks Assessment and Yield Prediction (ASPY), including increased spatial and temporal resolution of data, computerisation, and increased reliability of acoustic methods (Christie *et al.*, 1987a). The establishment of an acoustic assessment program on Lake Ontario, met several of the needs identified by ASPY, such as constructing a time series of fish abundance estimates (Christie *et al.*, 1987b). Acoustic estimates of prey fish biomass are now being used to help establish stocking policies and stocking rates in the Great Lakes. Yet another utility of acoustic information is its application to ecological issues. For example, these data from Lake Ontario have been used to develop spatial models of salmonine predation in Lake Ontario (Goyke and Brandt, 1993; Mason *et al.*, 1995; Mason and Brandt, 1996), for input to a biomass size spectrum model of Lake Ontario (Sprules and Goyke, 1994), and to aid in assessing the status of the offshore pelagic fish community in Lake Ontario during 1992.

5. Summary

Fisheries acoustics have been applied in the Great Lakes since the early 1960s, but not until recently has this technology been accepted for pelagic fish assessment. In this chapter, we present a general introduction to fisheries acoustics, a case study of Lake Ontario, and compare prey fish population estimates from Lake Michigan and Lake Ontario to gain insight into the carrying capacity of these lakes to support stocked salmonines. In Lake Ontario, prey fish biomass and numeric density varied spatially and seasonally during 1990–1992. Greatest mean fish densities occurred in the Kingston Basin region, 15.3 fish m^{-2} and 31.4 g m^{-2}, compared to the lake proper, 7.0 fish m^{-2} and 26.1 g m^{-2} for fall 1990. In the lake proper, numeric densities were consistently highest in the summer (13.9 fish m^{-2}) and decreased during the fall (9.5 fish m^{-2}), while biomass increased from summer to fall, 10.8 to 20.8 g m^{-2}. Correspondingly, acoustic estimates of mean fish weight increased from summer to fall, 0.74 to 2.18 g. During winter 1991–92, pelagic fish biomass decreased by 56% and numeric density declined by 76%, which is consistent with net-based observations of lower numbers of age-1 fish in spring 1992. We compared acoustic estimates of prey fish abundance in Lake Ontario to our previous estimates of prey fish abundance from Lake Michigan during the late 1980s when salmonids were food limited. Lake Ontario appeared to have four times the lakewide biomass of available prey fish and about six times the available prey biomass:predator ratio than Lake Michigan. Lake Ontario did not appear to exceed the capacity to support salmonines to the degree of Lake Michigan and may have been near or slightly below the capacity of the system to support continued salmonine production.

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