

RELATION OF SEA LAMPREY SIZE AND SEX RATIO TO SALMONID AVAILABILITY IN THREE GREAT LAKES

Kim A. Houston¹ and John R. M. Kelso²

Department of Fisheries and Oceans
Great Lakes Laboratory for Fisheries
and Aquatic Sciences
Canal Drive, Ship Canal P.O.
Sault Ste. Marie, Ontario P6A 1P0

ABSTRACT. Since 1980 the proportion of males appears to have increased to ~50% in the sea lamprey (*Petromyzon marinus*) populations of Lakes Superior and Huron following a period (1970-1980) of stability. In Lake Ontario, there has been a shift from an approximately equal sex ratio (1970-1980) to a slight preponderance (~60%) of males. Multiple regression analysis indicated that prey availability (reflected by salmonid stocking or commercial catch) was significantly related to the observed changes in length, weight, and proportion of males. We also found that, while sea lamprey length and weight may have stabilized in Lake Superior (1960 to present), sea lamprey have generally become larger in both Lakes Huron and Ontario. Again, prey availability was most closely related to weight of sea lamprey. Sex ratio and adult weight in Great Lakes sea lamprey appear to be related to prey availability and therefore may not be adequate indicators of the success of sea lamprey control.

INDEX WORDS: Lamprey, fish management, sea lamprey, salmon.

INTRODUCTION

Sea lamprey (*Petromyzon marinus*) in the Laurentian Great Lakes were smaller (Vladikov 1951, Hardisty 1971, Beamish 1979, Weise and Rugen 1987) and less fecund (Applegate 1950, Vladikov 1951, Wigley 1959, Manion 1972) than their marine counterparts. With the initiation of a control program to reduce sea lamprey abundance, mean lengths and weights of sea lamprey increased and the proportion of males in the population declined as their numbers declined (Smith 1971). Heinrich *et al.* (1980) and Torblaa and Westman (1980) examined size and sex data to 1978 and found that growth declined after chemical control but later increased, and that a shift to a preponderance of females occurred as populations declined. Smith (1971) recognized that factors other than sea lamprey abundance influenced sea lamprey size. Heinrich *et al.* (1980) found that in Lake Superior,

sea lamprey appeared larger when the control program had reduced lamprey numbers and when lake trout were more abundant.

Abundance of primary sea lamprey prey species (e.g., salmonids) has dramatically increased since the late 1970s in Lakes Ontario (Christie *et al.* 1987) and Superior (Krueger *et al.* 1986, MacCallum and Selgeby 1987) and probably also in Lake Huron (Collins 1988; data from the Great Lakes Fishery Commission (GLFC)). Because sea lamprey population characteristics are likely to respond to changes in prey density and/or fish community structure in general or to the sea lamprey control strategy in particular (Smith 1971, Heinrich *et al.* 1980, Torblaa and Westman, Odum 1985), we examined the 38 y of data now available for length, weight, and sex composition of Great Lakes sea lamprey populations from Lakes Ontario, Huron, and Superior. We first examined changes of these biological characteristics (length, weight, and proportion of male sea lamprey) to the present (1987) in populations from the three Great Lakes. Second, we related any change(s) evident in weight or sex composition to general control strat-

¹Present address: Department of Fisheries and Oceans
Habitat Research and Assessment
P.O. Box 5667
St. Johns, Nfld. A1C 5X1

²Author to whom correspondence should be addressed.

egy (e.g., pretreatment, barriers, chemical), an indicator of sea lamprey abundance (catches over time in a stream(s) for each lake), and prey abundance as indicated by salmonid catch and/or stocking.

METHODS

Data Collection

The Canadian Department of Fisheries and Oceans and the U.S. Fish and Wildlife Service have sampled spawning lamprey in streams from Lake Huron since 1951, from Lake Superior since 1953, and from Lake Ontario since 1968. Sea lamprey have not been a serious problem in Lake Erie (Pearce *et al.* 1980) and data were sparse. Although sea lamprey were common in Lake Michigan and an active control program has been in place since 1960 (Smith and Tibbles 1980), several interruptions in sampling occurred. Further, the available weight data for sea lamprey from Lake Michigan was used by Kitchell (in press) to examine their bioenergetics. Therefore, to avoid uncertainties and duplication, we excluded Lake Erie and Lake Michigan data from our analysis. Data on length, weight, and sex were available for ~25% of the 427 tributaries of the Great Lakes in which sea lamprey spawn. We used data wherever they were available (Table 1).

Because males and females were weighed and measured separately, we used Pearson correlation analysis to examine the correlation in length and weight between the sexes. There was no significant difference ($P < 0.05$) between the length and weight of males and females; therefore, we pooled data from both sexes. The length, weight, and sex ratio data from Lakes Superior, Huron, and Ontario were analyzed separately; however, we pooled the length, weight, and sex ratio data from all streams sampled in a lake since there was minimal variation among these variables (c.v. $< 10\%$) within a lake (Steel and Torrie 1960).

Salmonids (*Salvelinus namaycush*, *S. fontinalis*, *Salmo trutta*, *S. salar*, *Oncorhynchus mykiss*, *O. tshawytscha*, *O. kisutch*, and *O. gorbuscha*) have been stocked in each of the Great Lakes to increase abundance of lake trout or generate new fisheries (e.g., chinook, coho). Because these eight fish species may be among the preferred prey of sea lamprey (Johnson and Anderson 1980), we summed annual stocking and commercial catch for all salmonids. Records of salmonid stocking up to

1987 for Lakes Superior, Huron, and Ontario were obtained from the GLFC (M. A. Dochoda, GLFC, Ann Arbor, MI). Commercial catch statistics for all salmonid species were reported in Baldwin *et al.* (1979) and the GLFC annual reports (1978–1983). Commercial catch data for 1984 to present have not yet been compiled. While these data may only partly reflect salmonid abundance (e.g., incomplete reporting of commercial catches, no rigorous reporting of sport catches), no better database exists.

Data Analysis

Each time series of weight, length, and percent male sea lamprey was plotted using a Distance Weighted Least Squares (DWLS) smoothing which fitted a line through the data (Wilkinson 1988). Each point on the smoothed line was estimated by a weighted quadratic multiple regression on all points which allowed the curve to flex locally to better fit the data and to provide a visual representation of the shape of each time series. Autocorrelation analysis determined how closely each value was related to previous values in the series (i.e., if there were any significant lags in the data; Wilkinson 1988). In doing so, we were able to determine if the series was random or if there were indeed significant autocorrelations and/or potential trends. As well, a linear regression was fitted to each data set to test for trends.

Catch of spawning sea lamprey from an index stream(s) was used as a relative measure of abundance in each of the three Great Lakes. For Lake Superior, electrical barriers were continuously operated in the Betsy, Two Hearted, Sucker, Chocoma, Iron, Silver, Brule, and Amnicon rivers until 1978. Catches from these eight barriers were used to indicate sea lamprey abundance in Lake Superior. Catches from the Ocqueoc River were used as an indicator of sea lamprey abundance within Lake Huron, and catches from the Humber River were used for Lake Ontario.

For Lakes Superior and Huron, three "periods" (based on collection and/or control method) were identified: a) pre-chemical control, samples from electrical barrier and mechanical weirs only (Lake Superior pre-1958; Lake Huron pre-1958), b) initiation of chemical control and concurrent operation of electrical barriers (Lake Superior 1958–1979; Lake Huron 1958–1980), and c) chemical control only (Lake Superior 1979 to present; Lake Huron 1980 to present). These categories

TABLE 1. Great Lakes tributaries sampled for spawning sea lamprey used in the analysis.

LAKE SUPERIOR	YEARS SAMPLED	LAKE ONTARIO	YEARS SAMPLED
Amnicon River	1957-79, 1987	Duffin Creek	1980-87
Au Train River	1954-61, 1963-64	Graham Creek	1977-82, 85-87
Bad River	1986	Grindstone Creek	1982-87
Betsy River	1954-61, 1963-79, 1981-87	Humber River	1968-78, 1980-87
Big Garlic River	1981-87	Lakeport Creek	1986-87
Boot River	1987	Little Salmon River	1981-86
Brule River	1958-79, 1986-87	Lynde Creek	1980
Chocoday River	1954-61, 1963-70, 1972-75, 1979	Salem Creek	1981
Firesteel River	1954-64	Salmon River	1976-80
Furnace Creek	1963-70	Shelter Valley Creek	1978-82, 1984-87
Huron River	1954, 1963-65	Sterling Creek	1982, 1986-87
Iron River	1954-61, 1963-72, 1976-79, 1981-86	Sterling Valley River	1982-87
Little Carp River	1985	Wilmot Creek	1976-87
Little Gravel River	1980-81		
Mackenzie River	1980		
Middle River	1960-62, 1967, 1984-86		
Miners River	1963-64, 1966-68, 1970, 1981-85	LAKE HURON	YEARS SAMPLED
Misery River	1960-62, 1967-69, 1986-87	Albany Creek	1986-87
Pancake River	1980-83	Au Sable River	1986-87
Rock River	1963-70, 1981-87	Beaver River	1981
Sable River	1980-81, 1984	Blue Jay Creek	1967-77, 1980-81, 1984
Silver River	1954-61, 1963-79, 1987	Cheboygan River	1977-87
Stokely Creek	1981-85	East Au Gres River	1985-87
Sturgeon River	1962-68	Echo River	1980-82, 1987
Sucker River	1954-61, 1963-79, 1981-85	Kaskawong River	1967-77, 1980-87
Tahquamenon River	1981-87	Mindemoya River	1984
Two Hearted River	1955, 1963-79	Naiscoot-Harris River	1967-77
White River	1956-60	Ocqueoc River	1949-55, 1957, 1959-79, 1981-82
			1984-87
LAKE ONTARIO	YEARS SAMPLED	Silver Creek	1981
Bowmanville Creek	1976-87	Still River	1967-77, 1987
Bronte Creek	1980	Sucker Creek	1981
Catfish Creek	1981-85	Thessalon River	1981-87
Credit River	1980	Thunder Bay River	1986
		Tittabawassee River	1985
		Trout River	1981-82

were established to encompass major changes in the control strategy and may reflect relative differences in lamprey abundance. In Lake Ontario, electrical barriers were never used; therefore, only two "periods" were identified: a) pre-chemical control (pre-1971), and b) after the initiation of control (1971 to present). An analysis of variance (ANOVA) was performed to examine the possible effect of different control strategies ("periods") on the weight and proportion of male spawning sea lamprey.

Pearson correlation analysis was used to examine the correlations between sea lamprey weight and sea lamprey abundance, salmonid stocking, or salmonid catch. Pearson correlation analysis was also used to examine correlations between percent males

and sea lamprey abundance, salmonid stocking, or salmonid catch. We then used multiple regression to determine which of sea lamprey abundance, salmonid stocking, and salmonid catch had the greatest influence on sea lamprey weight or percent males (Snedecor and Cochran 1967).

RESULTS

Lake Superior

The data for Lake Superior, collected from 1953-1987, provided 35 y of continuous measurements of length and percent males in the sea lamprey spawning run. Weights were not measured in 1953. The proportion of males in the population

appeared to have changed through time in a cyclical pattern (Fig. 1), varying between 29 and 60% males. On the other hand, it appears that there was an initial decline in the length and weight of lamprey through to 1960 (from 460 to 430 mm and from 225 to 175 g), followed by cycling about some mean value (weight 172 ± 18 g; length 429 ± 12 mm). The autocorrelation analysis, indicated that a significant ($P < 0.05$) trend was present in length, weight, and proportion of males (Table 2). Regression analysis indicated that there was no significant trend in length and weight; however, there was a significant decrease in the proportion of males in the population ($b = -0.94$; $P < 0.05$).

Length and weight of sea lamprey were significantly correlated ($P < 0.05$); therefore, only weight was used in further analyses of change in sea lamprey size. ANOVA indicated a significant effect of treatment "period" on the weight of lamprey ($F = 7.1$, $P < 0.05$) but not on the proportion of males ($F = 2.8$, $P > 0.05$).

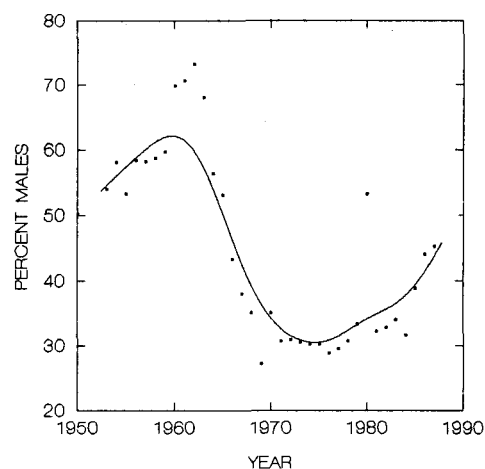
In the early 1950s, weights of sea lamprey declined dramatically as did the commercial catch of salmonids (Fig. 2b) and the total number of sea lamprey captured at the eight electrical barriers (Fig. 2a). After this decline in the 1950s, lamprey weight increased (Fig. 1). This increase in weight appeared to follow the increase in salmonid stocking in this lake (Fig. 2c). Pearson correlation analysis indicated that there was a significant correlation between weight of sea lamprey and commercial catch of salmonids ($r = 0.64$, $P < 0.05$). The proportion of males in the sea lamprey population, however, was apparently lower at higher salmonid stocking rates ($r = -0.76$, $P < 0.05$) and higher when abundance of sea lamprey was greater ($r = 0.63$, $P < 0.05$).

Multiple regression using sea lamprey abundance, salmonid stocking, and salmonid catch indicated that sea lamprey weight was significantly ($P < 0.05$) related to salmonid catch. The proportion of males was significantly related to both commercial catch of salmonids and salmonid stocking. Abundance of sea lamprey, as indicated by catches at the electrical barriers, was not related to sea lamprey weight or proportion of males.

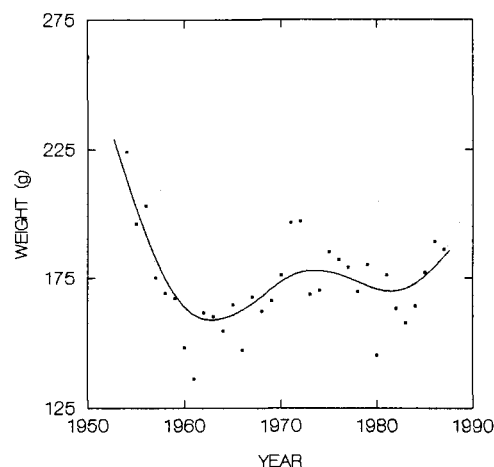
Lake Huron

Although a trap was operating on the Ocqueoc River in 1948, sea lamprey were not sexed or measured until 1950 (38 y of data) or weighed until 1951 (37 y of data). Data for sea lamprey popula-

A.



B.



C.

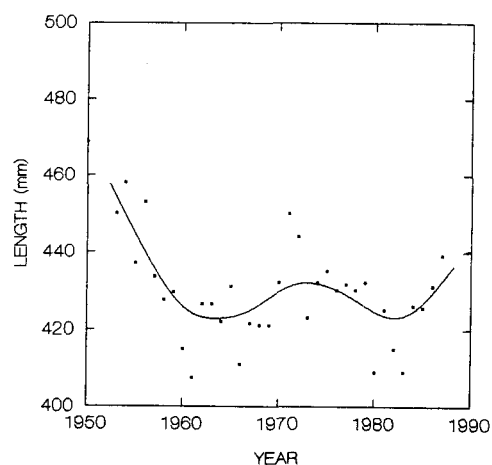


FIG. 1: Size and percent male sea lamprey in Lake Superior, 1953 to present. Smoothed line estimated using Distance Weighted Least Squares (DWLS) technique (see text). A. proportion of males; B. mean weight (g) of sea lamprey; C. mean length (mm) of sea lamprey.

TABLE 2. Summary of results from statistical analyses of data from three Great Lakes. (n/s = not significant at $P = 0.05$)

Statistical Test/ Variable	Lake Superior		Lake Huron		Lake Ontario	
	weight	% ♂	weight	% ♂	weight	% ♂
Autocorrelation (trend?)	+	+	+	+	+	n/s
Linear Regression (trend?)	+	n/s	+	+	+	n/s
ANOVA (treatment "periods")	+	n/s	+	+	+	n/s
Multiple Regression						
salmonid catch	+	+	n/s	n/s	n/s	n/s
salmonid stock	n/s	+	+	+	+	n/s
S/L abundance	n/s	n/s	n/s	n/s	n/s	n/s

tions from other streams were not available until 1967. There was an apparent steady decline in the proportion of male sea lamprey in Lake Huron (Fig. 3) until the early 1980s. Length and weight appeared fairly stable (413 ± 8 mm, 141 ± 8 g) through the 1950s, then began steadily increasing after 1960. Autocorrelation analysis (Table 2) indicated a significant trend in length, weight, and sex ratio of sea lamprey. Linear regression indicated that there was a significant decrease in the proportion of males ($b = 0.89$, $P < 0.05$) and increase in weight ($b = 2.85$, $P < 0.05$) and length ($b = 1.93$, $P < 0.05$) since the 1950s.

There was a significant difference among the three "periods" in both weight ($F = 9.8$, $P < 0.05$) and percent males ($F = 13$, $P < 0.05$). Weights of sea lamprey were initially low (131 g) while sea lamprey were apparently abundant and commercial catch of salmonids was high (Figs. 4a and 4b). After the initiation of chemical control in 1957–58, sea lamprey declined in the Ocqueoc River. Salmonid stocking was initiated in 1968; sea lamprey weight increased after this time as did salmonid stocking and catches (Fig. 4c).

Pearson correlation analysis indicated that sea lamprey were smaller when their abundance was greater ($r = 0.54$, $P < 0.05$) and lamprey weight was greater when salmonid stocking was higher ($r = 0.71$, $P < 0.05$). The proportion of males was higher at higher abundance of sea lamprey ($r = 0.64$, $P < 0.05$). The proportion of males in the sea lamprey population also decreased when salmonid stocking increased ($r = -0.66$, $P < 0.05$). Multiple regression analysis indicated that salmonid stocking and significantly related to both weight and

proportion of male sea lamprey in Lake Huron. There was, however, no significant relation between weight or proportion of males with abundance of sea lamprey.

Lake Ontario

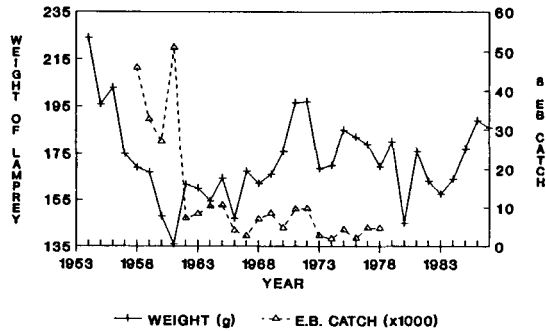
Sampling in Lake Ontario began in 1968, providing 20 y of data (Fig. 5). Lengths and weights of sea lamprey steadily increased until the early 1980s. The proportion of males increased gradually from a somewhat equal sex ratio to a slight preponderance (~60%) of males. The autocorrelation analysis indicated a significant trend in length and weight. However, autocorrelation analysis indicated that there was no strong trend in the proportion of males in the population (Table 2). Regression analysis also indicated no significant change in percent males ($b = 0.402$, $P < 0.05$) over time. Both weight ($b = 6.348$, $P < 0.05$) and length ($b = 4.554$, $P < 0.05$) increased from 1968 to present.

ANOVA indicated that there were significant differences in weight ($F = 11.6$, $P < 0.05$) between treatment "periods" but not in the sex ratio ($F = 2.3$, $P < 0.05$). Sea lamprey in Lake Ontario were initially small (415 mm, 150 g). After the initiation of chemical control in 1971, weight generally increased. At the same time, the stocking rate of salmonids increased (Fig. 6c). It appears that sea lamprey abundance may be cycling but this may be an artifact of changes in trapping methodology.

Pearson correlation analysis indicated that sea lamprey weight increased when stocking salmonids increased ($r = 0.74$, $P < 0.05$). There was no sig-

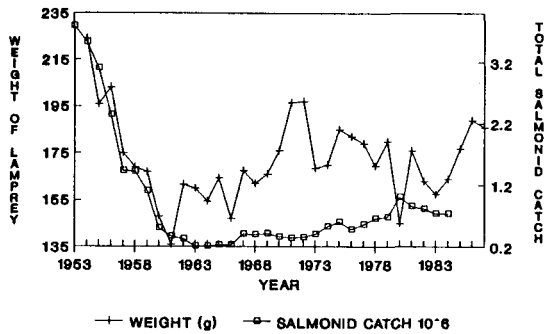
LAKE SUPERIOR DATA

a.



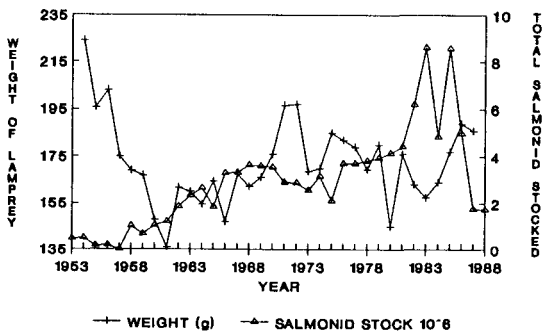
$R = -0.423$
 $P > 0.05$

b.



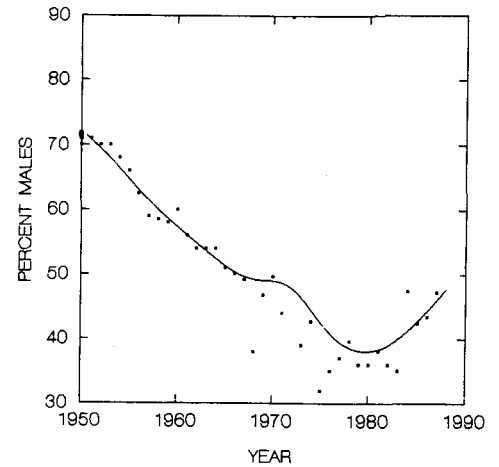
$R = 0.637$
 $P > 0.05$

c.

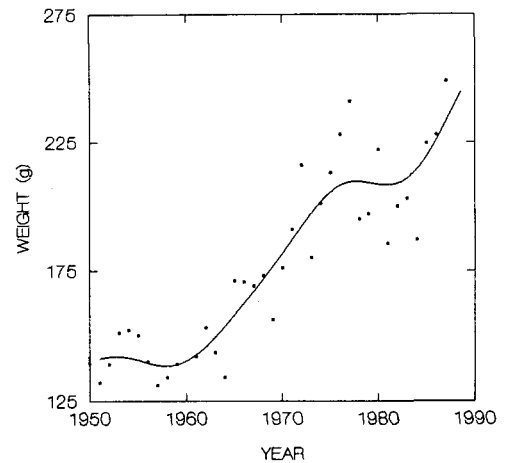


$R = -0.284$
 $P > 0.05$

A.



B.



C.

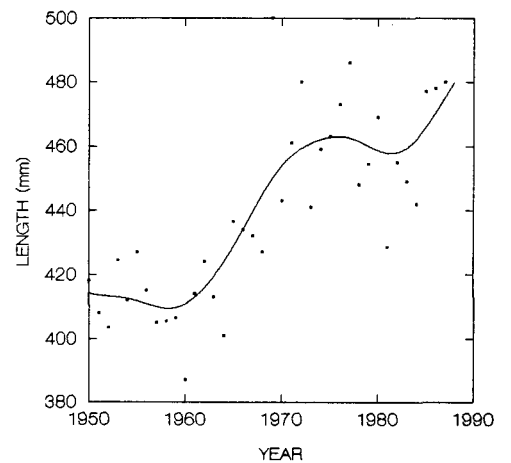


FIG. 2: Size (weight) of sea lamprey in relation to (a) relative abundance of sea lamprey as measured at eight electrical barriers; (b) total salmonid commercial catch; and (c) total salmonids stocked in Lake Superior.

FIG. 3: Size and percent male sea lamprey in Lake Huron, 1950 to present. Smoothed line estimated using DWLS technique. A. proportion of males; B. mean weight (g) of sea lamprey; C. mean length (mm) of sea lamprey.

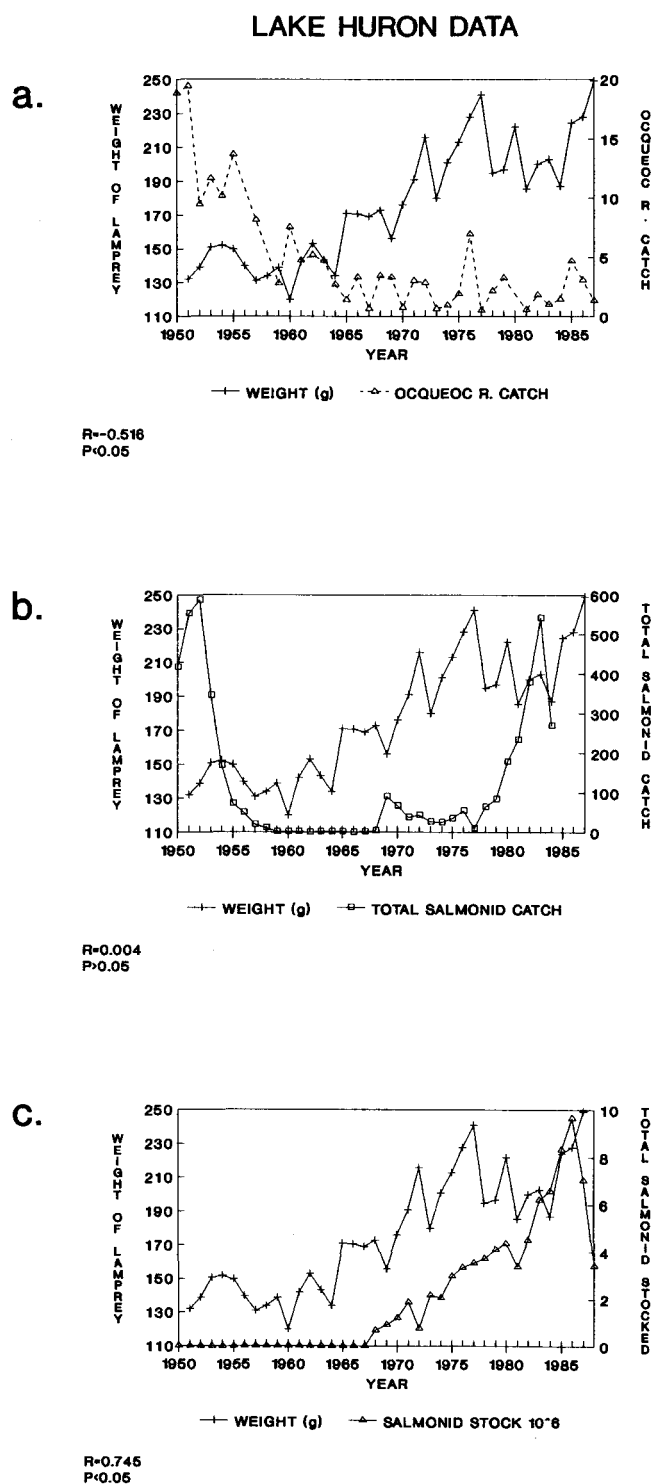
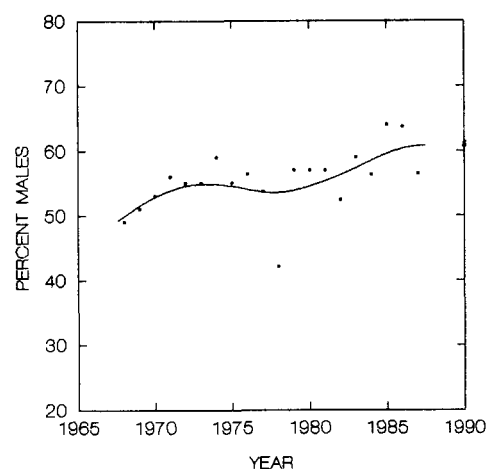
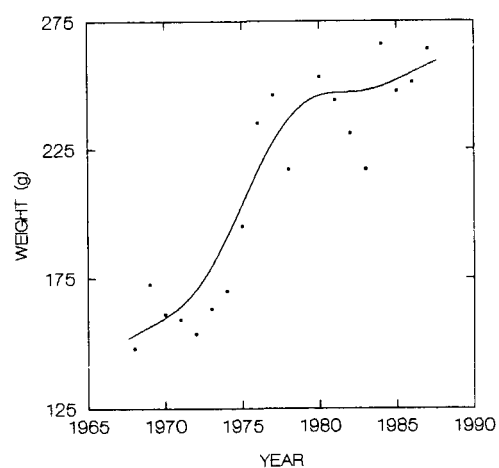


FIG. 4: Size (weight) of sea lamprey in relation to (a) relative abundance of sea lamprey as indicated by the Ocqueoc River catch of spawners; (b) total salmonid commercial catch; and (c) total salmonids stocked in Lake Huron.

A.



B.



C.

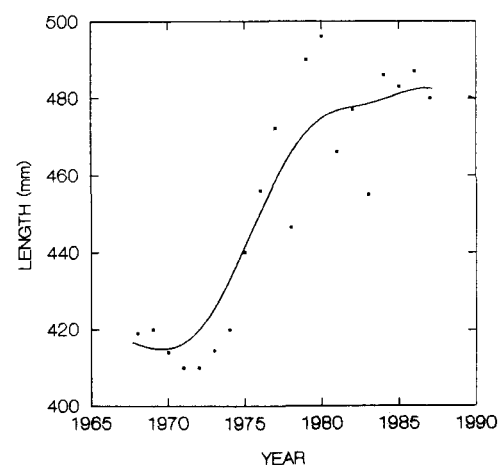
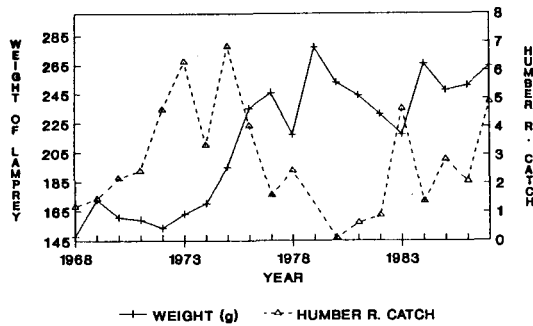


FIG. 5: Size and percent male sea lamprey in Lake Ontario, 1968 to present. Smoothed line estimated using DWLS technique. A. proportion of males; B. mean weight (g) of sea lamprey; C. mean length (mm) of sea lamprey.

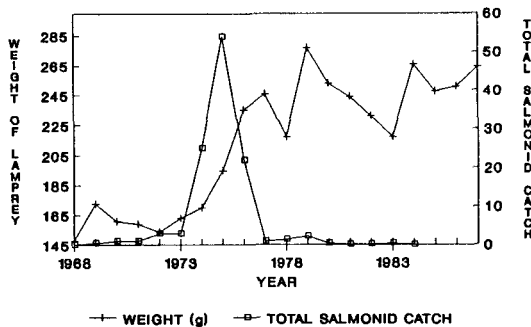
LAKE ONTARIO DATA

a.



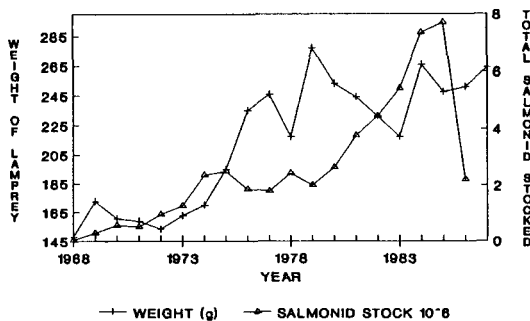
$R = -0.262$
 $P > 0.05$

b.



$R = -0.105$
 $P > 0.05$

c.



$R = 0.846$
 $P < 0.05$

FIG. 6: Size (weight) of sea lamprey in relation to (a) relative abundance of sea lamprey as indicated by the Humber River catch of spawners; (b) total salmonid commercial catch; and (c) total salmonids stocked in Lake Ontario.

nificant correlation between the percent males and sea lamprey abundance, salmonid stocking, or salmonid catch. Multiple regression indicated that weight of sea lamprey was significantly related to salmonid stocking only.

DISCUSSION

Odum (1985) suggested that biological parameters (e.g., length, weight, sex ratio) of a species will change in response to changes in population size, prey availability, or external pressures (e.g., control measures, environmental change). However, caution must be exercised as a variety of factors may affect any change(s) taking place. For sea lamprey within the Great Lakes, increased abundance of salmonids, differences in selection by trapping gear, time required by populations to readjust (predator or prey), alterations in environmental quality (see Beeton 1969), habitat alteration, or hydrologic and climatic cycles would affect changes in measured biological characteristics of the population. While we were able to examine the relation between sea lamprey size and sex with surrogates for their abundance and prey availability, we were only able to infer cause-effect.

Smith's (1971) early work (Table 3) examined the sex ratio of sea lamprey in Lake Superior (1953 to 1969) and Lake Huron (1951 to 1969). He found that males predominated in the early 1950s; however, there was a gradual shift to a preponderance of females. Heinrich *et al.* (1980) extended this examination of sex ratio to include data from Lakes Superior and Huron to 1978 and confirmed this shift from males to females. Heinrich *et al.* (1980) suggested that the sex ratio had stabilized at 30 to 40 percent males. Torblaa and Westman (1980) found the same trends in the North Channel of Lake Huron and in Lake Superior. In recent years (after 1980), the number of males has been increasing in Lakes Superior (Fig. 1) and Huron (Fig. 3, Table 3). In both lakes there was a significant relation among proportion of males, abundance of sea lamprey, and also salmonid stocking. The multiple regression, however, indicated that prey availability (as reflected by salmonid stocking in Lake Huron and commercial catch and stocking in Lake Superior) was most strongly related to observed sex ratios.

In Lake Ontario, however, there appeared to be only a slight shift from an approximately equal sex ratio (1970–1980) to a preponderance of males. Salmonid stocking, commercial catches, and sea

TABLE 3. Comparison of results from this study (since 1978) with those of Smith (1971) and Heinrich *et al.* (1980).

Lake	Variable	Smith (1971) to 1969	Heinrich <i>et al.</i> (1980) to 1978	This Study to 1987
Superior	% ♂	1950-53 equal ratio 1953-61 Increasing 1962-69 Decreasing	1971-78 Stable	1979-87 Increasing
	Size	1950's Decreasing	1962-72 Increasing 1973-78 Stable	1979-87 Increasing
Huron	% ♂	1950-52 Increasing 1952-69 Decreasing	1969-78 Stable	1979-87 Increasing
	Size	1950s Decreasing	1951-69 Stable 1969-77 Increasing	1980s Stable/ slight increase
Ontario	% ♂	—	1968-77 Stable	1968 Gradual increase
	Size	—	1968-73 Stable 1974-78 Increasing	1978-87 Stable

lamprey abundance did not appear to be related to the proportion of males in the population (based on ANOVA, Pearson correlation analysis, and multiple regression).

While the change in proportion of male sea lamprey has been pronounced in Lakes Superior and Huron, the causes of the changes are unclear. Hardisty (1971) suggested that, although significant departures from normal (equal?) sex ratios were found, the concept of labile sex determination was not valid for ammocoetes. Torblaa and Westman (1980), Heinrich *et al.* (1980), and Purvis (1979) implied that sex composition was density dependent and influenced by sea lamprey control programs. Our results did not dispute the influence of density reduction upon the proportion of males, but did indicate that prey availability (at least in Lakes Superior and Huron) may be related to the preponderance of males in sea lamprey populations. As the concept of labile sex determination is considered invalid for ammocoetes, the relation of sex ratio with adult sea lamprey density or measures of prey availability may be spurious. On the

other hand, the apparent relations prompt further evaluation of either the phenomenon or of the tenets of sex determination.

Because there was a significant difference in weight between treatment periods (ANOVA, Table 2), the possibility exists that differences resulted from differences in capture technology. However, direction of the change extended over more than one treatment period; therefore, we expect the changes did not result from differences in trapping (or control) technology.

The reason(s) for the trends in lamprey size remain speculative. Sea lamprey entered Lake Huron when food was abundant (i.e., fish stocks were high), natural predators on sea lamprey were likely non-existent, and control measures had not started (Smith 1971). As a result, the early declines in sea lamprey size in Lake Huron in response to control measures was expected (Table 3). By contrast, in Lake Superior, sea lamprey were subject to early pressures of control efforts; therefore, the sea lamprey population was likely held well below its carrying capacity. In addition, the food supply

for sea lamprey in Lake Superior has been replenished by increased salmonid stocking and/or enhanced survival or remnant native lake trout stocks. Finally, in Lake Ontario, it appears that sea lamprey may have been an integral part of the fish community at one time; however, as a result of increasing fishing pressure, food became limited and sea lamprey populations accordingly.

Smith (1971) initially described a decrease in size of sea lamprey from Lakes Huron (Ocqueoc River) and Michigan; he also described a slow decrease in size in sea lamprey from Lake Superior from 1953–1961. Heinrich *et al.* (1980) found that sea lamprey size increased after the initiation of control in each lake and that the sizes had generally stabilized by 1978. We observed that, while length and weight may have stabilized in Lake Superior (Fig. 1), sea lamprey have generally become larger in both Lakes Huron (Fig. 3) and Ontario (Fig. 5).

Smith (1971) suggested that factors other than sea lamprey abundance were influencing sea lamprey size. Heinrich *et al.* (1980) suggested that the increase in size was a result of reduction in sea lamprey numbers due to control, but indicated that stocking of salmonids may also have influenced sea lamprey size in Lake Superior. We found that, in Lakes Ontario and Huron, weight of sea lamprey was most strongly related to stocking rates of salmonids. Kitchell (In press) also found a relation between sea lamprey weight in Lake Michigan and salmonid stocking rates. In Lake Superior, however, sea lamprey weight was most closely related to commercial catch of salmonids. Sea lamprey weight was not significantly related to their abundance in Lakes Superior, Huron, or Ontario. These results generally indicate that prey availability, whether governed by increased stocking rates (Lakes Huron, Ontario, and Michigan) or recovery of remnant lake trout stocks (Lake Superior), was extremely important in determining sea lamprey weight and sex ratio.

The management implications of trend analyses of sea lamprey size and sex data (Table 3) are somewhat unclear. An apparent increase in mean size of sea lamprey may simply mean that more food is available through either increased prey abundance or decreased numbers of sea lamprey. As a result, the different trends identified by, particularly, Smith (1971), Heinrich *et al.* (1980), and ourselves reflect the response of sea lamprey populations to the management efforts prevalent during the respective periods of investigation. Apparently, control activities elicited early responses in both

sex composition and size of sea lamprey. Recently, enhanced salmonid stocks (and stocking) appear to more strongly influence the biological characteristics of sea lamprey populations, particularly in Lakes Superior and Huron. The possible increase in fecundity resulting from increased size of sea lamprey (Wigley 1959) could offset benefits accrued from sea lamprey management. Although factors responsible for changes in sea lamprey size or sex ratios may be unclear, these measures may still be useful indicators of the net benefits of both fishery management and sea lamprey control.

ACKNOWLEDGMENTS

We are deeply indebted to the Sea Lamprey Control Agents and the Great Lakes Fishery Commission for providing the data; their willing cooperation was most welcome. We are also grateful to R. J. Young and C. K. Minns for their advice on the statistical analysis and we thank G. Christie for his assistance with summarizing the salmonid stocking data. R. J. Young, C. K. Minns, and G. Christie made constructive comments on earlier drafts of the manuscript.

REFERENCES

- Applegate, V. C. 1950. *Natural history of the sea lamprey*. U.S. Dept. of Int. Fish & Wildl. Serv. Spec. Sci. Rep. Fish. 55.
- Baldwin, N. S., Saafeld, R. W., Ross, M. A., and Buettner, H. J. 1979. *Commercial fish production in the Great Lakes 1967–1977*. Great Lakes Fish. Comm. Tech. Rept. 3.
- Beamish, F. W. H. 1979. Migration and spawning energetics of the anadromous sea lamprey, *Petromyzon marinus*. *Environ. Biol. Fishes* 4:3–7.
- Beeton, A. M. 1969. Changes in the environment and biota of the Great Lakes. In *Eutrophication: causes, consequences, correctives*, pp. 150–187. Proceedings of Symposium. Nat. Acad. Sci. Washington, D.C.
- Christie, W. J., Scott, K. A., Sly, P. G., and Strus, R. H. 1987. Recent changes in the aquatic food web of eastern Lake Ontario. *Can. J. Fish. Aquat. Sci.* 44 (Suppl. 2):37–52.
- Collins, J. S. 1988. Changes in the North Channel fish community, with emphasis on pink salmon (*Oncorhynchus gorbuscha* Walbaum). *Hydrobiologia* 163:195–213.
- Great Lakes Fishery Commission. 1978. *Annual Report*. Great Lakes Fish. Comm. Ann Arbor, MI.
- . 1979. *Annual Report*. Great Lakes Fish. Comm. Ann Arbor, MI.
- . 1980. *Annual Report*. Great Lakes Fish. Comm. Ann Arbor, MI.

- _____. 1981. *Annual Report*. Great Lakes Fish. Comm. Ann Arbor, MI.
- _____. 1982. *Annual Report*. Great Lakes Fish. Comm. Ann Arbor, MI.
- _____. 1983. *Annual Report*. Great Lakes Fish. Comm. Ann Arbor, MI.
- Hardisty, M. W. 1971. Gonadogenesis, sex differentiation and gametogenesis. In *The Biology of lampreys*, ed. M. W. Hardisty and I. C. Potter, pp. 295-360. Volume 1. London: Academic Press.
- Heinrich, J. W., Weise, J. G., and Smith, B. R. 1980. Changes in biological characteristics of sea lamprey (*Petromyzon marinus*) as related to lamprey abundance, prey abundance, and sea lamprey control. *Can. J. Fish. Aquat. Sci.* 37:1861-1971.
- Johnson, B. G. H., and Anderson, W. C. 1980. Predatory-phase sea lampreys (*Petromyzon marinus*) in the Great Lakes. *Can. J. Fish. Aquat. Sci.* 37:207-2020.
- Kitchell, J. F. In Press. The scope for mortality caused by sea lamprey. *Trans. Amer. Fish. Soc.*
- Krueger, C. C., Swanson, B. L., and Selgeby, J. H. 1986. Evaluation of hatchery-reared lake trout for reestablishment of populations in the Apostle Island region of Lake Superior, 1960-84. *Fish culture in fisheries management*, ed. R. H. Stroud, pp. 93-107. Bethesda, MD: Amer. Fish. Soc.
- MacCallum, W. R., and Selgeby, J. H. 1987. Lake Superior revisited 1984. *Can. J. Fish. Aquat. Sci.* 44 (Suppl. 2): 23-36.
- Manion, P. J. 1972. Fecundity of the sea lamprey (*Petromyzon marinus*) in Lake Superior. *Trans. Am. Fish. Soc.* 4:718-720.
- Odum, E. P. 1985. Trends expected in stressed ecosystems. *Biosci.* 35:419-422.
- Pearce, W. A., Braem, R. A., Dustin, A. M., and Tibbles, J. J. 1980. Sea lamprey (*Petromyzon marinus*) in the Lower Great Lakes. *Can. J. Fish. Aquat. Sci.* 37:1802-1810.
- Purvis, H. A. 1979. *Variations in growth, age at transformation, and sex ratio of sea lampreys reestablished in chemically treated tributaries of the Upper Great Lakes*. Great Lakes Fish. Comm. Tech. Rept. 35.
- Smith, B. R. 1971. Sea lampreys in the Great Lakes of North America. In *The biology of lampreys*, ed. M. W. Hardisty and I. C. Potter, p. 207-247. Volume 1. London: Academic Press.
- _____, and Tibbles, J. J. 1980. Sea Lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936-78. *Can. J. Fish. Aquat. Sci.* 37:1780-1801.
- Snedecor, G. W., and Cochran, W. G. 1967. *Statistical methods*. Sixth Edition. Ames, Iowa: The Iowa State Press.
- Steel, R. G. D., and Torrie, J. H. 1960. *Principles and procedures of statistics*. New York: McGraw-Hill Book Company, Inc.
- Torblaa, R. L., and Westman, R. W. 1980. Ecological impacts of lampricide treatments on sea lamprey (*petromyzon marinus*) ammocoetes and metamorphosed individuals. *Can. J. Fish. Aquat. Sci.* 37:1835-1850.
- Vladikov, V. D. 1951. Fecundity of Quebec lampreys. *Can. Fish-Cult.* 10:1-14.
- Weise, J. G., and Rugen, P. C. 1987. Evaluation methods and population studies of larval phase sea lamprey. Section A. In *Workshop to evaluate sea lamprey populations "WESLP": Background papers and proceedings of the August 1985 Workshop*, B. G. H. Johnson (ed.). Great Lakes Fish. Comm. Special Publ. 87-2.
- Wigley, R. L. 1959. Life history of the sea lamprey of Cayuga Lake, New York. *U.S. Fish Wildl. Serv. Bull.* 154 (59):561-617.
- Wilkinson, L. 1988. *Systat: the system for statistics*. Evanston, IL: Systat, Inc.