

Population Biology and Management of Lake Champlain Walleye



**Lake Champlain
Basin Program**

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Lake Champlain Basin Program Technical Reports

1. *A Research and Monitoring Agenda for Lake Champlain.* Proceedings of a Workshop, December 17-19, 1991, Burlington, VT. Lake Champlain Research Consortium. May, 1992.
2. *Design and Initial Implementation of a Comprehensive Agricultural Monitoring and Evaluation Network for the Lake Champlain Basin.* NY-VT Strategic Core Group. February, 1993.
3. (A) *GIS Management Plan for the Lake Champlain Basin Program.* Vermont Center for Geographic Information, Inc., and Associates in Rural Development. March, 1993.

(B) *Handbook of GIS Standards and Procedures for the Lake Champlain Basin Program.* Vermont Center for Geographic Information, Inc. March, 1993.

(C) *GIS Data Inventory for the Lake Champlain Basin Program.* Vermont Center for Geographic Information, Inc. March, 1993.
4. (A) *Lake Champlain Economic Database Project. Executive Summary.* Holmes & Associates. March 1993.

(B) *Socio-Economic Profile, Database, and Description of the Tourism Economy for the Lake Champlain Basin.* Holmes & Associates. March 1993

(C) *Potential Applications of Economic Instruments for Environmental Protection in the Lake Champlain Basin.* Anthony Artuso. March 1993.

(D) *Conceptual Framework for Evaluation of Pollution Control Strategies and Water Quality Standards for Lake Champlain.* Anthony Artuso. March 1993.
5. *Lake Champlain Sediment Toxics Assessment Program. An Assessment of Sediment - Associated Contaminants in Lake Champlain - Phase 1.* Alan McIntosh, Editor, UVM School of Natural Resources. February 1994.

Lake Champlain Sediment Toxics Assessment Program. An Assessment of Sediment - Associated Contaminants in Lake Champlain - Phase 1. Executive Summary. Alan McIntosh, Editor, UVM School of Natural Resources. February 1994.
6. (A) *Lake Champlain Nonpoint Source Pollution Assessment.* Lenore Budd, Associates in Rural Development Inc. and Donald Meals, UVM School of Natural Resources. February 1994.

(B) *Lake Champlain Nonpoint Source Pollution Assessment. Appendices A-J.* Lenore Budd, Associates in Rural Development Inc. and Donald Meals, UVM School of Natural Resources. February 1994.

7. *Internal Phosphorus Loading Studies of St. Albans Bay. Executive Summary.* VT Dept of Environmental Conservation. March 1994.

(A) *Dynamic Mass Balance Model of Internal Phosphorus Loading in St. Albans Bay, Lake Champlain.* Eric Smeltzer, Neil Kamman, Karen Hyde and John C. Drake. March 1994.

(B) *History of Phosphorus Loading to St. Albans Bay, 1850 - 1990.* Karen Hyde, Neil Kamman and Eric Smeltzer. March 1994.

(C) *Assessment of Sediment Phosphorus Distribution and Long-Term Recycling in St. Albans Bay, Lake Champlain.* Scott Martin, Youngstown State University. March 1994.
8. *Lake Champlain Wetlands Acquisition Study.* Jon Binhammer, VT Nature Conservancy. June 1994.
9. *A Study of the Feasibility of Restoring Lake Sturgeon to Lake Champlain.* Deborah A. Moreau and Donna L. Parrish, VT Cooperative Fish & Wildlife Research Unit, University of Vermont. June 1994.
10. *Population Biology and Management of Lake Champlain Walleye.* Kathleen L. Newbrough, Donna L. Parrish, and Matthew G. Mitro, Fish & Wildlife Research Unit, University of Vermont. June 1994.

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APPENDIX A.

**LEGAL AND INSTITUTIONAL FRAMEWORK
GOVERNING ENVIRONMENTAL AND RELATED ACTIVITIES
IN THE LAKE CHAMPLAIN BASIN**

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Project Summary

The status of Lake Champlain walleye populations is of major concern to both anglers and fisheries biologists. Our objective in this project was to summarize data collected on Lake Champlain walleye from 1983 to 1992 and review recent literature to guide future assessment and research efforts.

From 1983 to 1992, 21,916 walleye were sampled during spring spawning in Lake Champlain and its adjacent tributaries. Based on length-at-age data, individual growth of spawning walleye was intermediate to that of walleye in other large lakes and we found no indication of particularly strong or weak cohorts.

Estimates of spawning population size and annual survival were calculated for Great Chazy River, South Bay and Poultney River walleye. Spawning population estimates for South Bay ranged from 161,292 to 323,186, for the Great Chazy River, from 1,990 to 7,457, and for the Poultney River from 2,703 to 11,160. Annual survival estimates varied from 0.48 to 1.0 for South Bay, from 0.23 to 0.94 for Great Chazy River, and from 0.05 to 0.78 for Poultney River spawning walleye. No data on survival to spawning age are available.

Spawning walleye tagged in South Bay and the Poultney River showed seasonal movements, moving northward through August, returning south during September-November and congregating near the spawning area from December to March. Great Chazy River walleye may disperse south toward the main lake after spawning.

Harvest rates (number harvested per hour) in daytime summer and winter creel surveys ranged from 0.00 to 0.08. Catch rates of anglers targeting walleye in spring 1991 ranged from 0.04 (Missisquoi River) to 0.22 (Winooski River) and harvest rates ranged from 0.03 (Missisquoi River) to 0.14 (Winooski River). From 1971 to 1991, springtime angling effort appeared to decrease on the Missisquoi River, harvest rates decreased on the Winooski River and harvest rates on the Lamoille and Missisquoi rivers and Otter Creek appeared stable. Opening day harvest rates of South Bay walleye anglers declined from 0.138 in 1984 to 0.045 in 1986. Mean total

length of walleye captured by diary cooperators from 1984 to 1991 increased in lake Zones 1,2 and 3. Nighttime harvest rates of diary cooperators appeared stable and exceeded 0.20 in the majority of years in Zones 2 and 4, however, there was a significant negative trend in daytime harvest rates in Zones 2 and 3.

Sea lamprey wounding rates on spawning walleye ranged from 0% to 42%; few fish exhibited multiple wounds. Females had higher wounding rates than males, and walleye from South Bay and the Poultney River appeared to have higher wounding rates than fish from more northern populations. Maximum lymphocystis infection rate was 19% of Great Chazy females.

Since 1986, over 12 million walleye fry have been stocked into Lake Champlain. Based on limited information, Lake Champlain adult walleye appear to forage primarily on rainbow smelt. Little information on the effects of pollutants on walleye was available, but we included a summary of materials potentially toxic to aquatic organisms found in the Lake Champlain basin.

We recommend increased monitoring and assessment of all walleye life stages, and increased research efforts to address recruitment, species interactions and stocking effectiveness. Based on available data, we can not recommend measures of success or changes in angling regulations to the management agencies.

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Introduction

Walleye (Stizostedion vitreum vitreum) have been an important sport fish species in Lake Champlain for more than 100 years (Halnon 1963) and the current status of Lake Champlain walleye populations is of major concern to both anglers and fisheries biologists. During recent years, anglers have reported perceived declines in walleye catch rates throughout the lake, but the information necessary to effectively managed Lake Champlain walleye has not been available. To complicate matters, recent changes in other species, e.g. increased salmonid stocking, anticipated declines in sea lamprey abundance, and invasion of exotics such as white perch (Morone americana) and zebra mussels (Dreissena polymorpha), could have significant effects on walleye. Piscivorous walleye may be in an unstable predator-prey relationship in Lake Champlain.

Although New York and Vermont biologists have routinely sampled walleye populations in recent years, the data have not been thoroughly summarized since 1983 (LaBar and Parren 1983). This document summarizes data collected on Lake Champlain walleye from 1983 to 1992. Our objective in this project was to use the data summary and a review of recent literature to provide management agencies with a guide for future assessment and research efforts. We developed this project as follows:

1. Detailed the biological information (age and growth, sexual maturity, spawning dates and locations, recruitment, survival rates, population sizes, harvest, genetic characterization, food habits, sea lamprey wounding rates, parasites and diseases) on Lake Champlain walleye by stock, (i.e., Missisquoi, Lamoille River, Great Chazy River, Winooski River, Poultney River and South Bay stocks) and compared this information to that in the scientific literature concerning walleye in other large lakes.
2. Compiled available information by stock, bringing the 1983 data summary up to date and including sport and commercial fishing regulations, stocking summaries, data collection efforts,

habitat alterations, spawning stream discharges during egg and larval stages, effects of sewage treatment discharges on water quality and heavy metal and pesticide information.

3. Recommended potential research and management strategies for obtaining the information needed to continue developing a Lake Champlain walleye management plan.

Taxonomy

Stizostedion ("pungent throat") vitreum ("glassy") vitreum Mitchill, is known by many common names, including walleye (used in this report), pickerel, yellow pickerel, yellow pike, yellow pike perch, walleye pike, wall-eyed pike, wall-eyed pike perch, and wall-eyed pickerel (Scott and Crossman 1990). The walleye is the largest member of the Percidae family (order Perciformes) in North America, averaging 330 - 508 mm (Scott and Crossman 1990). Walleye are known to hybridize with sauger (Stizostedion canadense) and blue pike (Stizostedion vitreum glaucom), although bluepike are now considered extinct (Festa et al. 1987).

Distribution

The walleye's native range is limited to the fresh waters of North America, with rare occurrences in brackish water (Scott and Crossman 1990). Its range extends from the Arctic circle near the Mackenzie River, Northwest Territories southeast along the southern shore of Hudson Bay to the St. Lawrence River and southward to the gulf coast of Alabama. Native North American walleye populations are generally found east of the Rocky Mountains and west of the Appalachian Mountains, but introduced populations are common in western reservoirs and along the Atlantic coast (Colby et al. 1979). The walleye shows a preference for large, semi-turbid lakes throughout the northern boreal and central and southern hardwood forests (Colby et al. 1979) and is native to Lake Champlain (Festa et al. 1987).

Lake Champlain

Lake Champlain extends 170 km (106 miles) from the Hudson-Champlain canal near Whitehall, New York to its outlet near Rouses Point, New York. The lake's political boundaries are formed by the states of New York and Vermont and the province of Quebec. Lake Champlain has a surface area (including numerous islands) of 1269 km² and a volume of 2.58×10^{10} m³ (Fisher 1968). At its widest point, Lake Champlain is 20.2 km across, mean width is 6.61 km, maximum depth is 122 m and mean depth is 19.4 m (Myer and Gruendling 1979). The lake basin has a generally parabolic shape with 50 percent of the water above 19.4 m, but many areas are deep, cold, and near-oligotrophic (Myer and Gruendling 1979). The major tributaries draining the 19,881 km² watershed are the Great Chazy, Saranac, AuSable, Bouquet, Missisquoi, Lamoille, Winooski, and Poultney rivers and Otter Creek (Fisher 1968) (Figure 1a).

Data Collection

Data collection efforts prior to 1983 are summarized in LaBar and Parren (1983). Since 1983, New York and Vermont fisheries personnel have conducted tagging operations in South Bay, Missisquoi Bay and several Lake Champlain tributaries (Table 1).

Creel surveys were conducted by the Vermont Department of Fish and Wildlife (VTF&W) during the summers of 1985 - 1987 and 1990 - 1992, during the spring of 1991, and during the winters of 1991 and 1992. In addition, between 18 and 46 walleye anglers have contributed angling diaries since 1984. Harvest information collected from creel surveys and the diary cooperators program was organized according to the five Lake Champlain management zones established by VTF&W and NYDEC (Figure 1b.) From 1984 to 1986, the success of South Bay anglers was monitored on the opening day of walleye season by the New York Department of Environmental Conservation (NYDEC) (Nashett 1986).

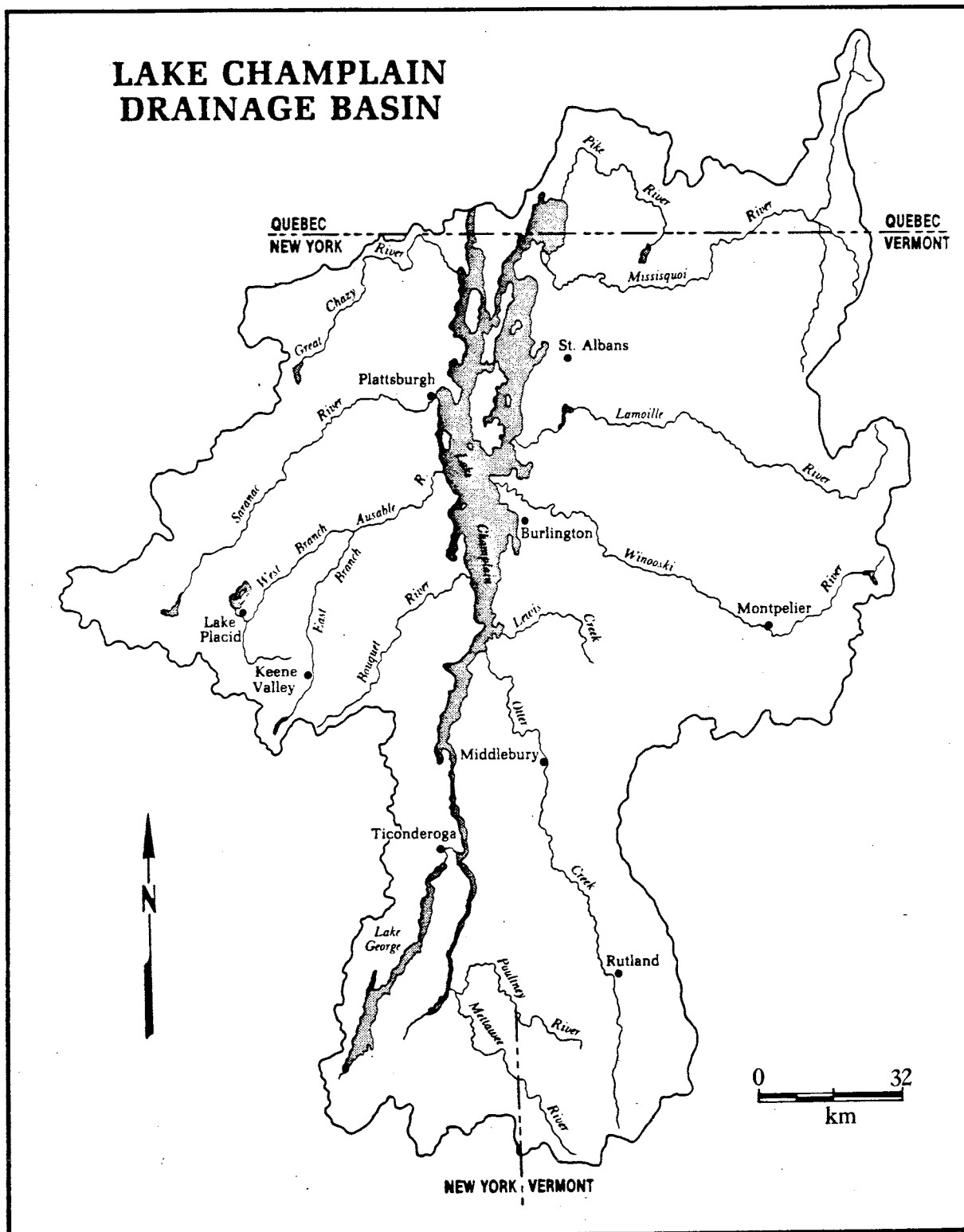


Figure 1a. Lake Champlain drainage basin (adapted from Verstaag 1987).

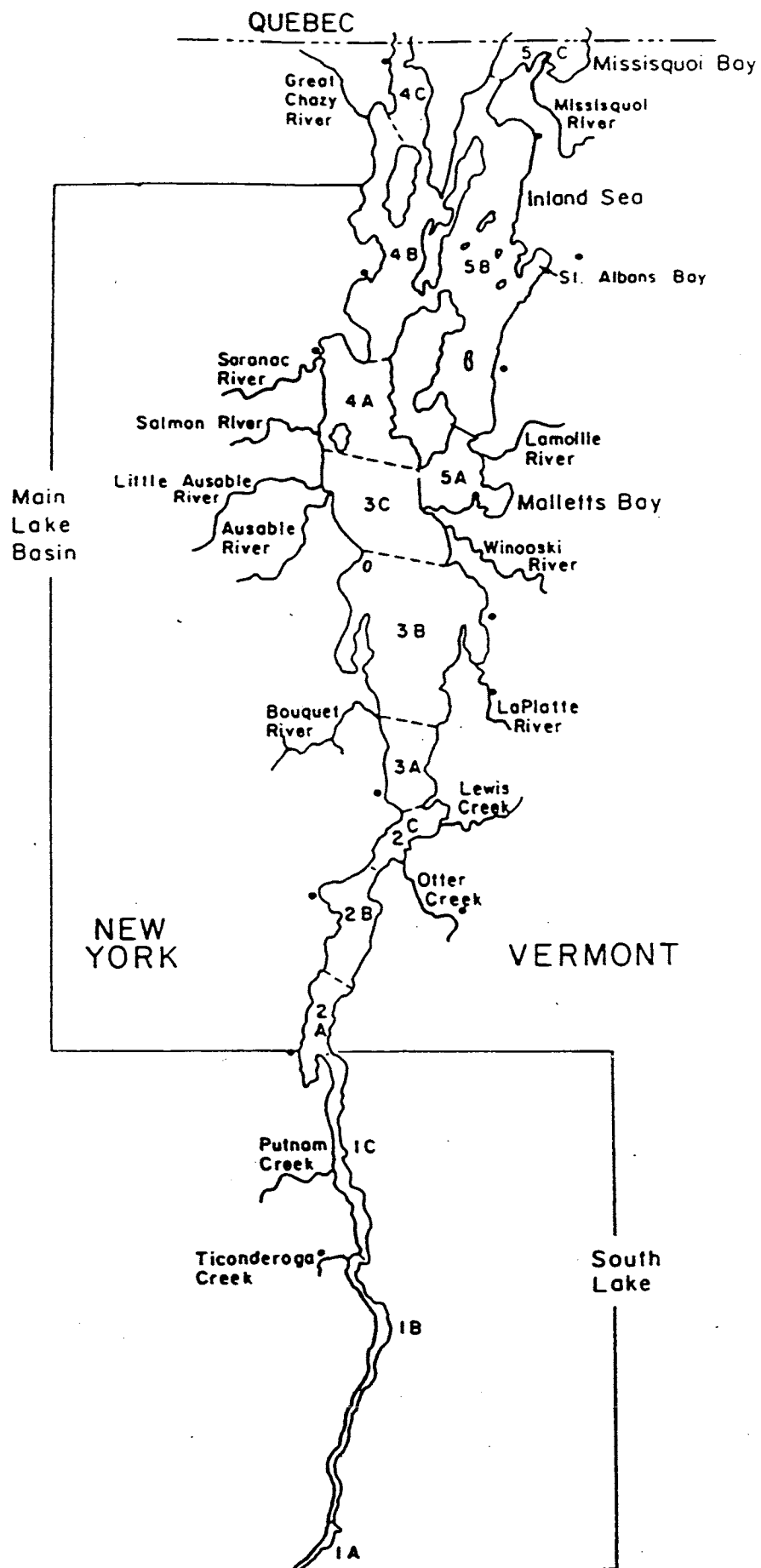


Figure 1b. Five Lake Champlain management zones established by VTF&W and NYDEC.

Table 1. Lake Champlain walleye populations sampled from 1983 to 1992 by New York Department of Environmental Conservation and Vermont Department of Fish and Wildlife.

Area	Year	Sampling Gear	Sampling Dates	Number Captured	Number Aged
South Bay	1983	Electrofishing	4/9;4/11	190	173
	1983	Trap Net	4/7 - 4/10	1235	1215
	1984	Electrofishing	4/10	32	32
	1984	Trap Net	4/10 - 4/16	3046	2373
	1985	Trap Net	4/2 - 4/9	3168	0
	1986	Trap Net	4/4 - 4/18	3314	118
	1987	Trap Net	4/8 - 4/21	3879	0
Great Chazy River	1983	Electrofishing	4/12 - 4/14;4/18 - 4/21	379	349
	1984	Electrofishing	4/23 - 4/26; 5/1 - 5/2	176	149
	1985	Electrofishing	4/15 - 4/17;4/22 - 4/24	498	222
	1986	Electrofishing	4/21 - 4/24	207	121
	1988	Electrofishing	4/8;4/9;4/10;4/11;4/12; 4/13;4/14	429	0
	1989	Electrofishing	4/10;4/11;4/12;4/13; 4/14;4/15;4/16;4/17; 4/18;4/19;4/20;	540	0
Lamoille River	1989	Electrofishing	4/17 - 4/19;4/21;4/24	162	153
	1990	Electrofishing	4/11;4/18;4/24;4/27; 4/30;5/2	301	299
	1991	Electrofishing	4/15 - 4/16	330	0
	1992	Electrofishing	4/20;4/28 - 4/29	410	0
Missisquoi River	1991	Electrofishing	4/15	181	0
	1992	Electrofishing	4/29	169	0

Table 1 (continued)

Area	Year	Sampling Gear	Sampling Dates	Number Captured	Number Aged
Missisquoi Bay	1985	Seine	4/10;4/13;4/15 - 4/19;	452	445
			4/22 - 4/26; 4/29 -		
			5/3;5/6 - 5/9		
	1986	Seine	4/14 -4/22;4/24 - 4/25;	436	427
			4/27 - 5/1;5/4 - 5/9		
	1990	Seine	4/14 - 4/16;4/21 -4/25;4/28 - 4/30; 5/2;5/5-5/9	118	0
Winooski River	1992	Electrofishing	5/1	142	0
Poultney River	1988	Electrofishing	4/6 - 4/8;4/11;4/12	570	0
	1989	Electrofishing	4/4;4/6;4/7;4/10 - 4/13	434	1
	1990	Electrofishing	4/6 - 4/9	549	3
	1991	Electrofishing	4/3;4/5;4/6	638	21
	1992	Electrofishing	4/6;4/8;4/9	650	399

Attempts to collect walleye by trawling have met with limited success (Larry Nashett, NYDEC, and Jon Anderson, VTF&W, personal communication). Currently, the Vermont Cooperative Fish and Wildlife Research Unit is conducting a study funded by the U.S. Fish and Wildlife Service to address walleye recruitment in Lake Champlain. In this study, larval walleye are collected as they leave spawning rivers and attempts have also been made to collect juvenile walleye in the pelagic zone.

Sampling Methods - Spawning Populations

From 1983 to 1992 walleye were sampled during spring spawning (early April to early May) in Lake Champlain and five adjacent tributaries (Table 1). New York Department of Environmental Conservation established 21 sampling sites in South Bay, and two sampling areas in the Great Chazy River. Vermont Department of Fish and Wildlife sampled one site in Missisquoi Bay and the Lamoille, Missisquoi, Poultney and Winooski rivers. Not every site was sampled every year (Table 1).

Three capture methods were used: trap netting, beach seining and electrofishing. Trap net cars 1.8 m deep with 1.9 cm-bar mesh and a 240-volt DC electroshocking boat were used to sample South Bay in 1983 and 1984, but South Bay was sampled only with traps nets from 1985 to 1987. Trap nets were set in 1.5 - 3.4 m of water. Great Chazy River walleye were collected using 240 - 300 volts from a DC electroshocking boat. Missisquoi Bay was sampled with beach seines. All other Vermont sites were electrofished.

Walleye were measured to the nearest mm and most were sexed, tagged (serially numbered jaw or Floy anchor tags) and released. Missisquoi River and Winooski River walleye were not tagged. Fish collected in South Bay and the Great Chazy River in 1983 and 1984 and the Poultney River in 1991 and 1992 were weighed to the nearest gram. A subset of Poultney River walleye were aged with spines, usually the second dorsal (Table 1). Subsets of fish from other locations were aged with scales (Table 1). The presence of sea lamprey wounds was

recorded for all sampled walleye, except those collected from the Poultney River in 1988. Externally visible parasites and diseases were noted at some sites and in some years (Figures 41 - 43).

Data Analysis

Data collected on Lake Champlain walleye from 1983 to 1992 were provided by VTF&W and NYDEC. The majority of the information had been computerized; however, each data base was recorded in a different format. Files were converted to formats compatible with the University of Vermont's mainframe VAX computer on which analyses were done using SAS (SAS Institute Inc. 1988).

In 1983 and 1984, South Bay was sampled with both trap nets and electrofishing gear. Relatively few walleye were obtained by electrofishing: 190 (13% of total) in 1983 and 32 (1% of total) in 1984. Overall mean lengths for each age class, except ages 7 and 8, and sex ratios of walleye collected with these two gears did not differ ($p > 0.05$). Therefore, electrofishing and trap netting samples were pooled for subsequent analyses.

Age and Growth - Spawning Populations

Mean age of female walleye sampled during spawning runs ranged from 6.35 years in the Great Chazy River to 9.81 years in the Poultney River and mean age of male walleye ranged from 4.87 years in the Lamoille River to 8.28 years in the Poultney River (Table 2). Mean age of female walleye was greater than that of male walleye for all stocks except South Bay. The oldest fish were female, except in South Bay 1986 and Poultney River samples.

Growth of individuals can vary markedly among and within bodies of water, as well as among and within cohorts. Individual growth of Lake Champlain walleye, based on length-at-age data, was intermediate to individual growth of two Great Lakes populations and Oneida Lake (Figures 2 - 5). Male walleye from areas in northern Lake Champlain (Great Chazy River, Missisquoi Bay and Lamoille River) appear to be larger and to maintain more rapid growth into later ages than males from southern areas (Poultney River and South Bay) (Figure 6). The oldest age classes were more abundant in southern stocks.

The pattern for females is less distinct (Figure 7). South Bay females were among the smallest at a given age. Although Missisquoi females were small at the youngest ages (3 and 4), they were among the largest in the older year classes. Lamoille River females showed a pattern similar to Missisquoi females.

Mean total lengths were not statistically compared among stocks because sampling methods were often inconsistent. For example, Missisquoi Bay walleye were collected with beach seines, 99% of walleye sampled from South Bay were collected in trap nets and Poultney River walleye were sampled by electrofishing (Table 1). Any differences in biological characteristics of walleye collected from these three sites could be due to site (stock) differences, but may also be due to differences in gear type used to sample each site. Differences in sampling years, dates and stations are likewise confounded with stock

Table 2. Number, mean and modal age of spawning walleye collected in Lake Champlain and its tributaries from 1983 to 1992.

Area	Males			Females		
	Number	Mean Age	Modal Age	Number	Mean Age	Modal Age
South Bay	955	7.49	8	2924	6.83	4
Great Chazy River	483	5.05	5	356	6.38	5
Missisquoi Bay	231	6.66	6	600	7.20	7
Lamoille River	364	4.87	5	84	6.45	7
Poultney River	311	8.28	10	104	9.81	8 and 10

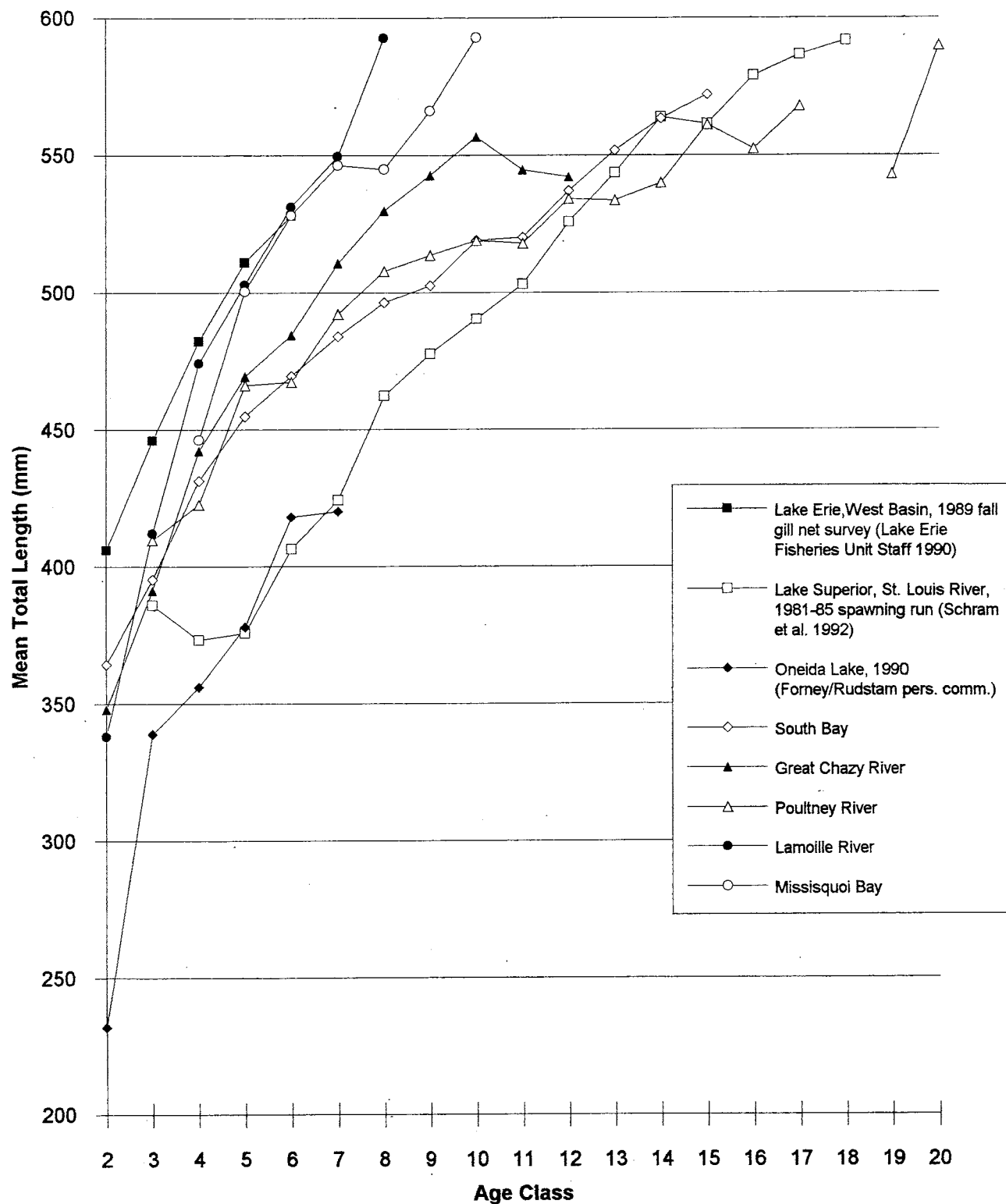


Figure 2. Length-at-age of male walleye from Lake Champlain, Lake Erie, Lake Superior and Oneida Lake.

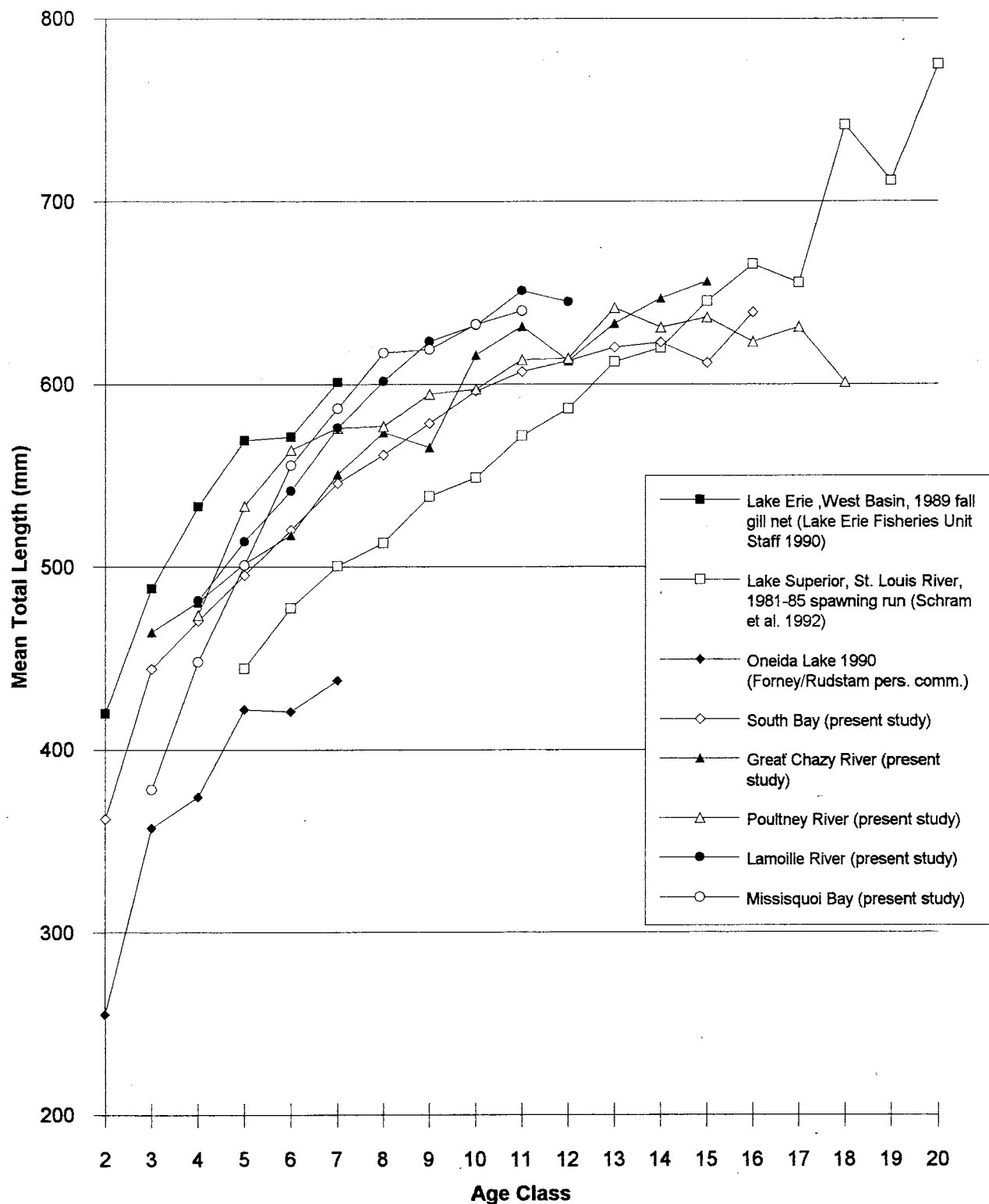


Figure 3. Length-at-age of female walleye from Lake Champlain, Lake Erie, Lake Superior and Oneida Lake.

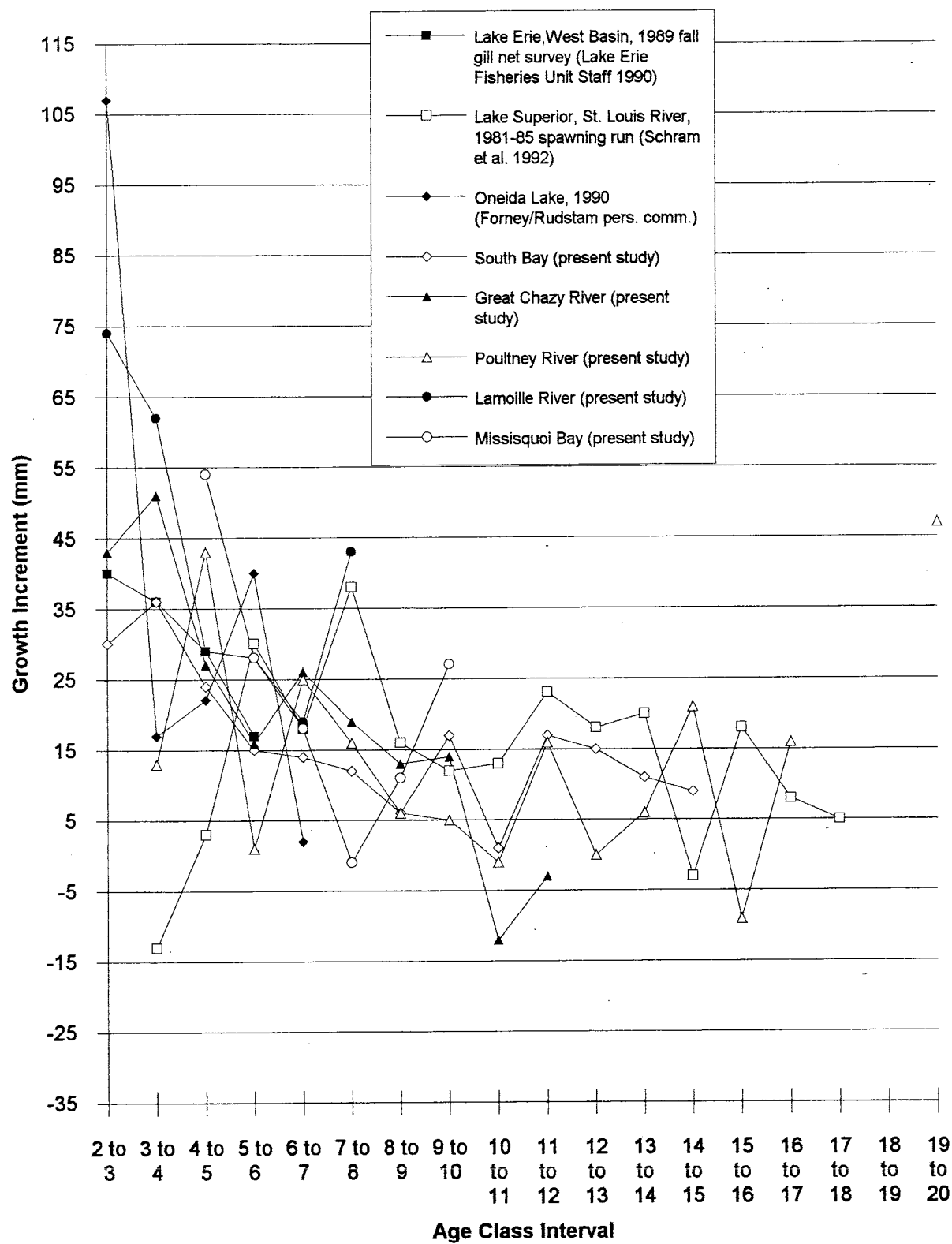


Figure 4. Mean annual growth increments of male walleye collected in Lake Champlain, Lake Erie, Lake Superior and Oneida Lake.

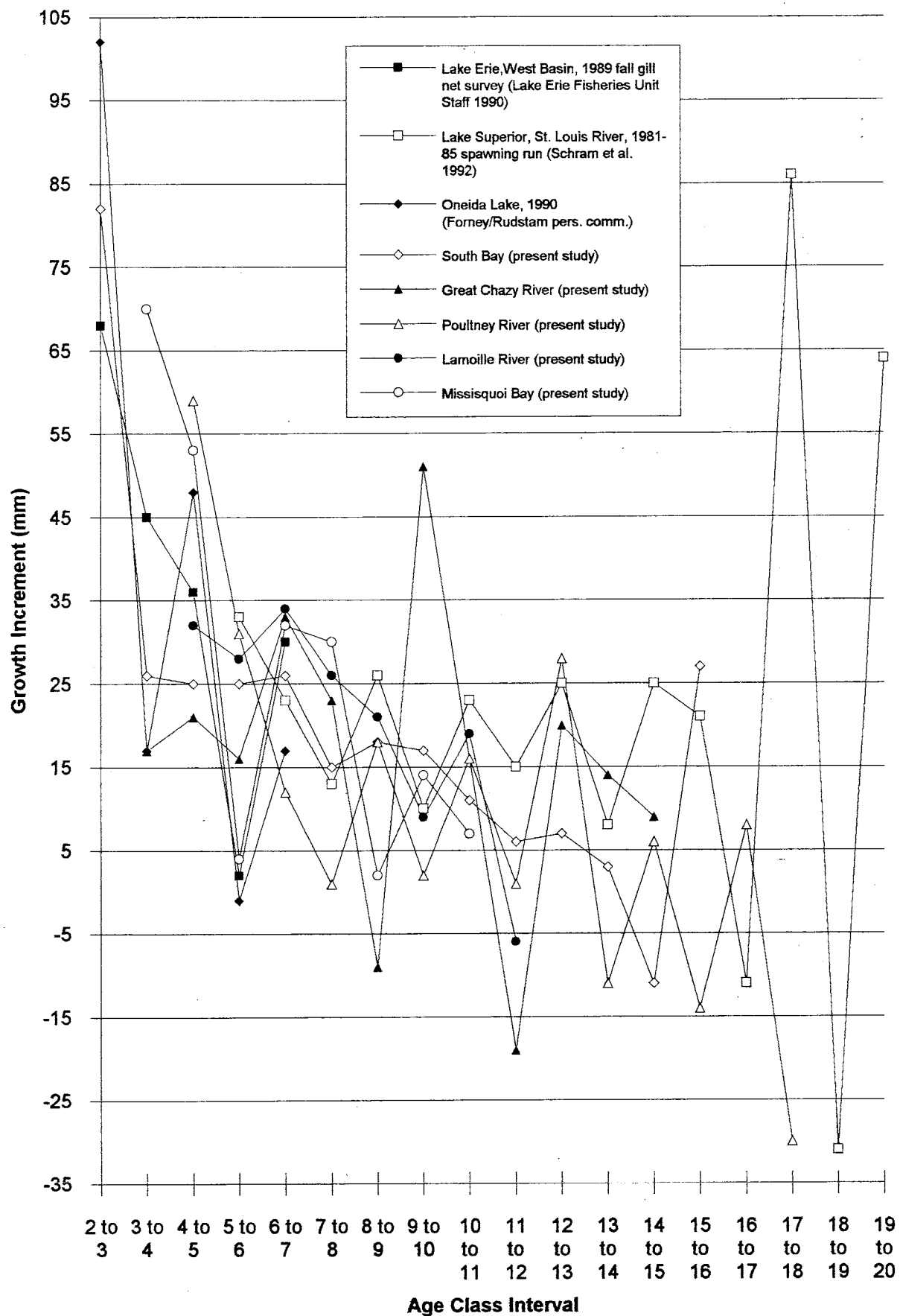


Figure 5. Mean annual growth increments of female walleye collected in Lake Champlain, Lake Erie, Lake Superior and Oneida Lake.

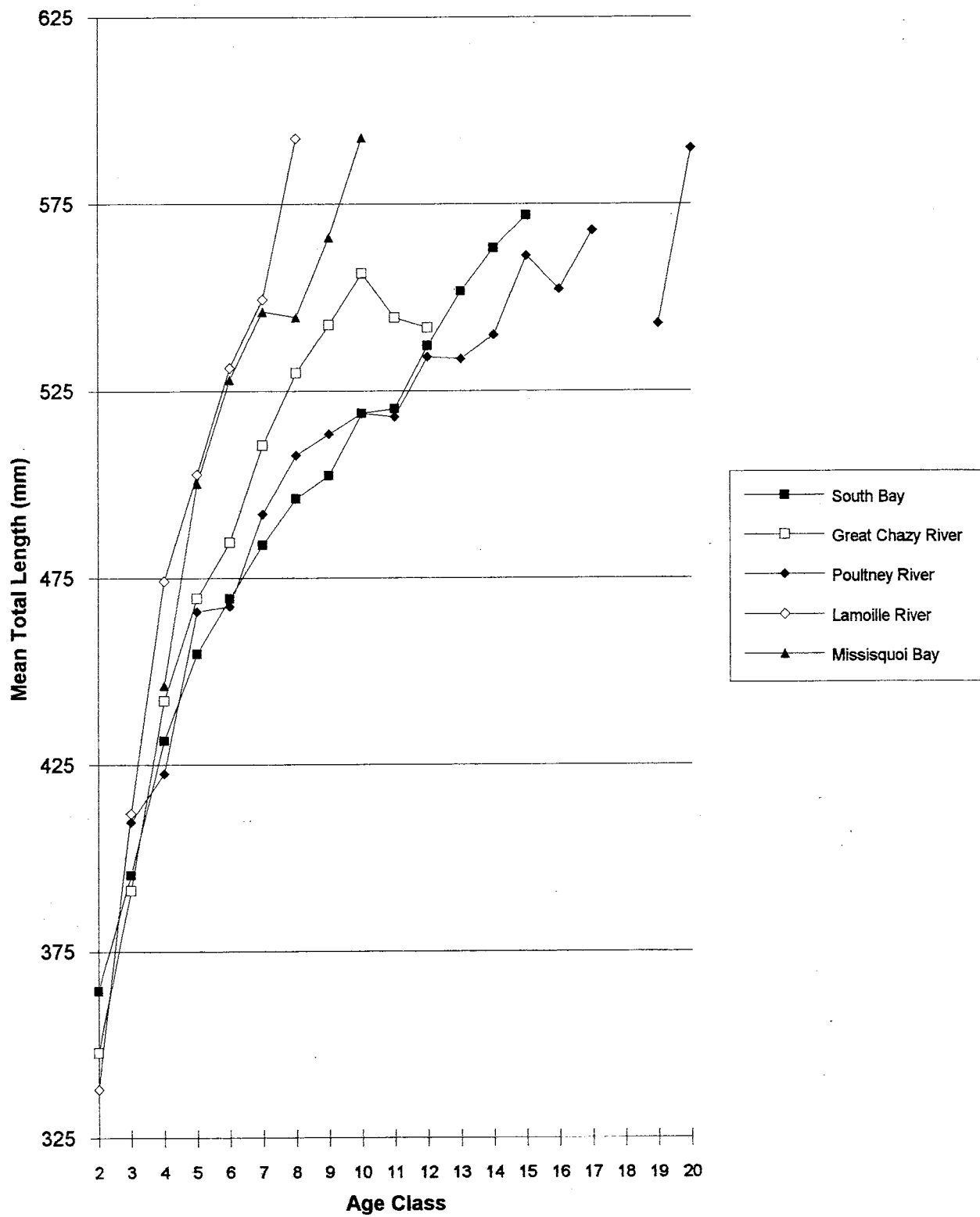


Figure 6. Length-at-age of spawning male walleye collected in Lake Champlain and its tributaries from 1983 to 1992.

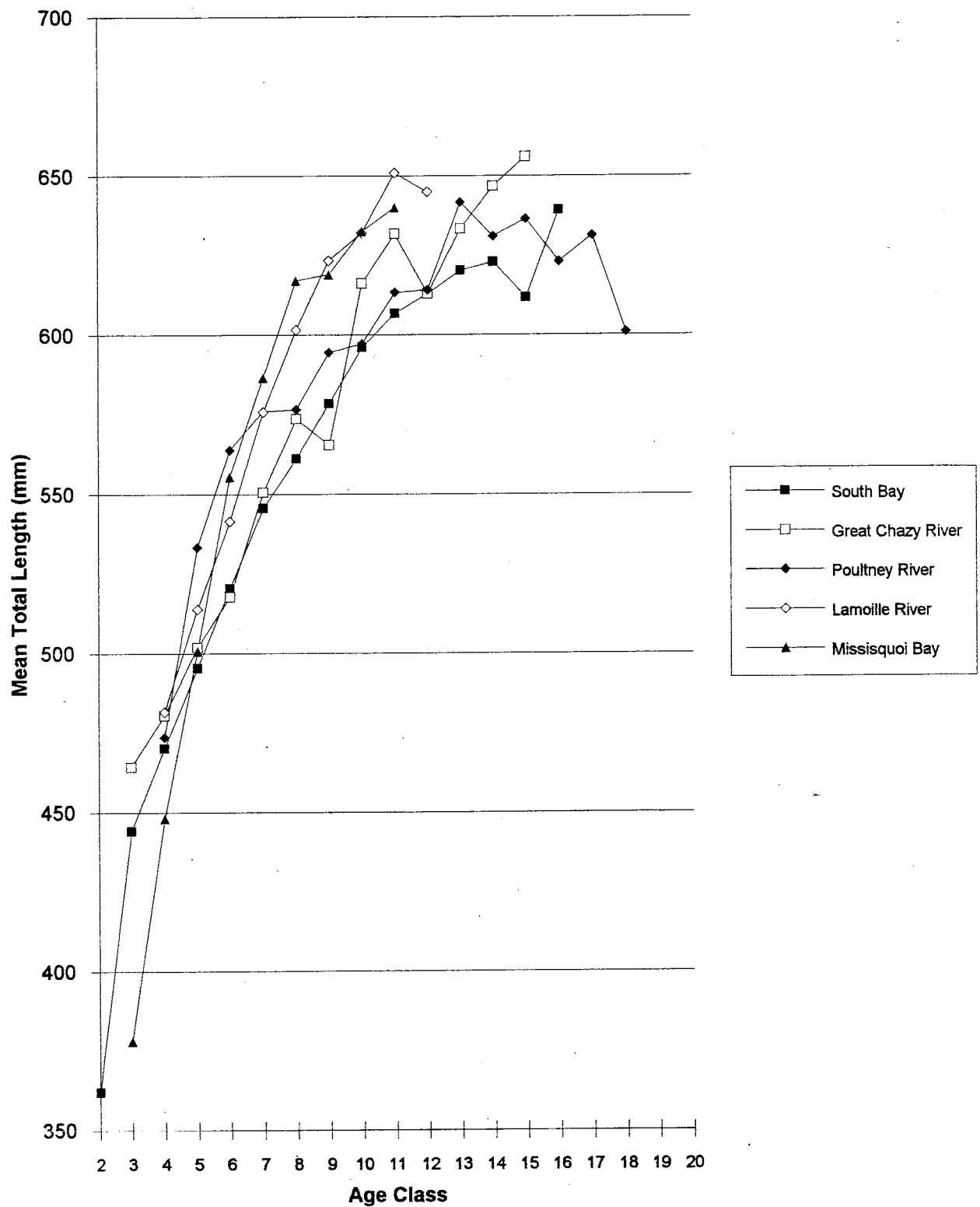


Figure 7. Length-at-age of spawning female walleye collected in Lake Champlain and its tributaries from 1983 to 1992.

in specific cases (Table 1). Therefore, statistical comparisons among stocks would be inappropriate because it would be impossible to attribute differences solely to stock differences. To compare Lake Champlain walleye stocks (e.g. mean total length, mean weight), consistent sampling methods are necessary.

Growth rates of males and females often differ after a certain age with females frequently attaining a larger size (Colby et al. 1979). Lake Champlain female walleye were usually larger at a given age than males (Figure 8). Walleye growth rates are commonly high during the first year of life then continually decrease until the 5th or 6th year (Colby et al. 1979). Growth rates for Lamoille River and Missisquoi Bay males did not appear to decrease with age, although age 9 was the oldest age class represented (Figure 6). Growth of males from the other 3 stocks did seem to gradually decrease after age 3 or 4 (Figure 6). In general, female growth rates showed a gradual decline after age 7 and often fluctuated after age 11, although sample sizes for the oldest age classes were often small (Figure 7).

Two important factors determining walleye growth rates are temperature and food consumption (Colby et al. 1979). Rate of food consumption and population density are often interrelated and may help explain why several authors (Koshinsky 1965; Beeton 1966; Priegel 1969; Moenig 1975; Baccante and Reid 1988; Hartman and Margraf 1992) have noted an inverse relation between walleye population density and growth rates. However, Kempinger and Carline (1977) found no relation between variations in annual adult walleye growth rates from 1955 to 1972 and population density or biomass in Escanaba Lake, Wisconsin.

Walleye year class size is known to fluctuate widely from year to year (Colby et al. 1979; Ritchie and Colby 1988). LaBar and Parren (1983) interpreted peaks in walleye age frequency distributions as evidence of strong year classes. We found no indication of particularly strong or weak cohorts in length frequency distributions, but sample sizes were small in many cases (Figure 9). Also, variation in individual growth rates can cause

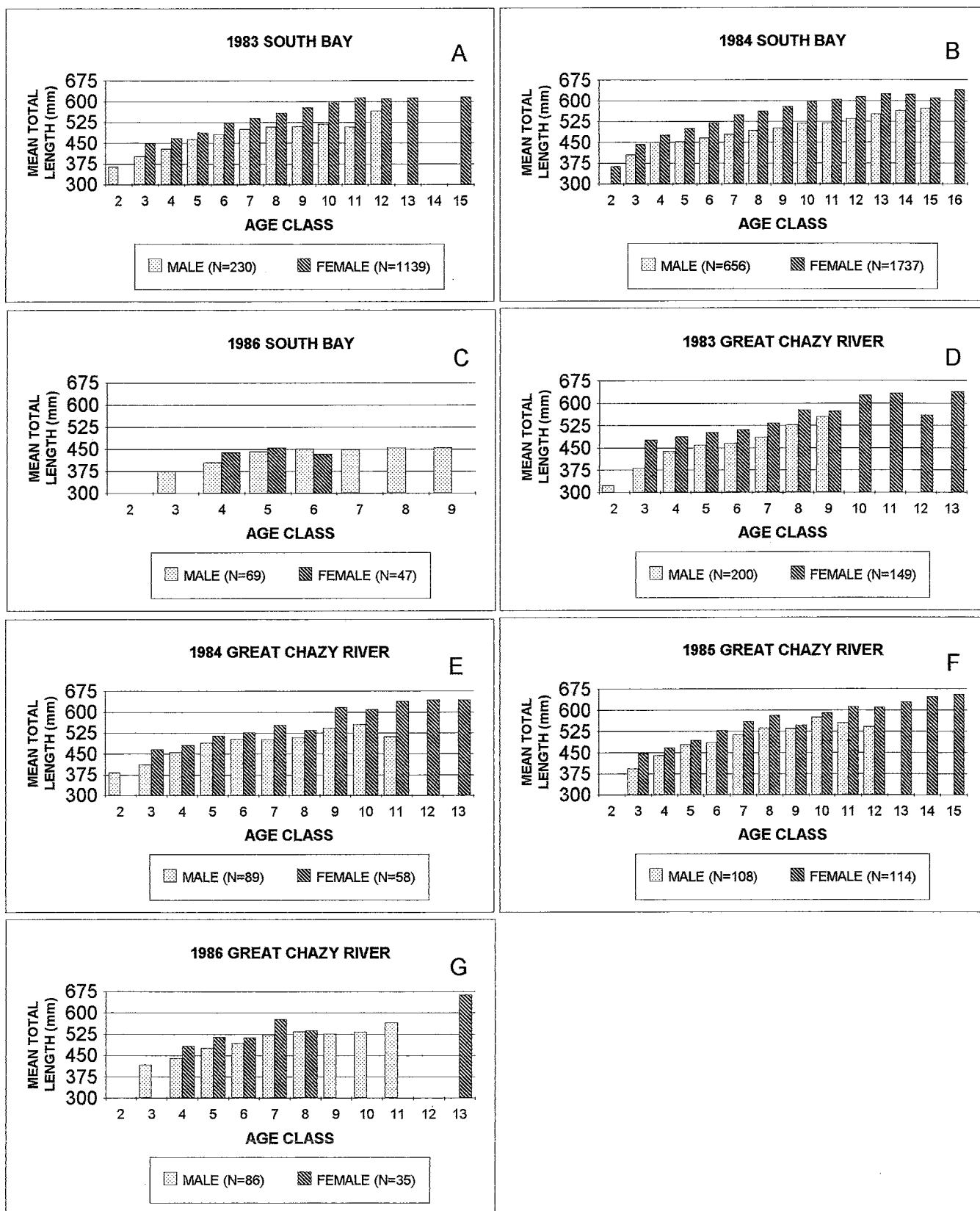


Figure 8. Mean total lengths of spawning male and female walleye collected in Lake Champlain and its tributaries from 1983 to 1992.

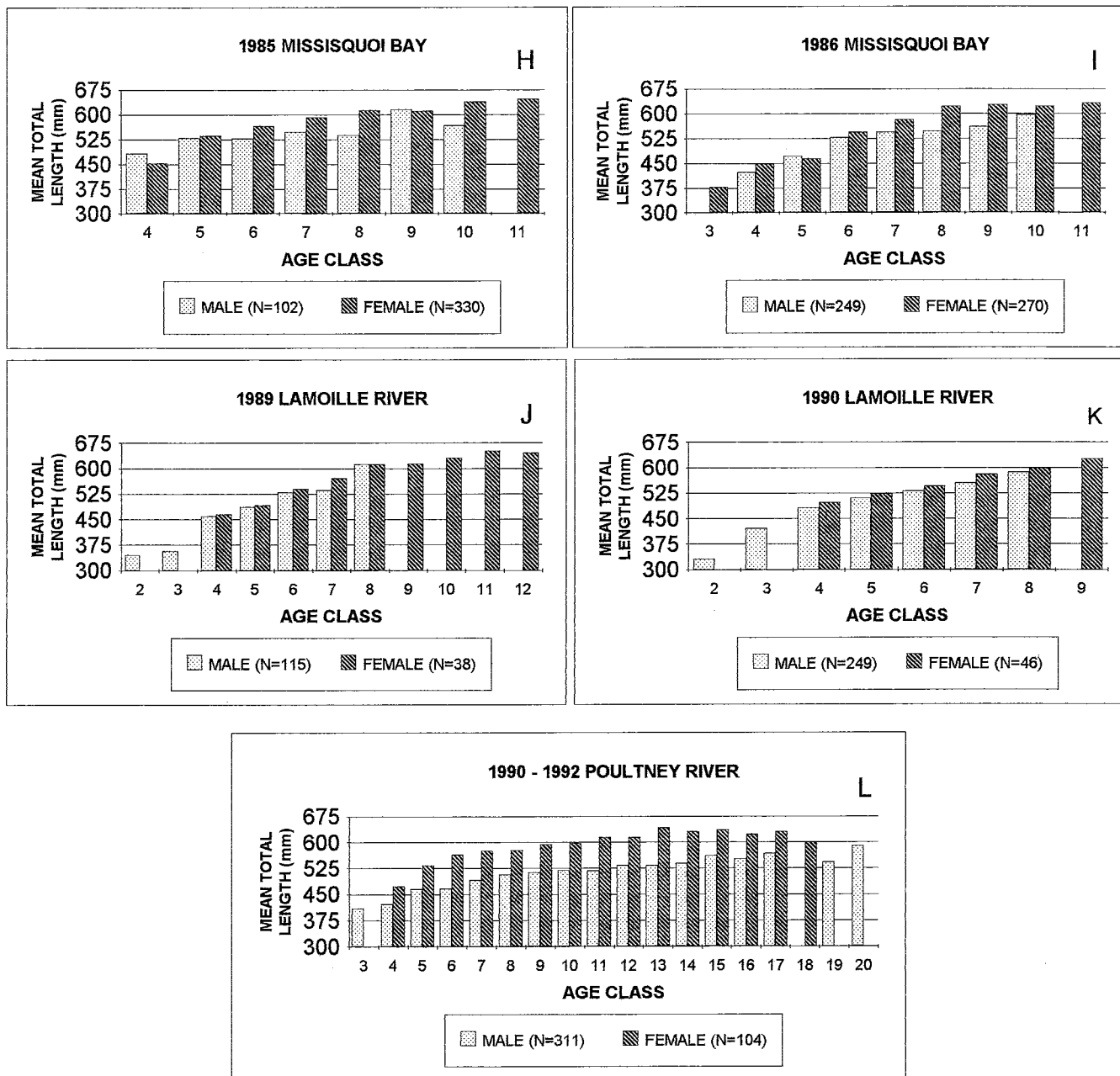


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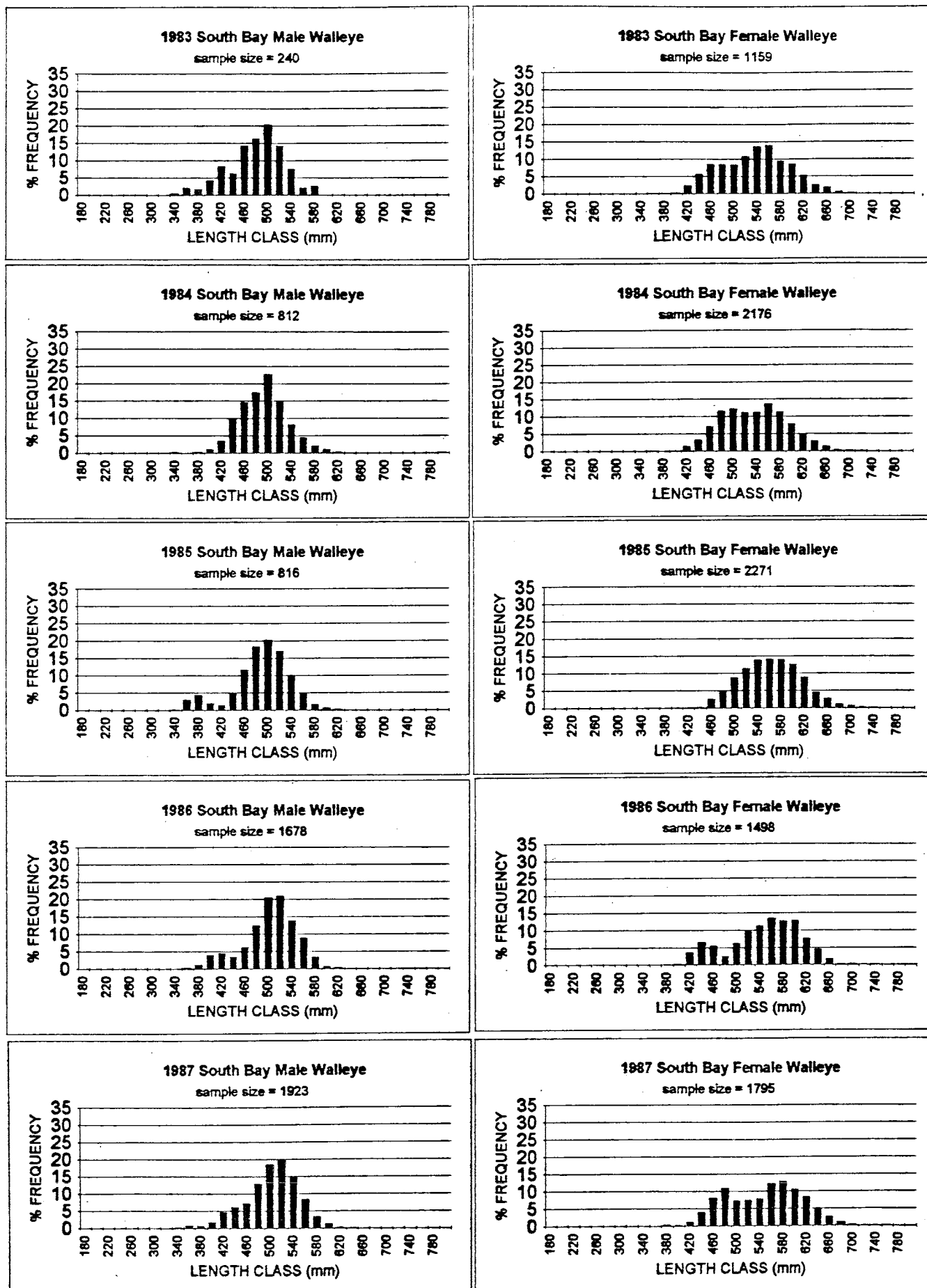


Figure 9. Length frequency distributions of spawning male and female walleye collected in Lake Champlain and its tributaries from 1983 to 1992.

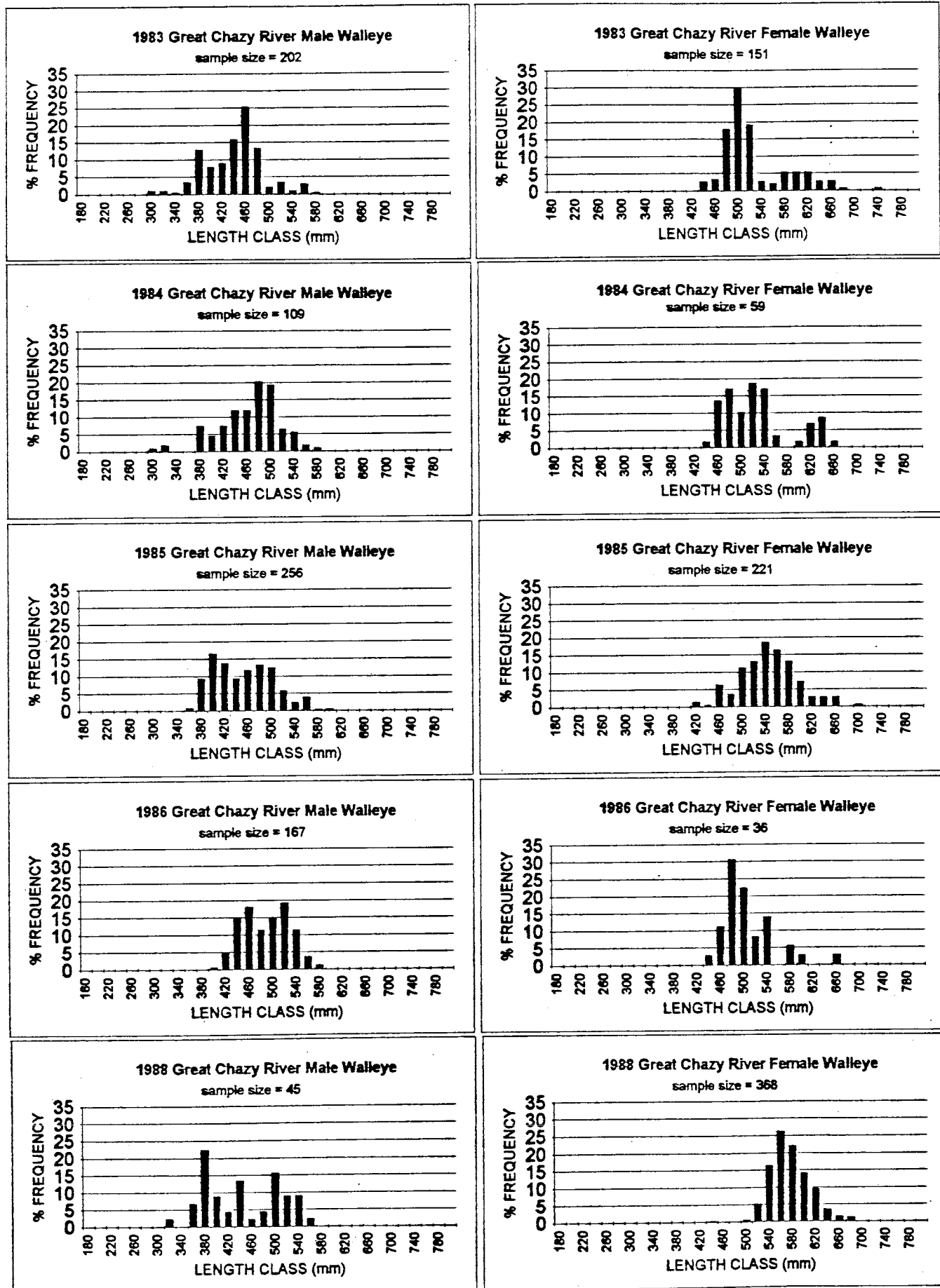


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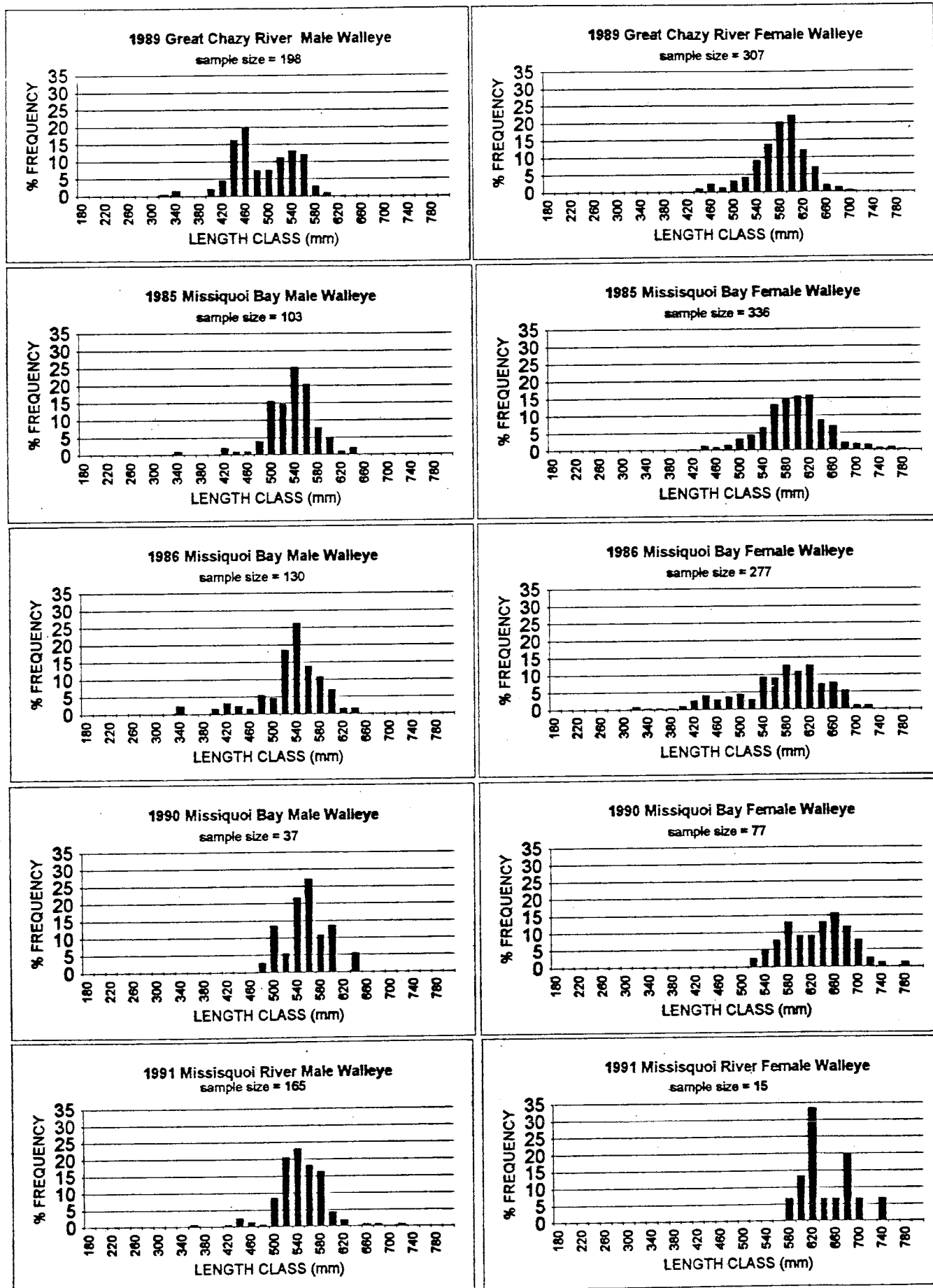


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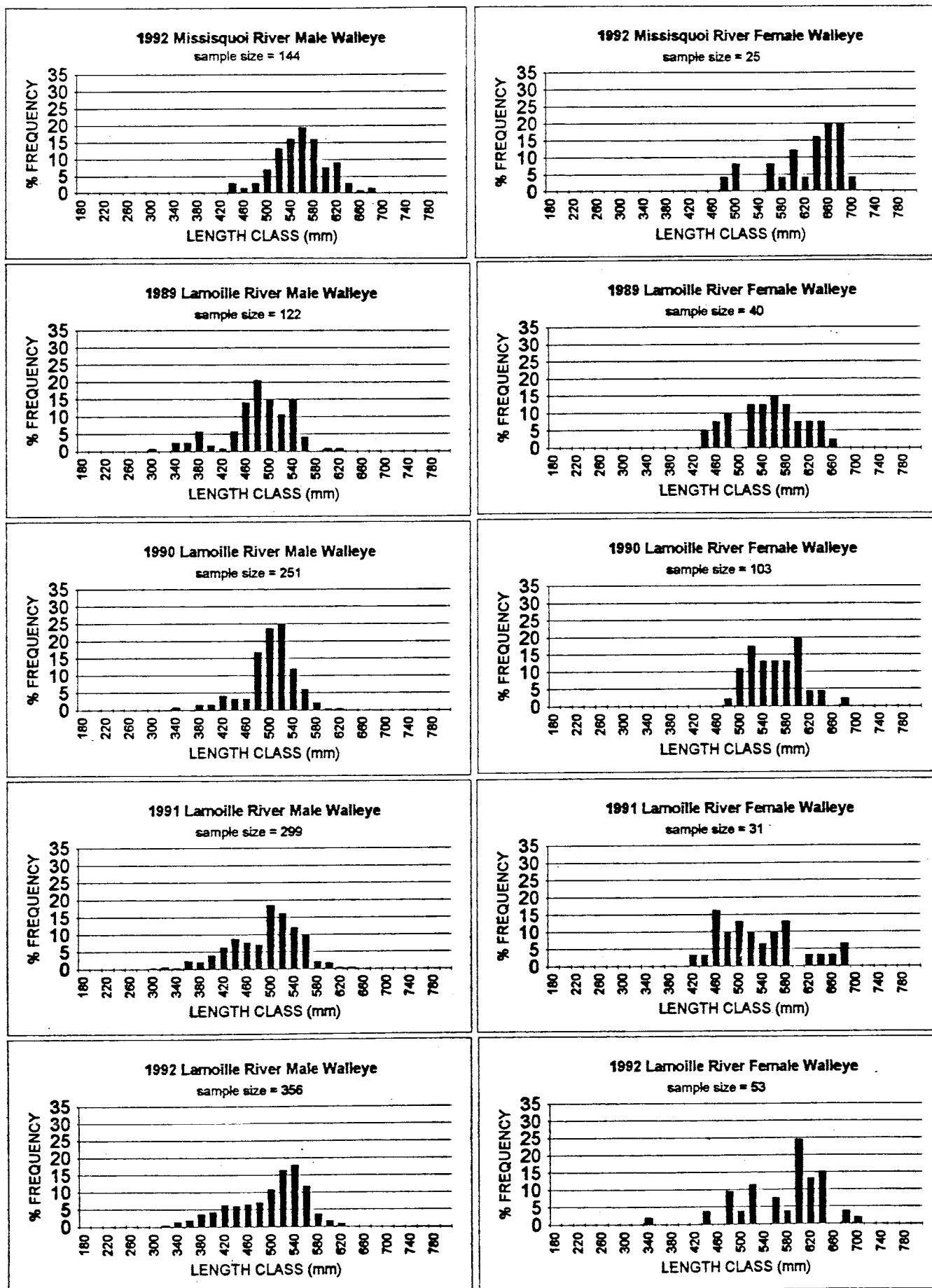


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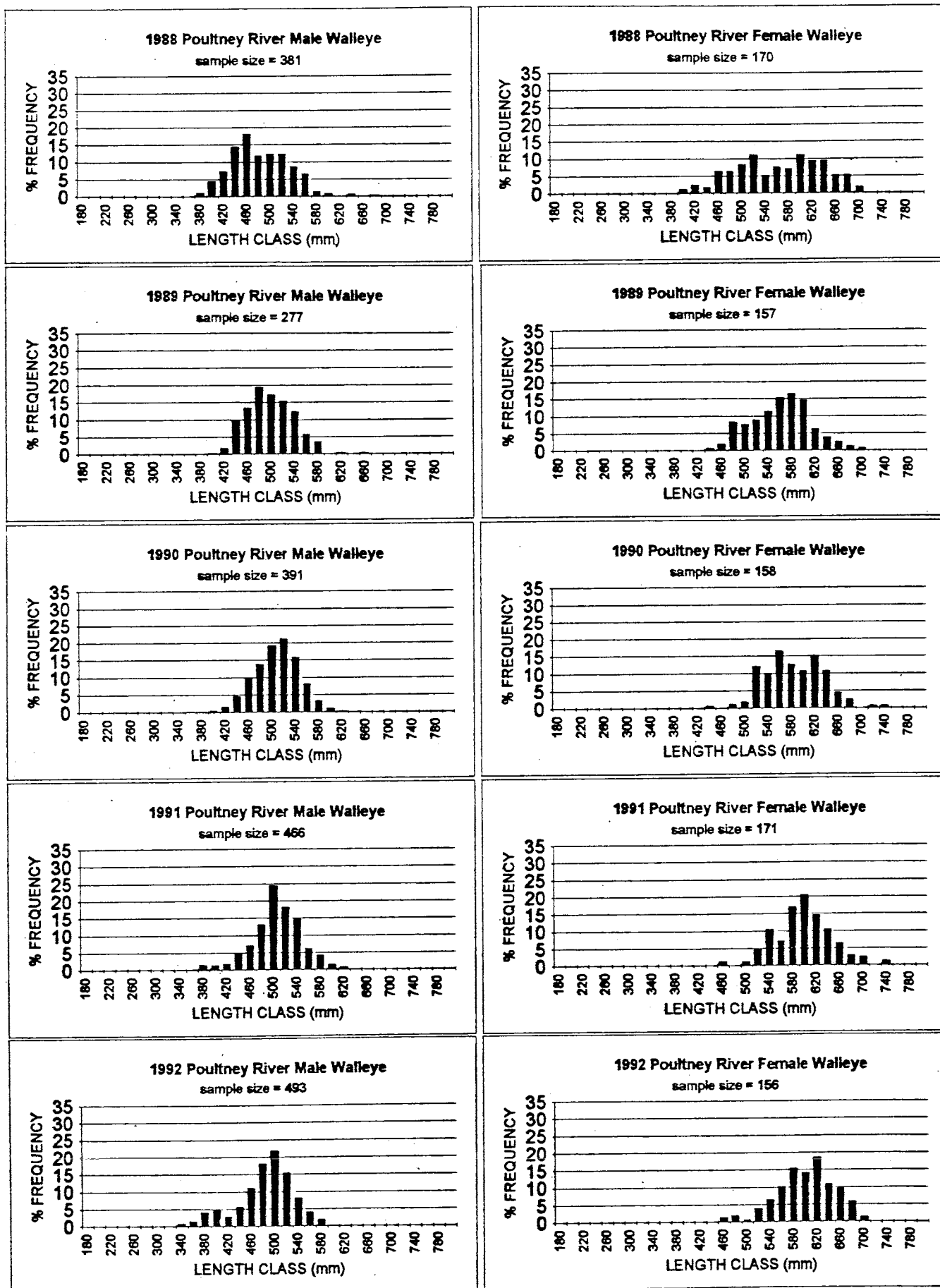


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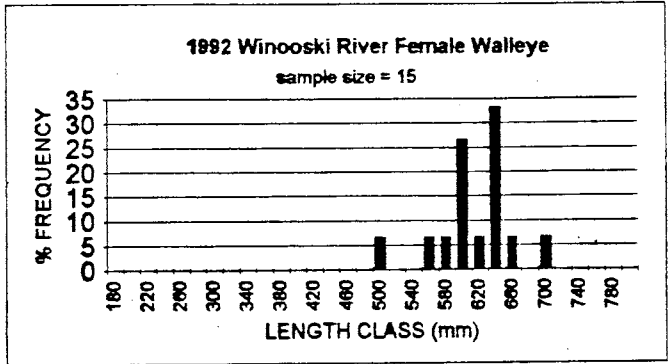
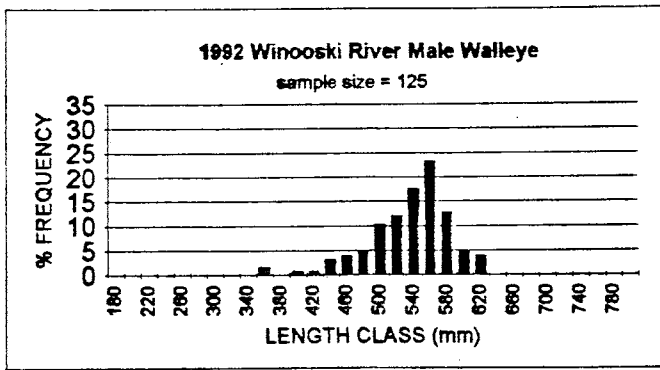


Figure 9 (continued).

overlaps in the length distributions of fish of different ages (Gulland 1983) (Figure 10) and walleye older than approximately age 7 or 8 can be difficult to age with scale samples (Belanger and Hogler 1982; Baccante and Sandhu 1983).

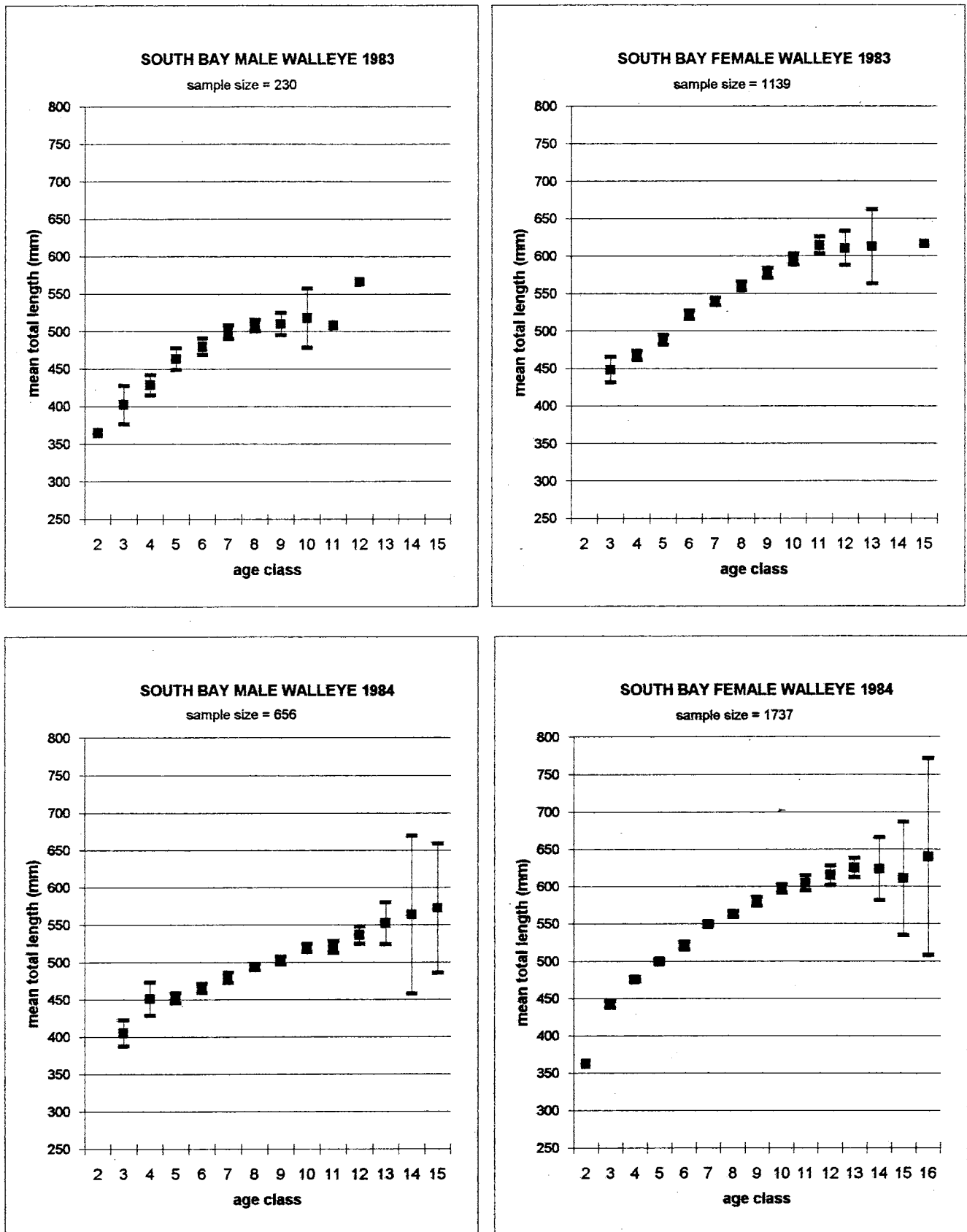


Figure 10. Length-at-age of spawning male and female walleye collected from Lake Champlain and its tributaries from 1983 to 1992 (error bars represent 95% CI).

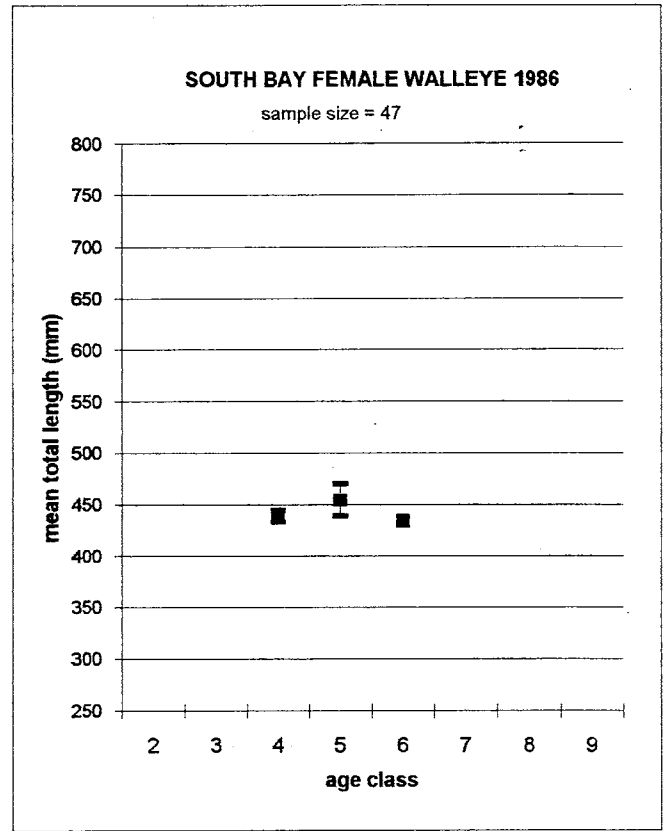
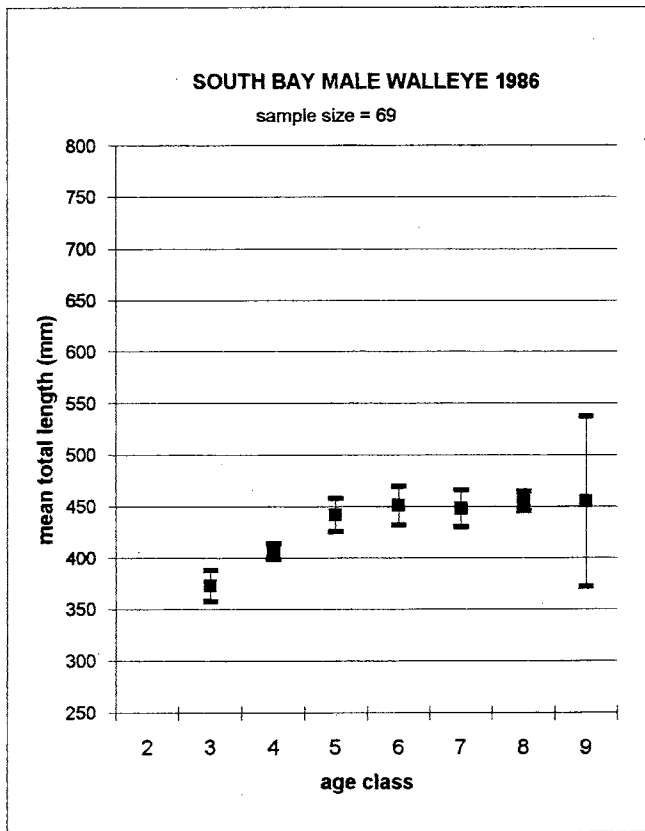


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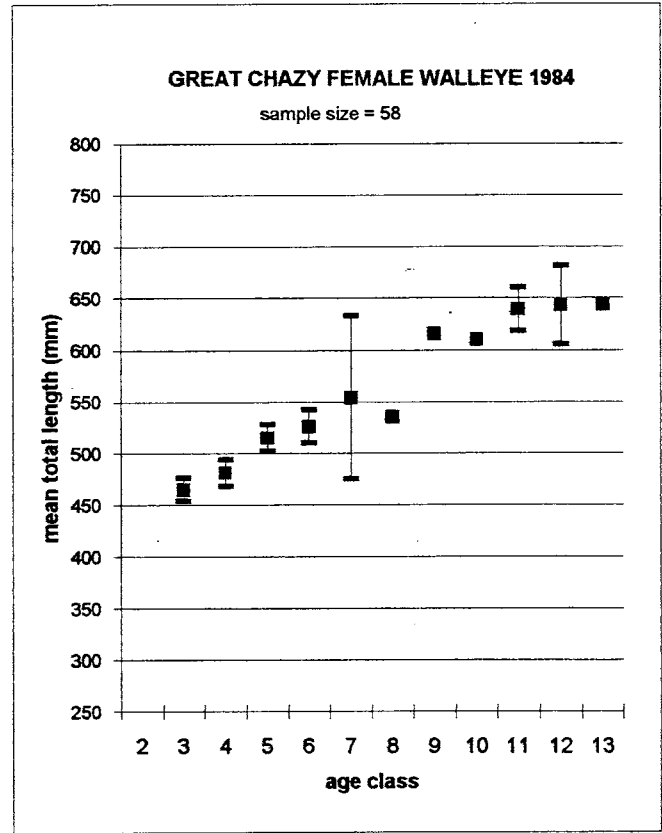
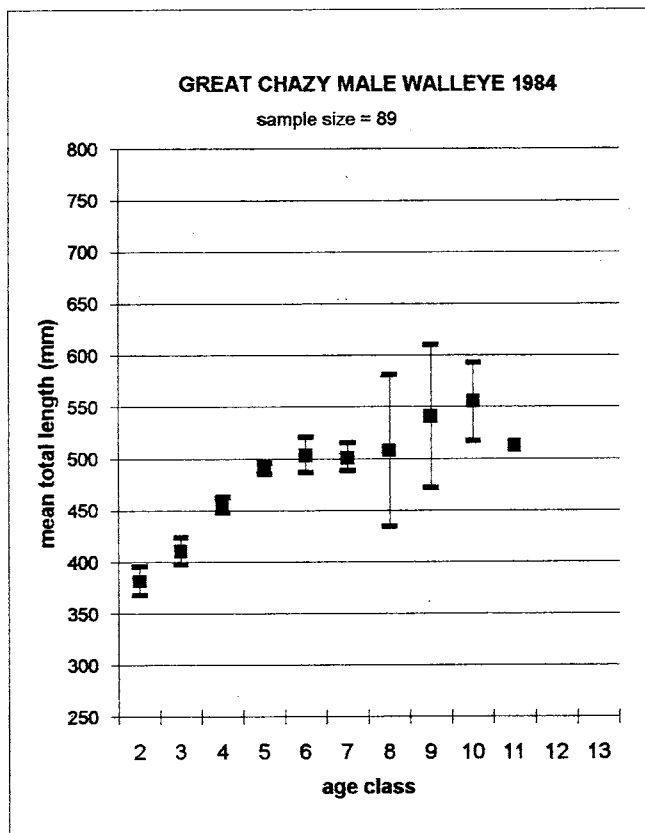
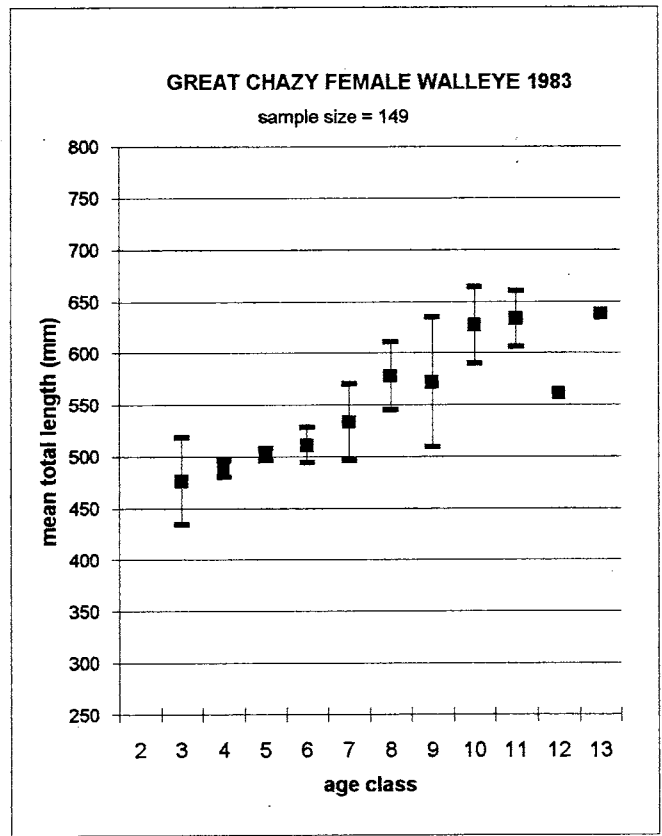
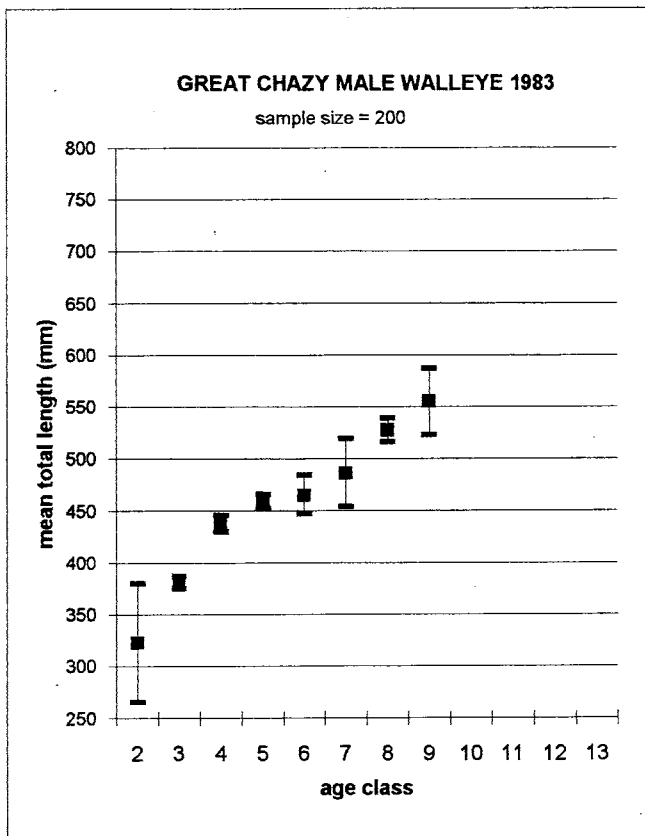


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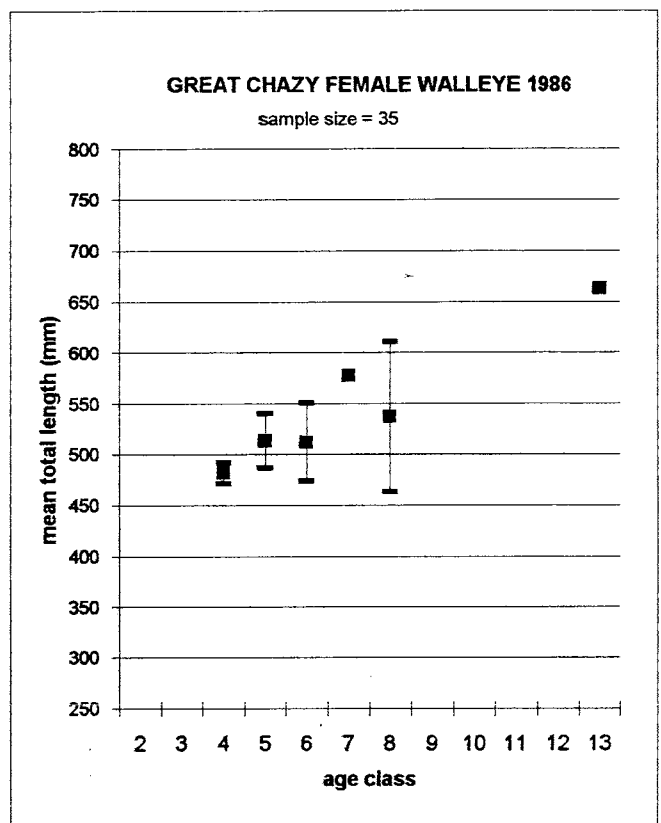
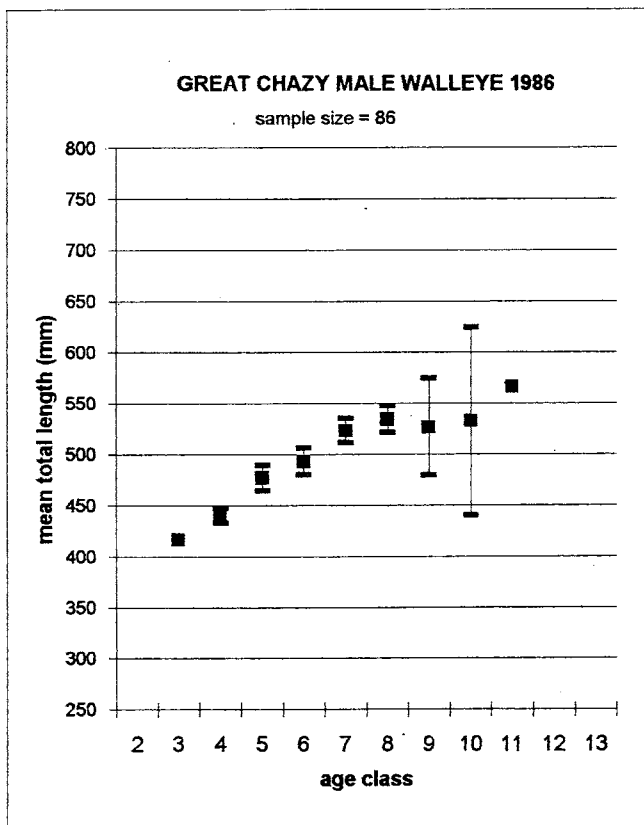
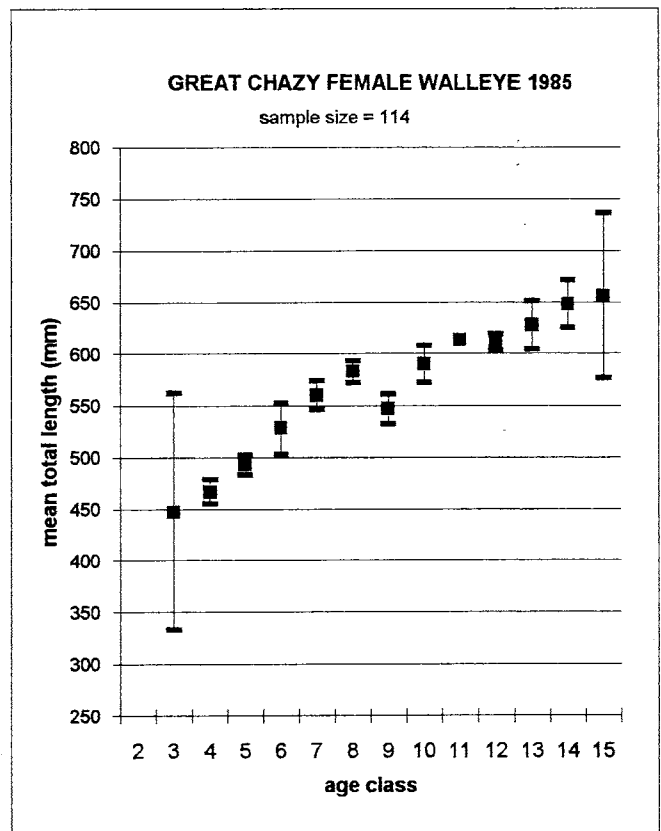
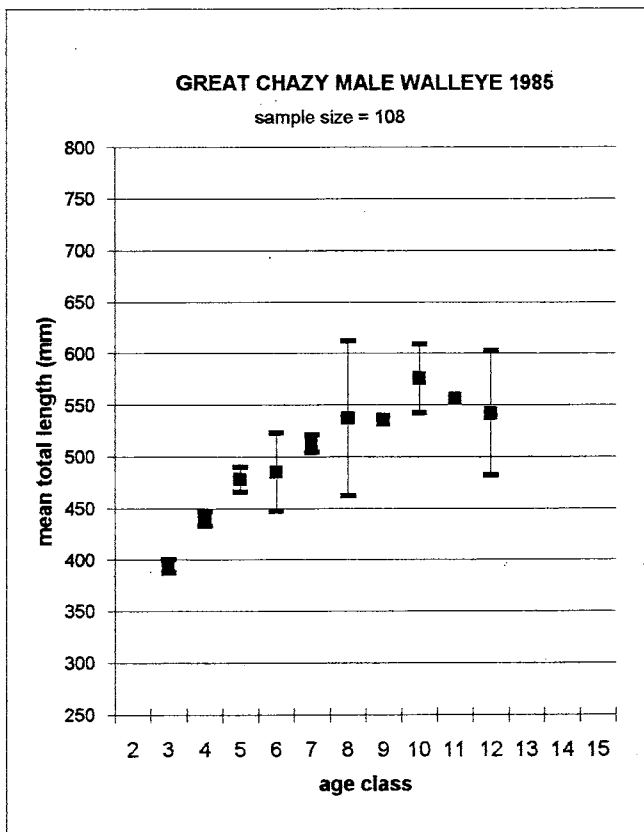


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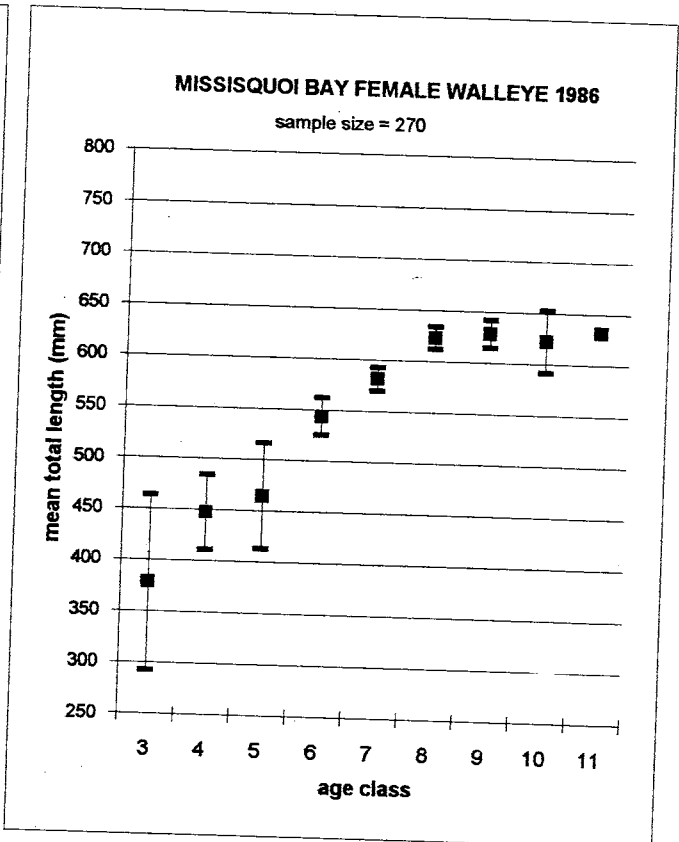
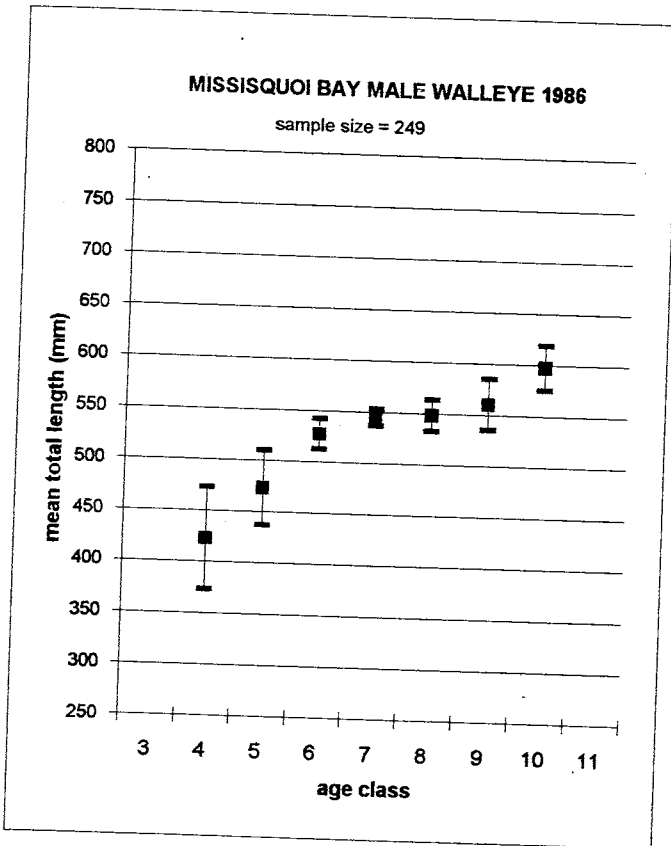
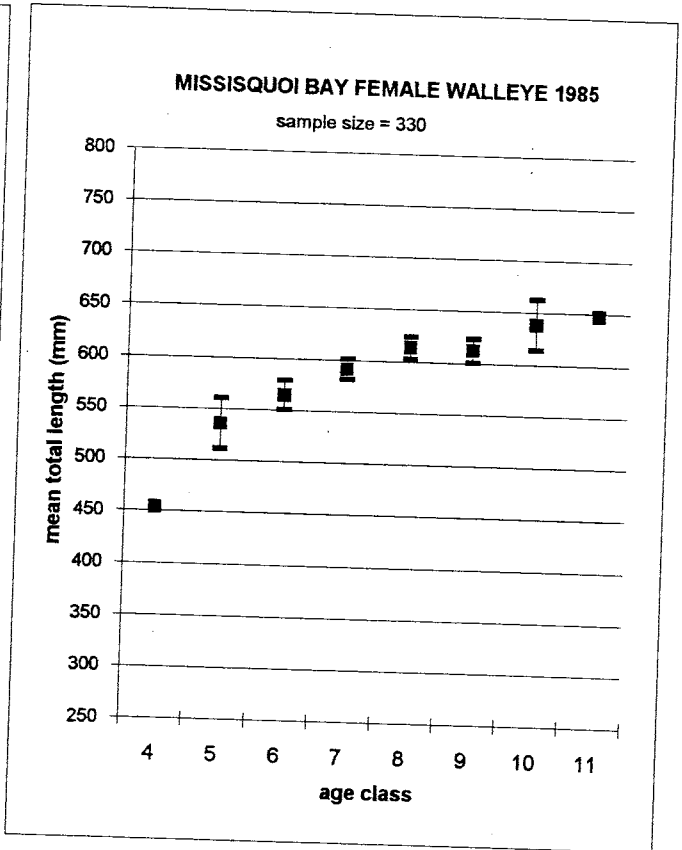
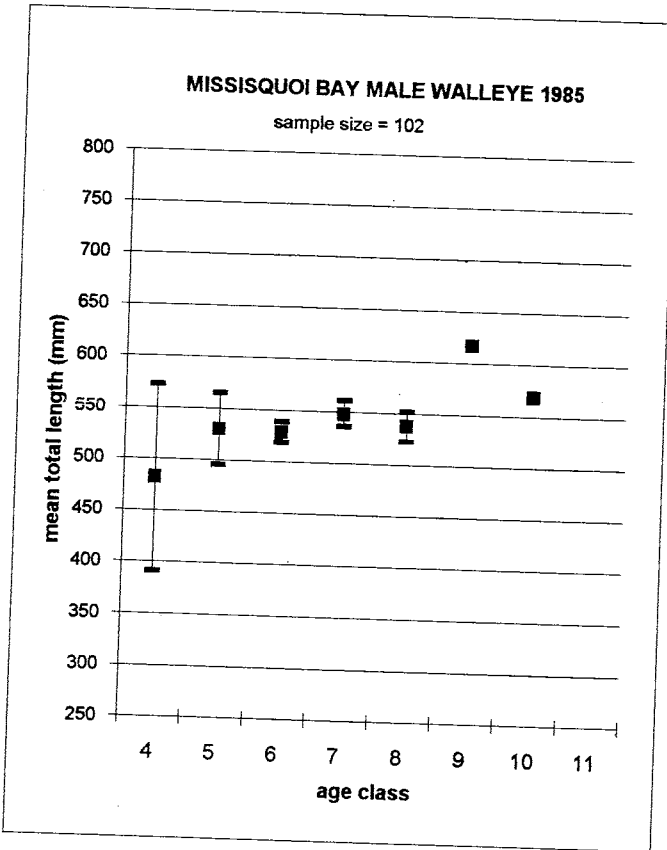


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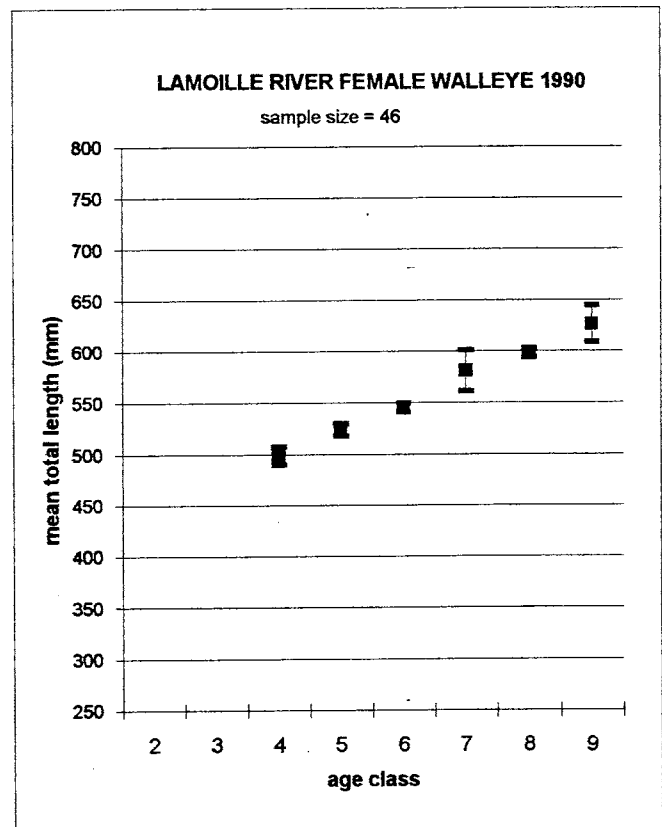
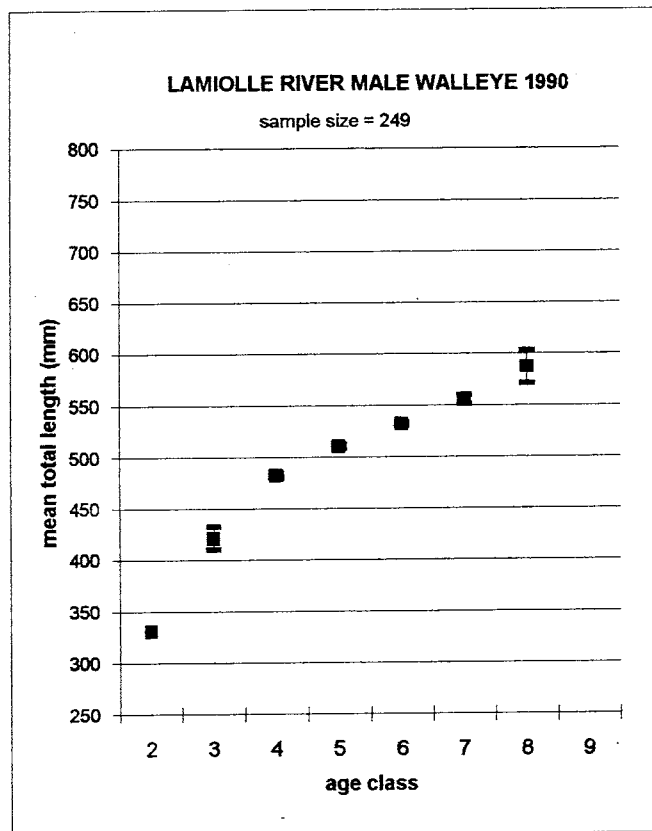
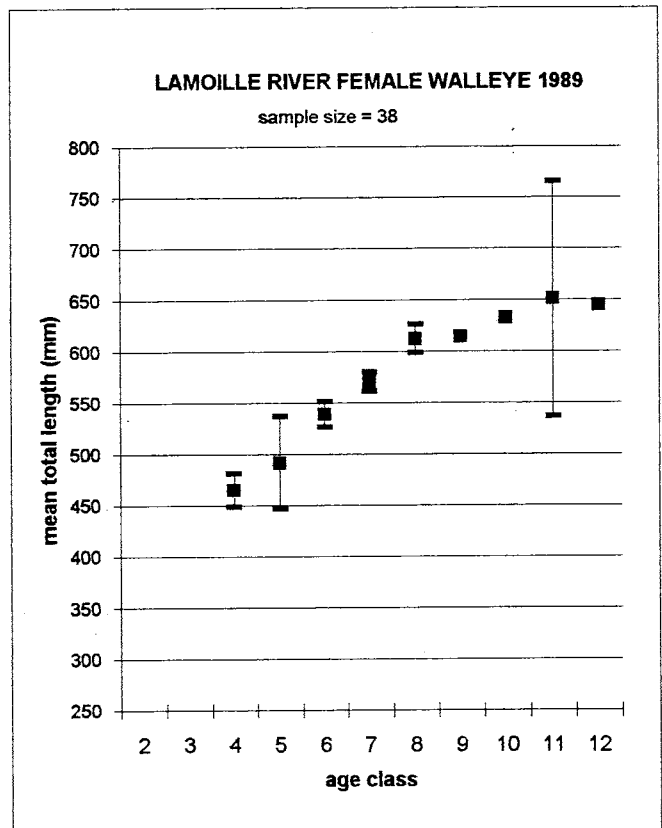
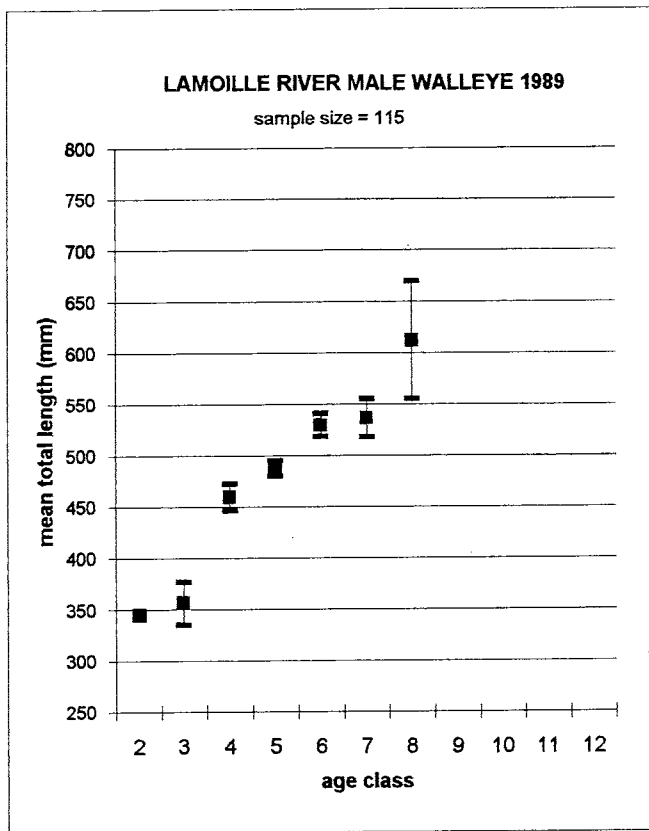


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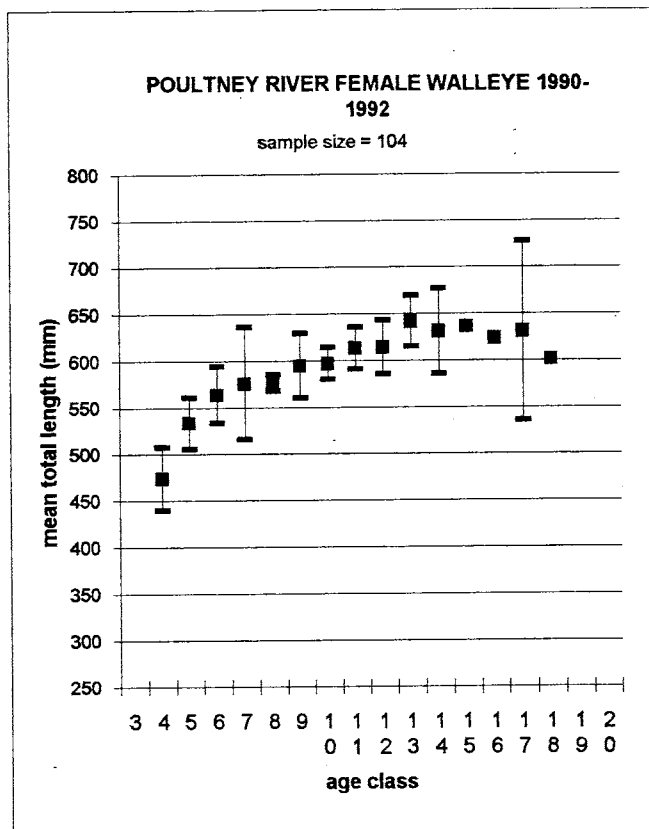
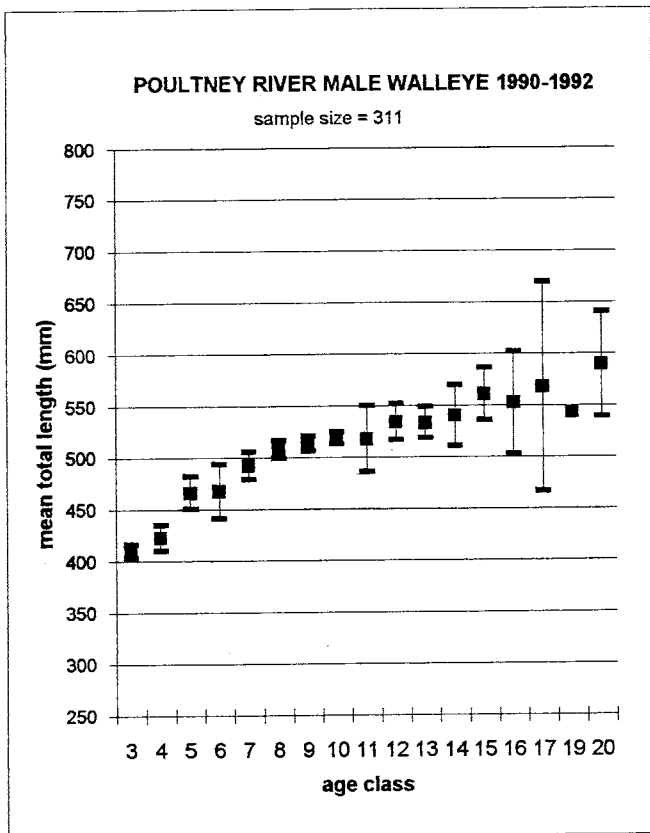


Figure 10 (continued)

Spawning

Dates and Locations

Spawning walleye were present at all sampled sites and on all sampling dates listed in Table 1. Otter Creek was also electrofished near Vergennes (Figure 1a) during several spring spawning seasons, but no walleye were found (Jon Anderson, VTF&W, personal communication). No other tributaries or lake sites were sampled during the spawning period between 1983 and 1992, however, other spawning sites may exist. For example, anglers report historic spawning sites in the Boquet and Ausable rivers in New York.

Relative abundance of male and female walleye on spawning grounds can indicate times of peak spawning: males often arrive first and remain for a period after females have left (Colby et al. 1979). Eschmeyer (1950) reported peak spawning activity for the season coincides fairly well with the minimum ratio of males to females on the spawning grounds. In Lake Champlain, dates during which the proportion of females was maximized varied from year to year at all sampling locations (Figures 11 - 15). Initiation of spawning activity can vary by up to four weeks on a year to year basis and depends on the thermal history and maturation state of the stock (Colby et al. 1979). Water temperature was recorded for South Bay and Great Chazy River samples, but no obvious relation between sex ratio and mean water temperature was noted (Table 3).

Consistently more male than female walleye were captured in Poultney and Lamoille River spawning runs (Table 3). The male to female ratio also exceeded 1.0 in both years the Missisquoi River was sampled (1991 and 1992) and in 1992 in the Winooski River (Table 3). In Missisquoi Bay, where walleye were collected by seining, females outnumbered males by a minimum of 2 to 1 in all 3 sampling years (1985, 1986 and 1990) when sampling dates were combined. Sex ratios varied in the Great Chazy River: from 1983 to 1986, males outnumbered females, but more females were collected in 1988 and 1989. In South Bay, more females were captured from 1983 to 1985, but the majority of fish collected in 1986 and 1987 were male.

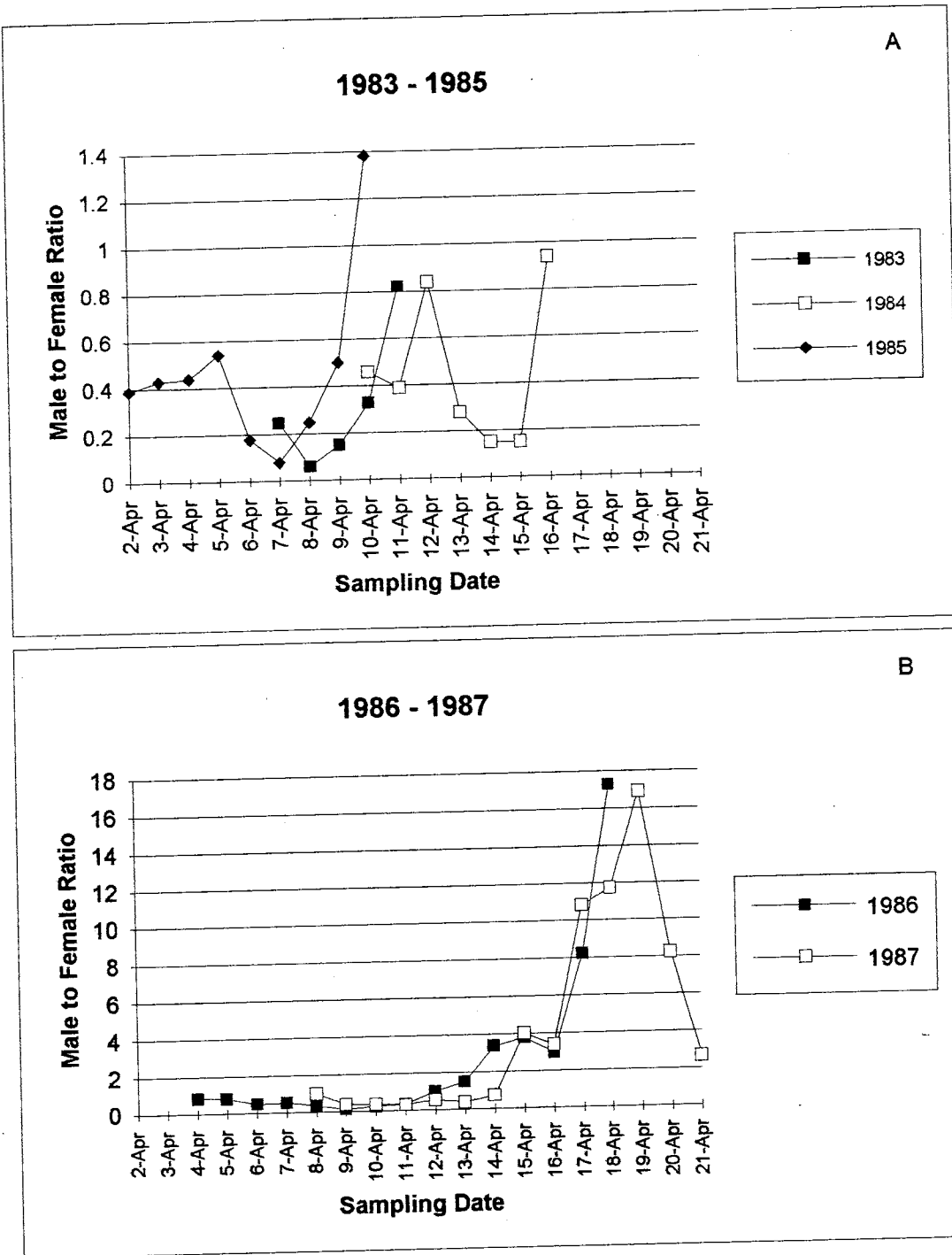


Figure 11. Ratio of spawning male to female walleye in South Bay from 1983 to 1987.

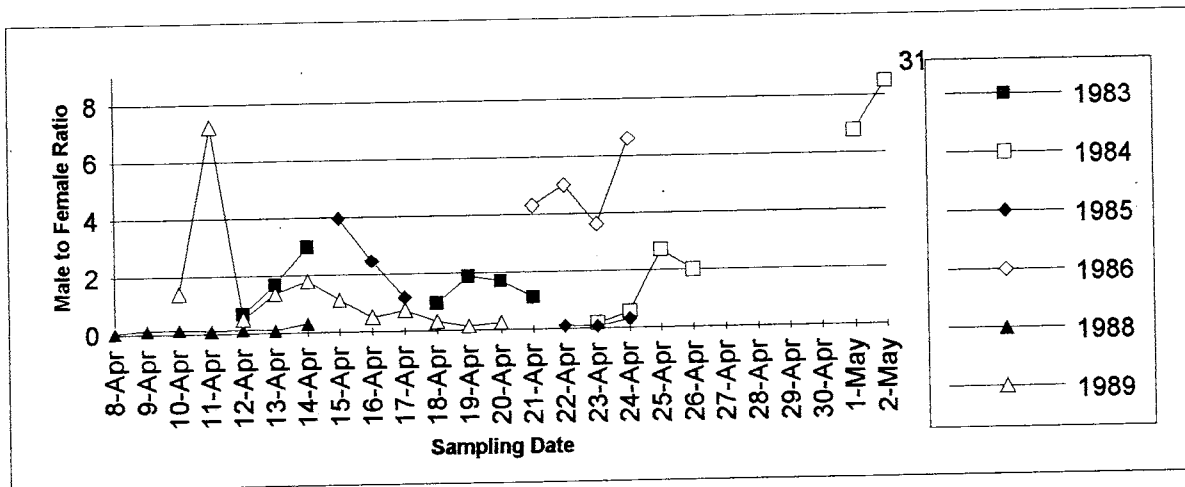


Figure 12. Ratio of spawning male to female walleye in the Great Chazy River from 1983 to 1989.

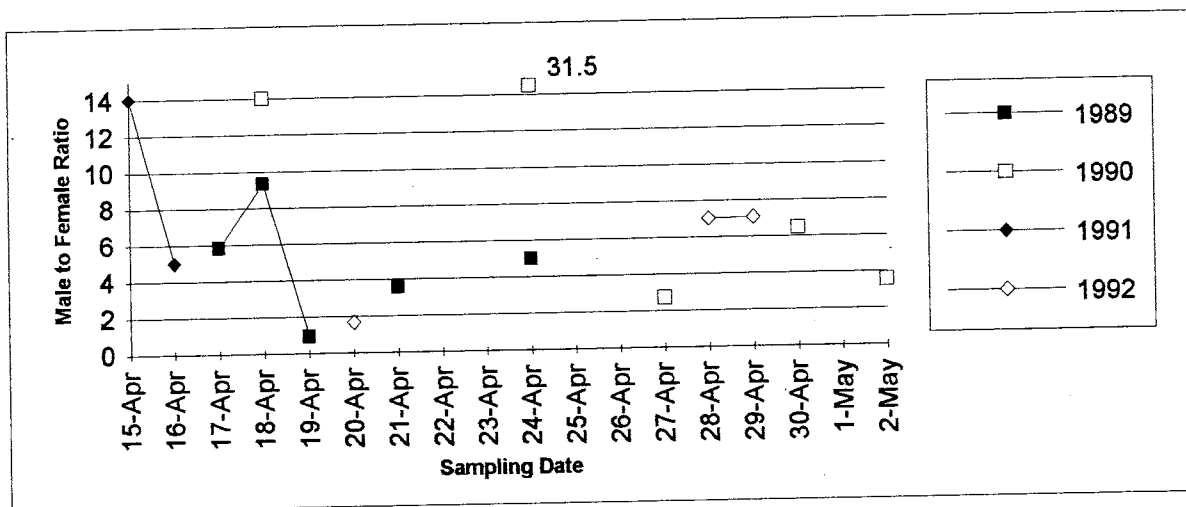


Figure 13. Ratio of spawning male to female walleye in the Lamoille River from 1989 to 1992.

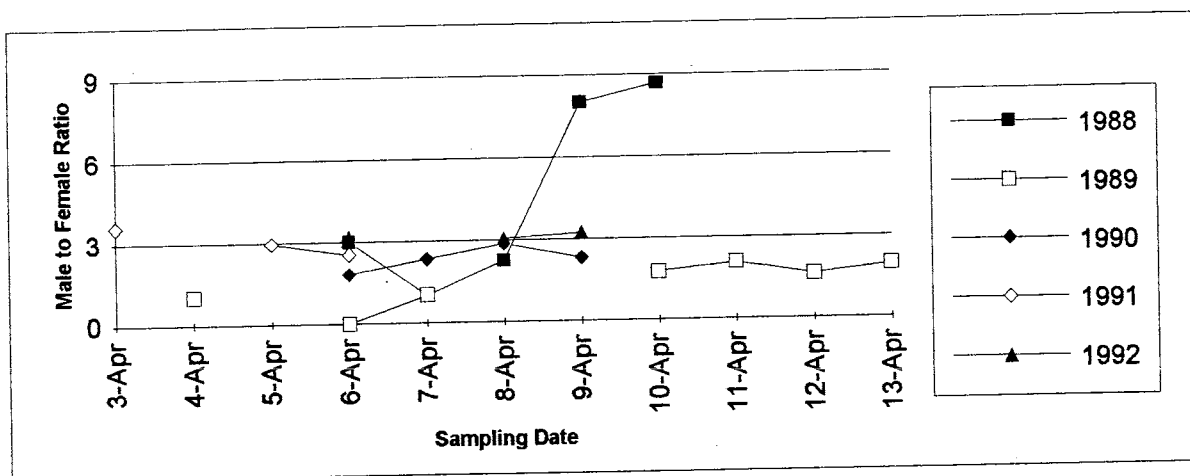


Figure 14. Ratio of spawning male to female walleye in the Poultney River from 1988 to 1992.

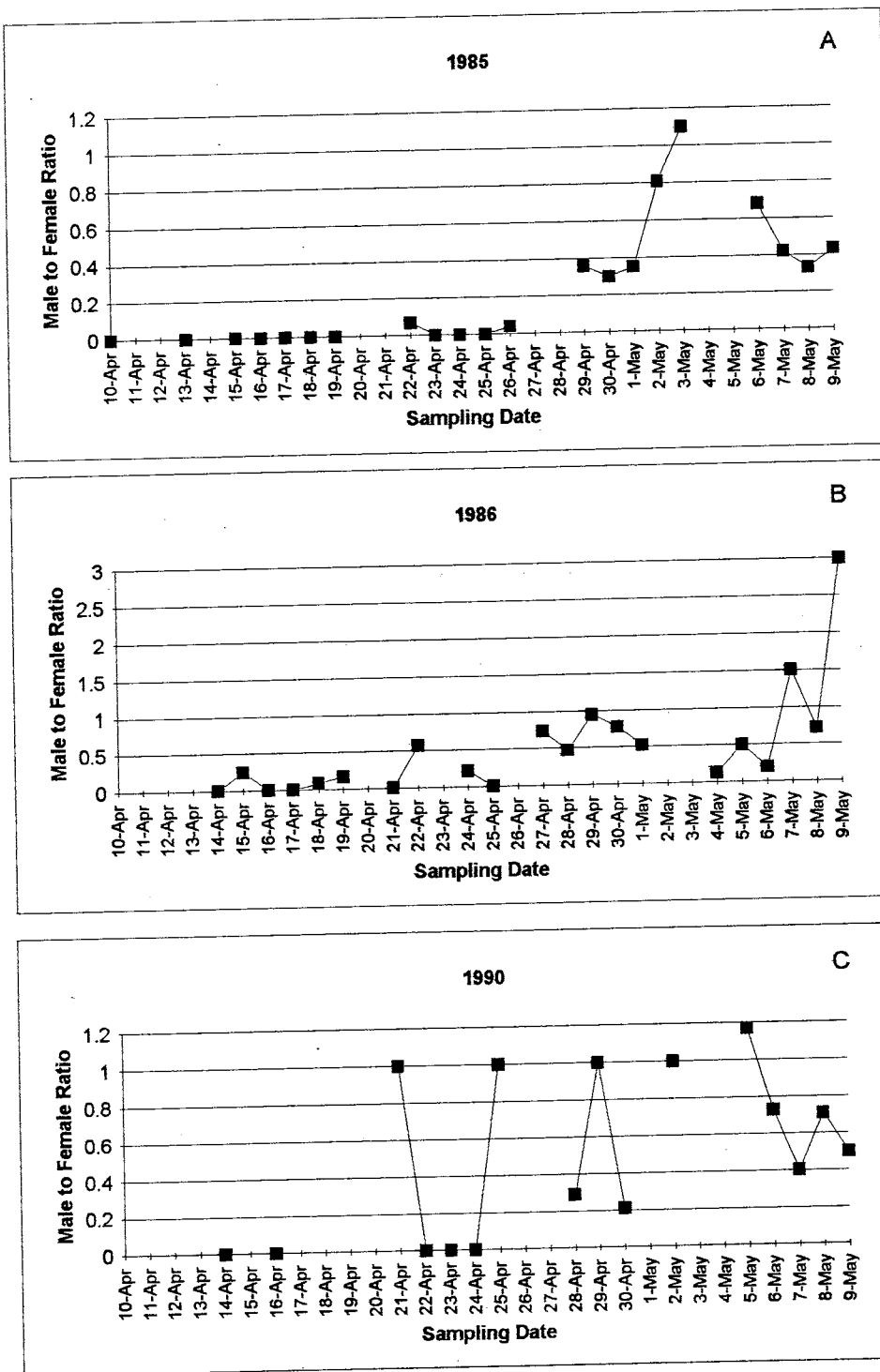


Figure 15. Ratio of spawning male to female walleye in Missisquoi Bay from 1985 to 1990.

Table 3. Ratio of male to female walleye in spawning population samples. Mean water temperatures not available for Vermont populations.

Stock	Year	Sampling Period	Mean Water Temp. (° C)	Number of Males	Number of Females	Male to Female Ratio
Great Chazy River	1983	4/12 - 4/21	3.6	202	151	1.34
	1984	4/23 - 5/02	9.0	109	59	1.85
	1985	4/15 - 4/24	8.3	256	221	1.16
	1986	4/21 - 4/24	11.0	167	36	4.64
	1988	4/08 - 4/14	8.4	45	368	0.12
South Bay	1989	4/10 - 4/20	7.0	198	307	0.64
	1983	4/07 - 4/11	6.4	240	1159	0.21
	1984	4/10 - 4/16	6.8	812	2176	0.37
	1985	4/02 - 4/09	5.6	816	2271	0.36
	1986	4/04 - 4/18	6.6	1678	1498	1.12
Missisquoi Bay	1987	4/08 - 4/21	8.0	1923	1795	1.07
	1985	4/10 - 5/09		103	336	0.31
	1986	4/14 - 5/09		130	277	0.47
	1990	4/14 - 5/09		37	77	0.48
	1988	4/06 - 4/12		381	170	2.24
Poultney River	1989	4/04 - 4/13		277	157	1.76
	1990	4/06 - 4/09		391	158	2.47
	1991	4/03 - 4/06		466	171	2.73
	1992	4/06 - 4/09		493	156	3.16
	1989	4/17 - 4/24		122	40	3.05
Lamoille River	1990	4/11 - 5/02		251	103	2.44
	1991	4/15 - 4/16		299	31	9.65
	1992	4/20 - 4/29		356	53	6.72
	1991	4/15		165	15	11.00
Missisquoi River	1992	4/29		144	25	5.76
Winooski River	1992	5/01		125	15	8.33

Sexual Maturity

Knowledge of sexual maturity and fecundity can help in understanding the causes of fluctuating year-class strength (Wolfert 1969; Baccante and Reid 1988) and help fisheries managers refine harvest regulations to protect reproductively important segments of the population. Male walleye usually reach sexual maturity between ages 2 and 4, and around 280 mm total length (Scott and Crossman 1990). Females normally mature from 3 to 6 years of age and 356 - 432 mm in length (Scott and Crossman 1990). Grinstead (1971) reported finding sexually mature age-I males and age-II females in an Oklahoma reservoir with exceptionally good first year growth rates. In contrast, the majority of male and female walleye did not spawn until age 7 in Lac la Ronge, Saskatchewan (Rawson 1957).

Less than 1% (44 fish) of all walleye collected from Lake Champlain spawning grounds were classified as immature. Without collecting immature fish, it is difficult to identify age of sexual maturity. Schram et al. (1992) defined age of 100% maturity as the most common age class captured during spawning. Using that definition, Lake Champlain walleye mature late because the modal age of males collected during spawning was between 5 and 10 and female modal age ranged from 4 to 10 (Table 2). In relatively cold lakes, like Lake Champlain, maturity is often delayed, but longevity increased (Colby and Nepszy 1981). However, age to sexual maturity is considered inversely related to growth rate (Hile 1954; Forney 1965; Wolfert 1969; Moenig 1975; Wootton 1990) and growth rates of Lake Champlain walleye appear to be good (Figures 2 and 3). Heavily exploited stocks tend to mature at a younger age (Wolfert 1969; Spangler et al. 1977).

Wolfert (1969) attributed a decrease in age of sexual maturity of Lake Erie walleye to a sharp reduction in walleye abundance. He also speculated that higher fecundity among walleye from the western basin of Lake Erie than those from the eastern basin could be due to differences in genetics and/or food supply. Baccante and Reid (1988) reported that burrowing mayflies (*Hexagenia limbata*) were a significant component of

walleye diets in two Ontario lakes and noted decreases in walleye fecundity during years when this prey was not abundant. Baccante and Reid (1988) concluded that because walleye fecundity appears responsive to changes in food supply, some indication of forage adequacy can be gained by comparing fecundity of populations from similar habitats.

Seasonal Movement Patterns of Tagged Walleye

Historically, angler tag returns have indicated that spawning walleye tagged in Missisquoi Bay do not disperse outside the Inland Sea (management Zone 5) and walleye tagged in the Lamoille River are rarely returned from sites other than Mallets Bay (Figure 1b) (Jon Anderson, VTF&W, personal communication). Seasonal movements of walleye from South Bay, the Poultney River and the Great Chazy River were assessed from angler tag return information. Walleye tag information was obtained from NYDEC for South Bay and the Great Chazy River. From 1983 to 1987, 14,820 walleye from South Bay were captured, tagged and released during mid-April. From 1983 to 1986 and 1988 to 1989, 1,967 walleye from the Great Chazy River were tagged and released. Tag information was obtained from VTF&W for Poultney River walleye. From 1988 to 1992, 2,841 walleye from the Poultney River were tagged during mid-April. Information on the date and place of recapture was obtained from angler tag returns.

Lake Champlain was divided into five tag return areas (Figure 16). Tag return areas 1-3 correspond to management Zones 1 - 3 established by VTF&W and NYDEC, but tag return areas 4 and 5 do not correspond to management Zones 4 and 5 (Figure 1b).

Walleye from South Bay and the Poultney River were tagged in Zone 1 at the southern end of the lake. Walleye from the Great Chazy River were tagged in Zone 5 at the northern end of the lake. Return sites reported by anglers were assigned to the appropriate area. The number of tag returns in each month of the year was tabulated for each return area. Returns were further divided on the basis of whether walleye were caught during the year (April-March) immediately after they were tagged (same year returns), or at a later date (other year returns). Same vs. other year returns were compared to determine if seasonal movements were repeated every year. Return months were grouped to increase sample size as follows: April-May, June, July, August, September-November and December-March. Data were analyzed using SAS (SAS Institute Inc. 1988).

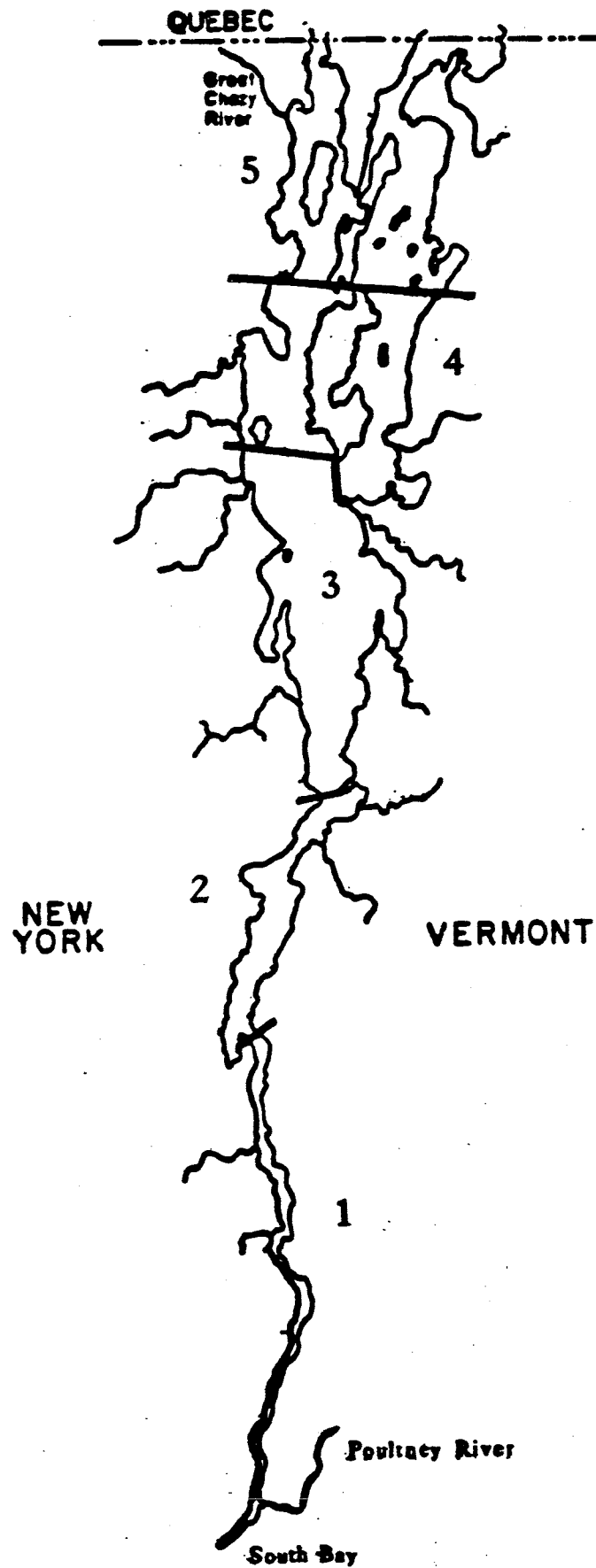


Figure 16. Map of Lake Champlain including three tagging sites (South Bay, Poultney River, Great Chazy River) and 5 angler tag return areas.

A total of 935 of the 14,280 South Bay tagged walleye (316 same year, 619 other year) were recaptured and reported with return month, year and site. There was a 6.6% recapture rate. Return site distributions of same year and other year returns were compared by months with Wilcoxon's nonparametric rank sum test. Distributions were not significantly different ($p>0.05$), indicating movements are not specific to the time fish were tagged, but may repeat on a seasonal basis. Although sample size becomes smaller, a detailed account of this seasonal movement of walleye from South Bay is obtained by dividing Lake Champlain into 18 sections (Figure 17) and observing 12 months. Figure 18 shows the migration cycle for the first 12 months after spawning. South Bay walleye exhibit an immediate post-spawn dispersal through the main lake (sections 11-13), which continues through September. October-November returns show the beginning, and December-March returns show the return to, the southern end of Lake Champlain. All returns were combined to increase sample size in representing seasonal movements (Figure 19). Since the opening of walleye season was changed to May in 1984 and there were no longer April returns, these two months were combined. Walleye originally collected in South Bay show a post-spawn dispersal up the lake through August, begin to return south during September-November and congregate closer to their spawning area during December-March.

A total of 62 of the 2,841 Poultney River tagged walleye were recaptured and reported with return month, year and site, which was a 2.2% recapture rate. Although the sample size is very small, Poultney River walleye showed the same general seasonal movement as walleye that spawn in South Bay (Figure 20). It appears that Poultney River walleye begin to return south sooner than those tagged in South Bay, however, the sample size is too small to draw this conclusion.

A total of 13 of the 1,967 Great Chazy River tagged walleye were recaptured and reported, which was a 0.7% recapture rate. Although the sample size is very small, the

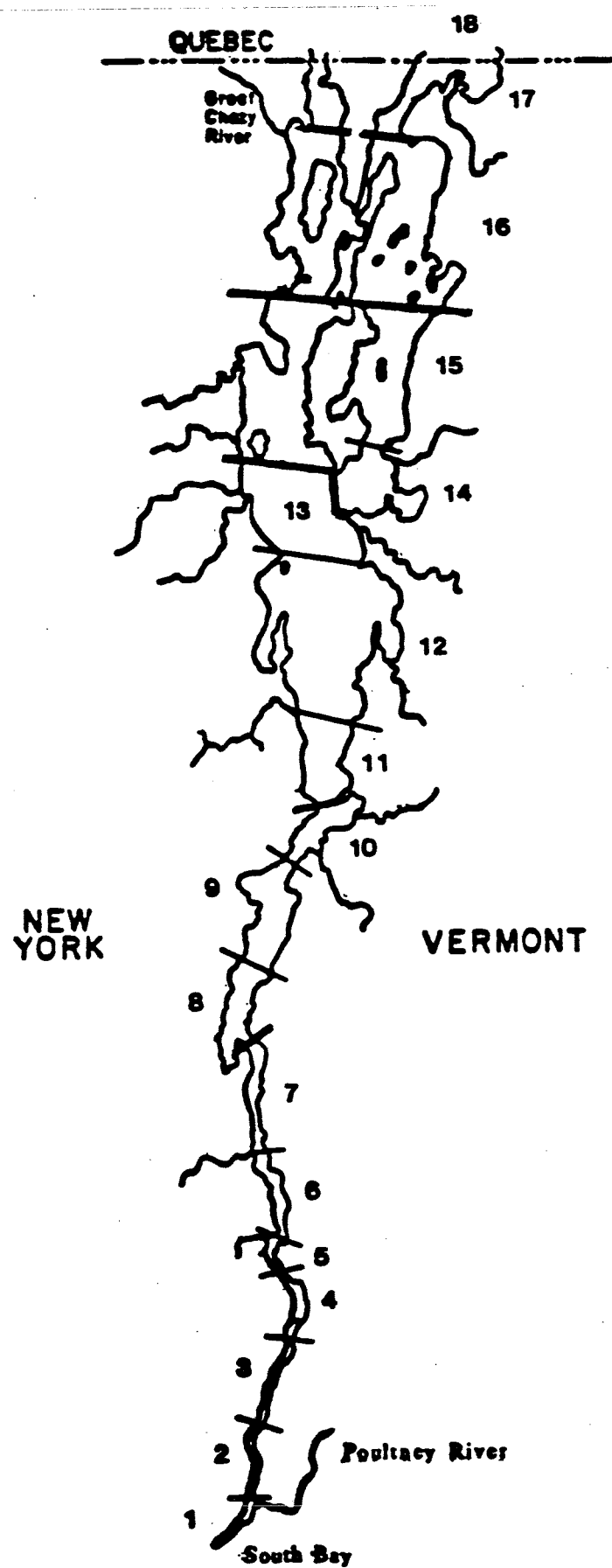


Figure 17. Map of Lake Champlain including three tagging sites (South Bay, Poultney River, Great Chazy River) and 18 angler tag return sections.

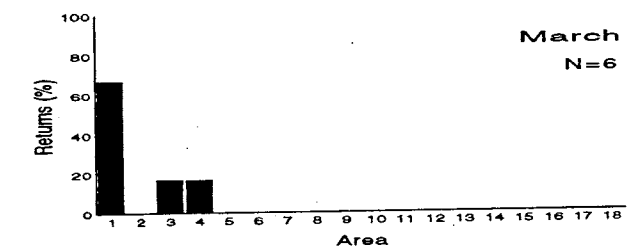
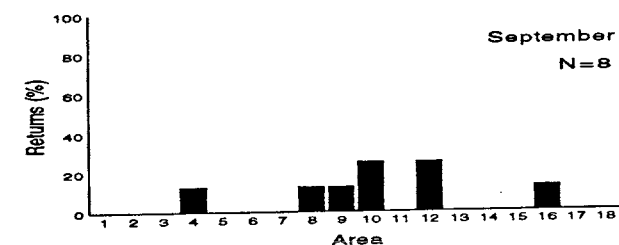
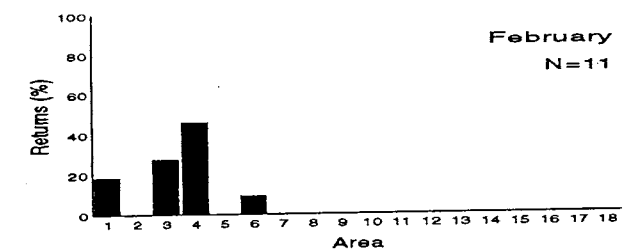
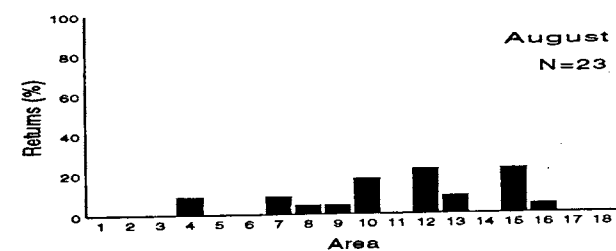
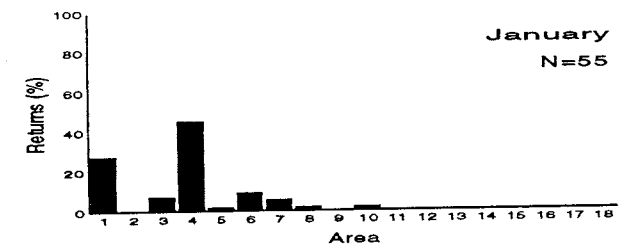
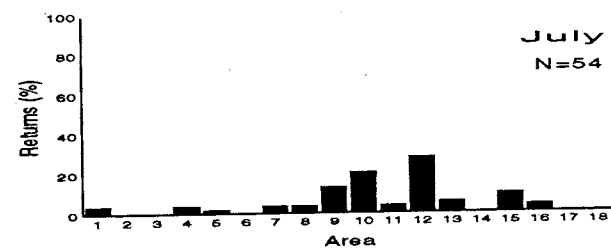
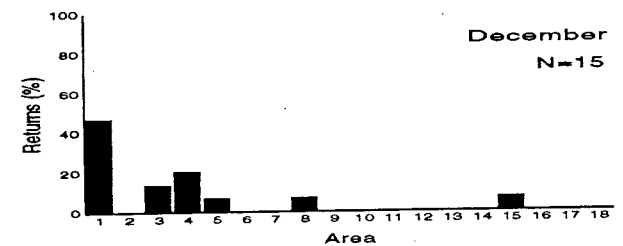
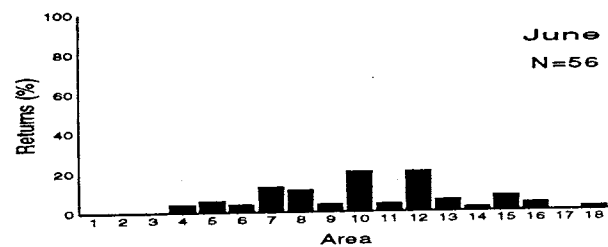
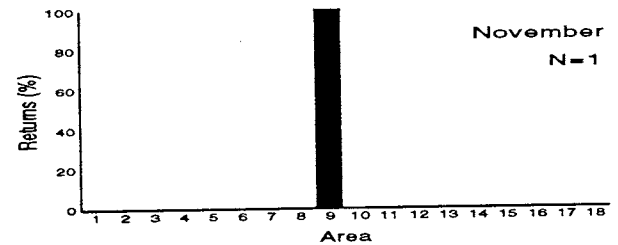
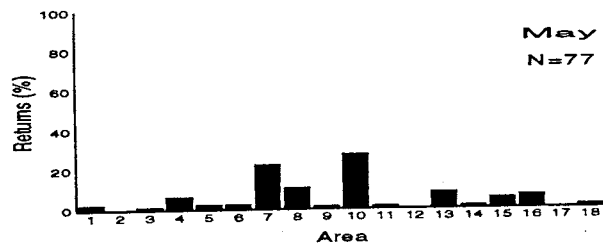
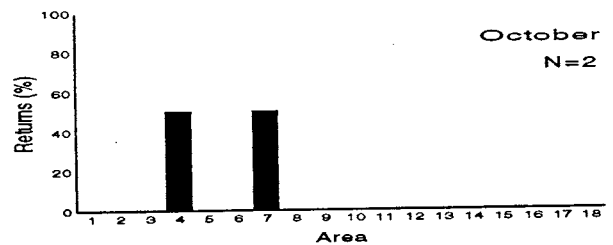
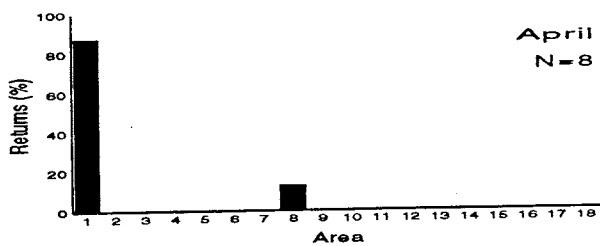


Figure 18. South Bay same year walleye returns (%; by month) from areas 1-18 during 1983-1987.

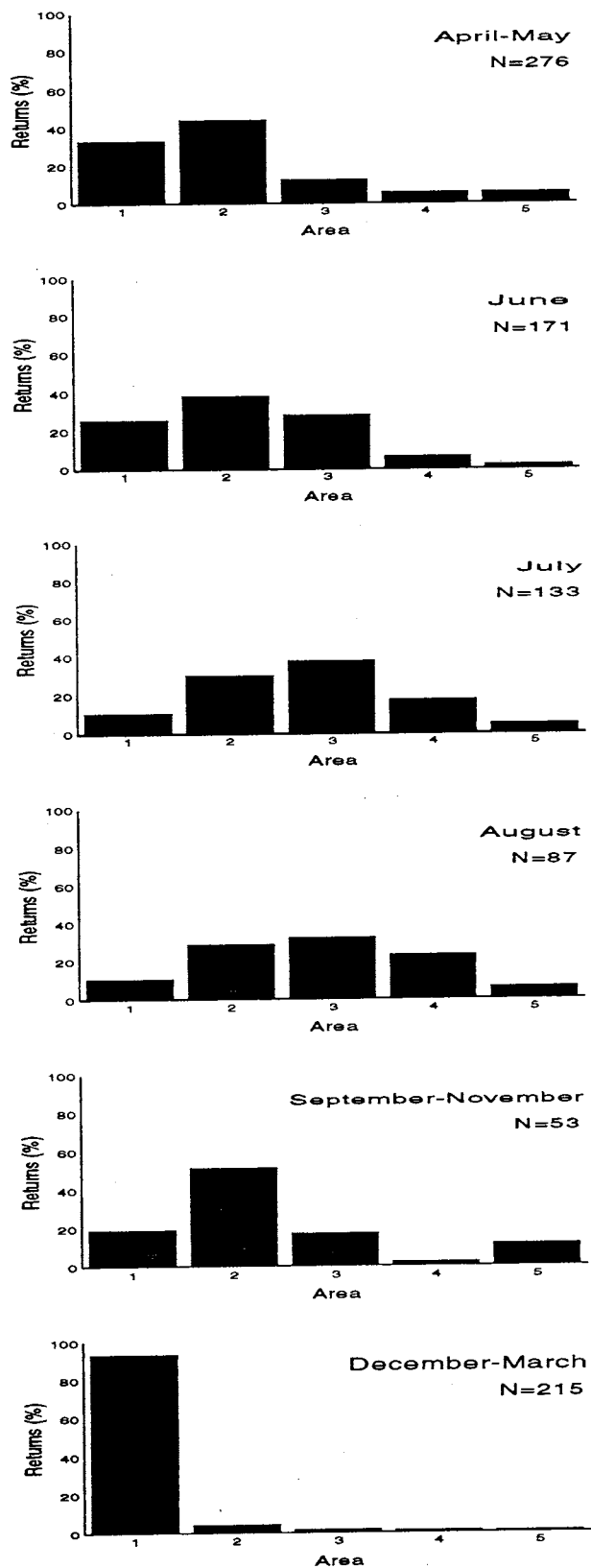


Figure 19. All South Bay walleye returns (%; by six time periods) from areas 1-5 during 1983-1987.

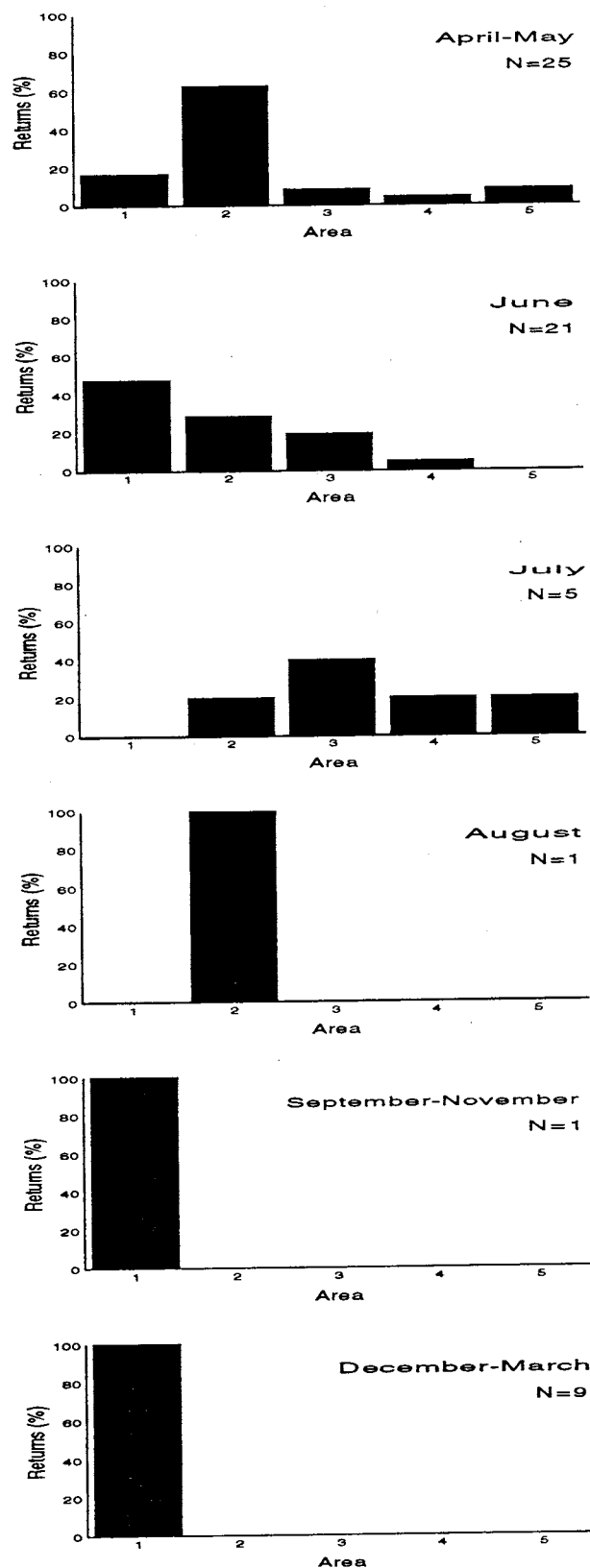


Figure 20.

All Poultney River walleye returns (%; by six time periods) from areas 1-5 during 1988-1992.

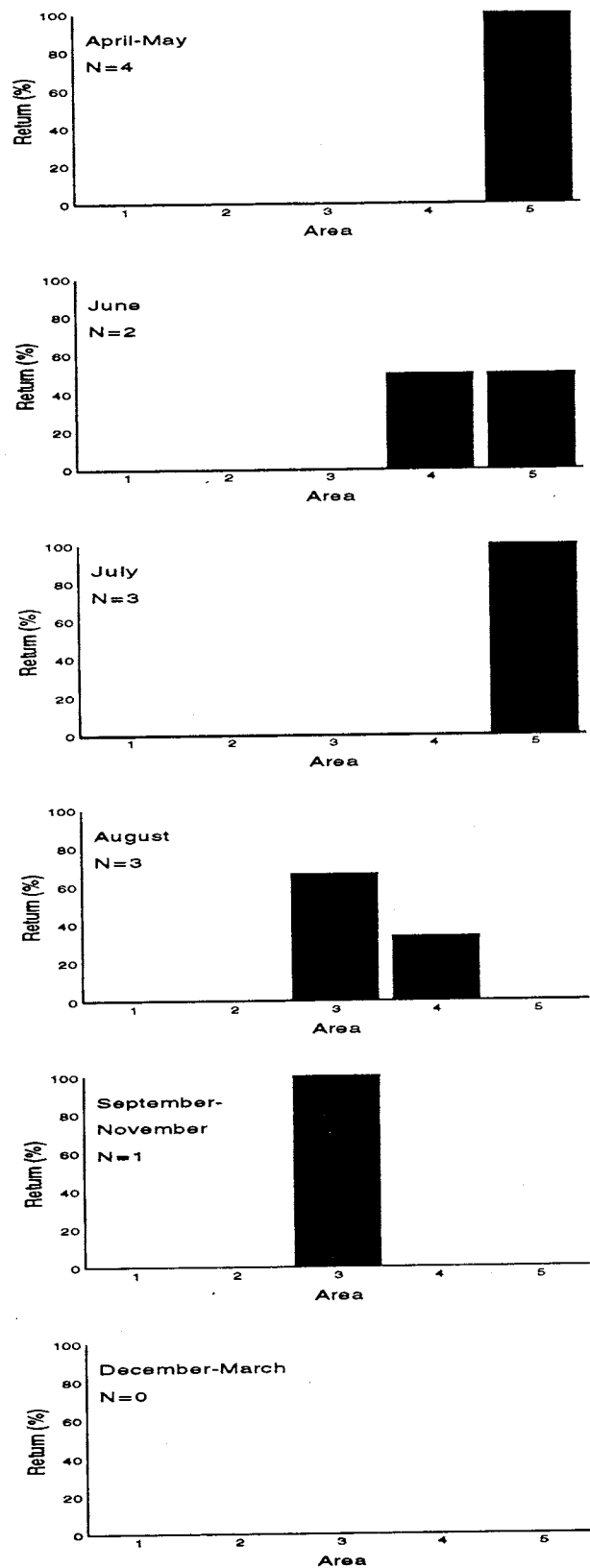


Figure 21. All Great Chazy River walleye returns (%; by six time periods) from areas 1-5 during 1983-1986 and 1988-1989.

recapture information indicates that Great Chazy River walleye show a post-spawn dispersal towards the main lake (Figure 21).

The most common return sites were areas 2 and 3 (Figure 16) from April-November. The beginning of area 2 is approximately 50 km north of South Bay. Walleye from South Bay and the Poultney River show long range movements in post-spawn dispersal. After spawning in early April, six fish from South Bay (same year returns) were recaptured in the northern-most area (area 5) in May. These fish traveled more than 100 km in less than two months, an average rate of at least 1.7 km/day. For comparison, Schram et al. (1992) found some walleye moving from Fond du Lac to Lake Superior at a maximum rate of 1.3 km/day. Ferguson and Derksen (1971) found one walleye to migrate 280 km from the Thames River (Lake St. Clair) spawning area to Saginaw Bay, Lake Huron, in only 31 days, a rate of 9 km/day.

Same vs. other year returns showed similar trends. This trend of other year returns may indicate cycling or seasonal events. Other studies have found that walleye tend to return to the same spawning area every year (Smith et al. 1951; Colby et al. 1979). Ferguson and Derksen (1971) found clear results of movements from early spring to summer repeated during several years of tagging. Available tag return data from Lake Champlain walleye show similar movement patterns.

Results of South Bay, Poultney River and Great Chazy River tag returns support those of Ferguson and Derksen (1971) and Colby et al. (1979) who describe a short spawning period (March-April), a feeding period (May-November) and an overwintering period (December-March) for walleye. Paragamian (1989) observed walleye in the Cedar River, Iowa, to concentrate and spawn within a very short time period. After spawning, tagged and returned walleye from South Bay and the Poultney River quickly disperse throughout the lake. Previous studies have shown post-spawning dispersal of walleye to often be rapid and to a considerable distance (Smith et al. 1951; Colby et al. 1979). This walleye movement pattern was also observed by Spangler et al. (1977) in the Canadian waters of

Lake Huron and by Ferguson and Derksen (1971) in the Thames River spawning population. Post-spawn movements of walleye from the Great Chazy River are considerably less than those of South Bay and Poultney River walleye (Figures 19 - 21). Schram et al. (1992) suggest that movement is a result of limnological and/or biological factors, including lake or stream morphometry, currents, water temperature, turbidity and food availability. According to Olson et al. (1978), some adult walleye migrate between a home spawning and home feeding area. There is often a wide dispersal during summer months that suggests fish from the same spawning area use separate feeding areas (Olson et al. 1978). Also, Holt et al. (1977) observed little relation between release point location of walleye and areas moved to after release in Lake Bemidji, Minnesota, suggesting mixing of fish coming from different spawning areas, as evidenced with returned walleye from South Bay and the Poultney River in Lake Champlain. Ferguson and Derksen (1971) also observed mixed stocks in summer feeding areas. Holt et al. (1977) found that types and amount of food available may be important in regulating the distance traveled to these areas because mean daily distance moved by walleye was least during the summer when food was available.

Post-spawn dispersal in Lake Champlain may be related to feeding. According to Knight et al. (1984), walleye select soft-rayed prey. From 1993 trawl catches in Lake Champlain, Zone 1 consists of predominantly spiny-rayed prey (white perch, Morone americana), and the main basin in Zone 3 consists of predominantly soft-rayed prey (rainbow smelt, Osmerus mordax). Stomach samples of walleye from the main basin have consisted mainly of smelt (Kirn 1986; LaBar and Parrish, unpublished data). If walleye prefer smelt over white perch, they would have to migrate from the southern end (South Bay and Poultney River fish) or stay in the northern end of Lake Champlain (Great Chazy River fish).

By December-March, the South Bay and Poultney River walleye have congregated in the southern end of the lake. No walleye from the Great Chazy River were returned

December-March. Ferguson and Derksen (1971) also observed a reversal in post-spawning migration in late fall to early spring. This migration away from the feeding area to the wintering ground adjacent to the spawning areas is the overwintering migration (Nikolsky 1963). Walleye that use such an area do so from December-March (Ferguson and Derksen 1971; Colby et al. 1979).

We must insert a cautionary note regarding our determination of walleye movement in Lake Champlain. This study may be biased by differences in fishing effort. Reported movement trends are accurate if fishing effort is similarly distributed across lake areas and return periods. Adequate fishing effort data were not available to compare with migration results and we do not know if fishing effort varied by return area. However, we can speculate that effort probably varied by month because late fall/early winter months had the fewest tag returns.

Recruitment, Survival, Population Sizes of Spawning Walleye

From 1983 to 1992, 21,916 walleye were sampled during spring spawning in Lake Champlain and its adjacent tributaries (Table 4). Two-thirds of these fish (65.7%) were collected in South Bay. Combining catches from the two areas sampled in southern Lake Champlain (South Bay and Poultney River) accounts for 78.3% of the walleye collected. These percentages reflect absolute catch and do not include measures of effort expended to collect samples.

Too few fish were recaptured in Lamoille River (N=5) and Missisquoi Bay (N=0) samples to estimate population sizes. Missisquoi River and Winooski River walleye were not tagged so population estimates based on recaptured fish were not possible for these rivers.

Estimates of spawning population size, annual survival and recruitment to the spawning population were calculated for the Great Chazy River, South Bay and Poultney River using two open population models: Jolly-Seber and Bailey (Ricker 1975) (Tables 5 - 7). Plotting the log of the number of recaptured fish versus time did not produce straight lines, indicating survival was variable between years (Ricker 1975). It was assumed that new individuals were recruiting to the spawning population each year. Bailey's and Jolly-Seber were used because they do not assume constant survival and allow estimates of additions to the population (recruitment) as well as losses (survival). Both models were modified for small sample sizes.

Petersen single census (Ricker 1975) estimates are included for comparison with past population size estimates calculated with that method (Table 5). However, because survival appeared to vary with year and recruitment was not assumed to be negligible, the Petersen model may overestimate true population sizes and may be inappropriate.

Table 4. Number of spawning walleye sampled in Lake Champlain and its tributaries from 1983 to 1992 (includes recaptured fish).

Area	Sampling Year										Total
	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	
South Bay	1,425	3,078	3,168	3,314	3,879						14,864
Great Chazy River	379	176	498	207		429	540				2,229
Missisquoi Bay			452	436				118			1,006
Poultney River						570	434	549	638	650	2,841
Lamoille River							162	301	330	410	1,203
Missisquoi River									181	169	350
Winooski River										142	142
All Sites	1,804	3,254	4,118	3,957	3,879	999	1,136	968	1,149	1,371	22,635

Table 5. Walleye population estimates. Numbers in parentheses are 1 standard deviation for Jolly-Seber and Bailey estimates, and 95% confidence intervals for Petersen estimates.

Stock Year	South Bay			Great Chazy River			Poultney River		
	Jolly-Seber (SD)	Bailey (SD)	Petersen (95% CI)	Jolly-Seber (SD)	Bailey (SD)	Petersen (95% CI)	Jolly-Seber (SD)	Bailey (SD)	Petersen (95% CI)
1983			350,396 (203,128 - 656,993)			7,612 (3,954 - 16,025)			
1984	197,788 (72,453)	163,191 (75,370)	251,206 (182,965 - 356,116)	6,531 (2,948)	5,869 (2,686)	6,216 (3,673 - 11,223)			
1985	263,078 (60,352)	323,186 (97,222)	374,318 (257,467 - 565,829)	3,664 (1,110)	2,692 (2,029)	7,422 (4,386 - 13,402)			
1986	161,292 (35,254)	226,931 (65,576)	215,275 (165,689 - 279,380)	7,457 (2,977)	5,914 (2,811)	10,477 (5,443 - 22,057)			
1987		137,503							
1988				3,642 (1,133)	2,414 (1,431)	5,904 (4,226 - 8,545)			118,699 (35,969 - 215,816)
1989					1,990		3,732 (4,245)	5,764 (---)	14,238 (8,829 - 24,234)
1990							8,018 (3,246)	11,160 (5,007)	20,521 (12,726 - 34,929)
1991							5,037 (1,721)	6,070 (2,450)	8,543 (6,332 - 11,492)
1992								2,703	

Table 6. Bailey's population estimates for walleye collected in Lake Champlain and its tributaries from 1983 to 1992 (modified for small sample size).

Stock Year	South Bay			Great Chazy River			Poultney River		
	Population Est	Survival	Recruitment	Population Est	Survival	Recruitment	Population Est	Survival	Recruitment
1983		0.479			0.711				
1984	163,191	1.000	37,044	5,869	0.433	0			
1985	323,186	0.606	29,087	2,692	0.797	1,429			
1986	226,931		0	5,914	0.230	2,555			
1987	137,503								
1988				2,414		1,308		0.049	
1989				1,990			5,764	0.784	0
1990							11,160	0.296	5,033
1991							6,070		1,159
1992							2,703		

Table 7. Jolly-Seber population estimates for walleye collected in Lake Champlain and its tributaries from 1983 to 1992 (small sample modification).

Stock Year	South Bay			Great Chazy River			Poultney River		
	Population Est	Survival	Recruitment	Population Est	Survival	Recruitment	Population Est	Survival	Recruitment
1983		0.487			0.855				
1984	197,788	1.000	63,316	6,531	0.555	42			
1985	263,078	0.517	25,284	3,664	0.941	4,016			
1986	161,292			7,457	0.311	1,323			
1987									
1988				3,642				0.054	
1989							3,732	0.576	5,873
1990							8,018	0.276	2,825
1991							5,037		

Jolly - Seber stochastic model:

$$\beta_i = \frac{(M_i + 1)(K_i)}{R_i + 1} + m_i + 1$$

$$N_i = \frac{(\beta_i)(C_i + 1)}{m_i + 1}$$

$$S_i = \frac{\beta_{i+1}}{\beta_i - m_i + M_i}$$

$$B_i = N_{i+1} - S_i(N_i - C_i + M_i)$$

where,

β_i = number of marked fish in the population just prior to capturing the i th sample

R_i = number of fish recaptured at time i

N_i = number of fish in the population just prior to capturing the i th sample

S_i = survival rate from time i to time $i + 1$

M_i = number of fish newly marked

K_i = number of fish recaptured later than time i of fish marked before time i

m_i = number of fish recaptured at time i

C_i = number of fish examined for marks at time i

B_i = number of fish added to the population between times i and $i + 1$ and

surviving to time $i + 1$.

Bailey's deterministic model:

$$N_t = \frac{(M_t)(C_{t+1})(R_{t-1, t+1})}{(R_{t-1, t} + 1)(R_{t, t+1} + 1)}$$

$$S_{t-1, t} = \frac{(M_t)(R_{t-1, t+1})}{(M_{t-1})(R_{t, t+1} + 1)}$$

$$r_{t, t+1} = \frac{(R_{t-1, t})(C_{t+1} + 1)}{(C_t)(R_{t-1, t+1} + 1)}$$

where,

N_t = population estimate at time t

M_t = number of fish newly marked at time t

C_t = number of fish examined for marks at time t

C_{t+1} = number of fish examined for marks at time $t+1$

$R_{t-1, t+1}$ = number of fish tagged at time $t-1$ and recaptured at time $t+1$

$R_{t-1, t}$ = number of fish tagged at time $t-1$ and recaptured at time t

$R_{t, t+1}$ = number of fish tagged at time t and recaptured at time $t+1$

$S_{t+1, t}$ = survival rate between time $t-1$ and time t

$r_{t, t+1}$ = rate of accession of new recruits between time t and time $t+1$

Petersen's single census model:

$$N = MC/R$$

where,

N = size of population at time of marking

M = number of fish marked

C = number of fish captured and examined for marks

R = number of marked fish recaptured

Spawning population estimates for South Bay ranged from 161,292 (Jolly-Seber) in 1986 to 323,186 (Bailey's) in 1985 (Table 5). Spawning population estimates for the Great Chazy River were considerably lower than for South Bay, ranging from 1,990 (Bailey's) in 1989 to 7,457 (Jolly-Seber) in 1986. Poultney River estimates ranged from 2,703 (Bailey's) in 1992 to 11,160 (Bailey's) in 1990. No trends were noted in survival or recruitment rates, but population estimates cycled up and down in alternate years.

Information on recruitment of walleye to the Lake Champlain sport fishery is not available. Madenjian and Carpenter (1991) describe recruitment variability as the central problem facing fishery scientists and a significant cause of uncertainty in fisheries management. Although attempts to establish a relation between the number of spawning adults and the strength of subsequent year classes have been largely unsuccessful (Gulland 1983), abundance estimates of a given age class are often used to predict recruitment to subsequent age or size classes. For example, a high correlation between gill net catches of age-0 walleye in a given year and age-1 walleye the following year in six Kansas reservoirs allows managers to use estimates of age-0 abundance to predict recruitment to age-1 (Willis 1987). A similar correlation between age-0 and age-1 walleye abundance measured with electrofishing catch per effort data has been reported for Wisconsin lakes (Serns 1982, 1983). The Lake Erie Walleye Task Group of the Great Lakes Fishery Commission uses fall gill net catches of age-1 walleye to predict the number of fish that will recruit to age-2 the following year (Knight et al. 1993).

Forney (1962a), however, suggests that annual variability in overwinter mortality the first year may obscure any relation between fall abundance of age-0 walleye and the abundance of age-1 walleye the following year. Forney (1961) also reported efforts to index the abundance of age-0 walleye in Oneida Lake were seriously hampered by annual shifts in the distribution of the population.

Being able to identify strong and weak year classes allows managers to more effectively adjust harvest regulations to avoid over- or under-exploitation. Schneider and Leach (1977) noted that the decline of several Great Lakes walleye stocks from 1800 to 1975 could be traced to a series of weak year-classes.

LaBar and Parren (1983) estimated survival rates from 1953 to 1964 for south lake (Zone 1), Great Chazy River and Missisquoi Bay stocks using Chapman and Robson's proportional age-class method. LaBar and Parren's (1983) calculations included only walleye 6 to 10 years old. The Chapman-Robson approach assumes recruitment and

survival remain constant for each year class (Everhart and Youngs 1981). These assumptions were probably violated for the 1983 - 1986 walleye year classes, but survival rates were calculated for these years using Chapman-Robson to allow comparison with the survival estimates of LaBar and Parren (1983).

Annual survival rate estimates for 6 to 10 year old spawning walleye collected from 1983 to 1986 from south lake and Missisquoi Bay stocks appear similar to LaBar and Parren's (1983), 1953 - 1962 estimates (Table 8). Estimated average annual survival from 1958 to 1961 for Great Chazy walleye was 0.68 (LaBar and Parren 1983) compared with 0.53 - 0.60 from 1983 to 1986 (Table 8).

Survival rates of Lake Champlain walleye appear to be similar to survival rates reported from other large-lake systems. Survival of Lake Superior (Nipigon Bay) walleye larger than 356 mm was estimated at 0.45 by Ryder (1968) for the period 1955 to 1957. In Escanaba Lake, Wisconsin, adult walleye survival averaged 0.53 from 1960 to 1969 (Kempinger and Carline 1977). Forney (1962b) sampled spawning walleye in Oneida Lake, New York from 1957 to 1959 and reported annual survival rates of 0.45 to 0.87.

Table 8. Chapman-Robson annual survival estimates for Lake Champlain walleye (ages 6 to 10). Estimates for years prior to 1983 from LaBar and Parren (1983).

Stock	Year	Annual Survival Rate
south lake	1961 - 1962	0.60
	1983	0.61
	1984	0.65
	1986	0.55
Great Chazy River	1958 - 1961	0.68
	1983	0.58
	1984	0.53
	1985	0.60
	1986	0.57
Missisquoi Bay	1953, 1956 - 1962	0.54
	1985	0.58
	1986	0.59

Harvest

Commercial Fishing

The Canadian government ended commercial walleye fishing in 1971 because of concern about mercury contamination (Anderson 1974). There is no commercial fishing of walleye currently allowed on Lake Champlain (Brian Chipman, VTF&W, personal communication). Historic rates of commercial walleye harvest in Lake Champlain were summarized by LaBar and Parren (1983).

Angling Regulations

Angling regulations in the form of creel, size and season restrictions, have been a major focus of walleye management for Lake Champlain. Creel limits, the number of walleye an angler may harvest per day, do not protect stocks from overharvest, but serve to divide the catch among individual anglers (Noble 1980). Minimum size limits have been used to protect young fish until they reach a legally harvestable size. Everhart and Youngs (1981) caution that size limits do not increase brood stock if small fish protected from fishing mortality are lost to a subsequent increase in natural mortality. Size and creel limits are most effective when productivity is low, fishing pressure is high, and for species prone to widely fluctuating population levels (Noble 1980; Brousseau and Armstrong 1987). Walleye are particularly vulnerable to capture during spawning, when large groups congregate in shallow water. Lake Champlain walleye are currently protected by a closed season during the spawning period. Recent walleye sport fishing regulations on Lake Champlain are presented in Tables 9 and 10. Information on size at age of walleye harvested in the Lake Champlain sport fishery is limited to that provided by the small number of anglers who returned jaw tags, making it difficult to evaluate how changes in fishing regulations would affect walleye or their prey.

Table 9. Vermont walleye sport fishing regulations for Lake Champlain (adapted from Vermont Digest of Fish and Wildlife Laws 1978 - 1985).

Year	Daily Creel Limit	Possession Limit	Minimum Length	Season
1978	5	10	381 mm (15 inches)	Last Saturday in April to March 15 south of Crown Point Bridge. No closed season rest of lake.
1984	5	10	457 mm (18 inches)	Last Saturday in April to March 16 in Mallets Bay and the Inland Sea. Second Saturday in May to March 16 on remainder of lake.
1985	5	10	457 mm (18 inches)	First Saturday in May to March 15 entire lake.

Table 10. New York walleye sport fishing regulations for Lake Champlain (Jennie Sausville, NYDEC, personal communication).

Year	Daily Creel Limit	Minimum Length	Season
1982/83	5	381 mm (15 inches)	Last Saturday in April to March 15 south of Crown Point Bridge. No closed season rest of lake.
1984/85	5	381 mm (15 inches)	First Saturday in May through March 15 entire lake.
1991/92	5	457 mm (18 inches)	First Saturday in May to March 15 entire lake.

Catch Rates

Catch rates (number of walleye caught per angler hour) and harvest rates (number of walleye creel per angler hour) are commonly used measures of fishing quality, but it should be noted that acceptable catch and harvest rates for walleye are often lower than those for other sport fish. For example, a catch rate above 0.10 (1 walleye every 10 hours) is considered a good fishery (Festa et al. 1987). In contrast, trout and bass anglers average 0.50 fish per hour in many New York waters (Festa et al. 1987) and the Vermont Department of Fish and Wildlife (1993) has recommended targeting 0.50 rainbow (Oncorhynchus mykiss), brook (Salvelinus fontinalis) or brown (Salmo trutta) trout per hour as an average catch rate for Vermont lakes and streams.

There is generally a positive correlation between catch rate and walleye density (Festa et al. 1987), but even dramatic changes in catch or harvest rates between years do not necessarily indicate changes in walleye abundance (Forney 1980; Johnson and Staggs 1992). Forney (1980) observed that harvest rates in Oneida Lake increased from 0.08/hr in 1958 to 0.34/hr in 1959 even though walleye abundance was similar in both years. Forney (1980) suggested that because prey were scarce in 1959, walleye were more likely to pursue angling bait. Possible changes in vulnerability of walleye to angling should be considered when comparing catch or harvest rates. Long-term trends in catch or harvest rates can be more indicative of underlying changes in walleye abundance (Tyler and Gallucci 1980; Sigler and Sigler 1990).

Festa et al. (1987) examined catch rates of anglers targeting walleye in several lakes and concluded that catch rates between 0.05 and 0.10 per hour represented fair quality walleye fishing and that catch rates exceeding 0.20 per hour were above average. The current walleye sport fishery on the Michigan and Ontario portions of Lake Erie is considered exceptional with catch rates between 0.20 and 0.50 fish per angler hour (Knight et al. 1993). In comparison, 1992 walleye catch rates in the New York portion of Lake Erie were only 0.06 fish per angler hour (Culligan et al. 1993). Culligan et al. (1993)

speculated that differences in distribution and catchability were responsible for the variability in catch rates among different portions of Lake Erie.

Creel Surveys (refer to Figure 1b for lake zone locations)

Winter ice-fishing creel surveys were conducted in Zone 1 in 1952 - 1955 (Halnon 1956) and 1991 (MacKenzie 1992b.) Halnon (1952) defined Zone 1 as extending from Maple Bend in West Haven, Vermont to the south side of the Lake Champlain Bridge in Addison, Vermont. MacKenzie (1992b) included the area south of Maple Bend to East Bay in Zone 1 and divided the zone into four areas: 27, 28, 29 and 30. Halnon's (1952) Zone 1 corresponds approximately to the portion of Lake Champlain included in areas 27, 28 and 29 defined by MacKenzie (1992b). Both MacKenzie (1992b) and Halnon (1952, 1953, 1955, 1956) included information from the New York side of Lake Champlain in creel results. Results of the creel surveys conducted during the 1950's were compared with information collected from areas 27, 28 and 29 in 1991 (Table 11).

Average total length varied from 420 to 460 mm during the 1950's surveys, but had increased to 544 mm in 1991 (Table 11). It is difficult to compare angler effort and walleye harvest for the two time periods because the 1991 figures represent creel data extrapolated to estimate total effort and harvest during the entire creel period, but data from the 1950's surveys include only the effort and harvest of anglers actually surveyed.

Halnon (1952) estimated that fishing intensity measured in the 1952 creel was 1/7th of the effort expended throughout Zone 1 during the entire 1952 winter fishing season. Multiplying the 1952 figures by 7 yields an angler effort of 44,744 hours and a harvest of 1,561 walleye. In comparison, 41,931 angler hours and 1,283 harvested walleye were estimated for the 1991 winter season. It should be noted that the 1952 creel represented primarily weekday fishing (71% of creel days), but the majority of creel days in the 1991 survey were weekends or holidays (58% of creel days). Since fishing effort was lower on

Table 11. Summary of winter creel surveys conducted in Lake Champlain Zone 1, excluding area 30, during the years 1952 - 1956 and 1991.

Creel Period	No. weekdays in Creel (%)	No. weekend days in Creel (%)	Angler effort (hours)	No. of walleye harvested	Ave. total length (mm)	No. walleye harvested per angler hour
01/02/52 - 03/28/52	15 (71)	6 (29)	6,392	223	420 a	0.035
12/14/52 - 03/26/53	17 (67)	7 (33)	6,080	196	460 a	0.032
12/19/53 - 03/23/54	17 (67)	7 (33)	7,056	227	445 a	0.032
01/08/55 - 03/20/55	6 (100)	0 (0)	1,969 a	123 a	438 a	0.062 a
01/07/91 - 03/15/91	10 (42)	14 (58)	41,931 b	1,283 b	544 c	0.031 b

a Includes data from Vermont side of Lake Champlain only.

b Extrapolated to entire creel season.

c Includes walleye from area 30.

weekdays (Halnon 1956), figures from the 1952 survey may have been higher had the same proportion of weekend/holiday days been used in 1952 as in 1991.

The number of walleye harvested per angler hour during the 1950's winter creel surveys varied from 0.032 in 1953 and 1954 to 0.062 in 1955 (Table 11). The 1991 winter creel harvest rate of 0.031 walleye per angler hour was similar to rates recorded in the 1950's.

Vermont personnel conducted daytime, stratified, roving creel surveys on Lake Champlain during the summers of 1985 (Zones 1-4), 1986 (Zone 3), 1987 (Zones 5A and 5B) and 1991 (Zone 1). Sampling procedures and dates for these surveys can be found in Anderson (1990b) and MacKenzie (1992a). Harvest rates ranged from 0.01 to 0.05 walleye per angler hour (Table 12).

Information on the walleye fishery was incidentally collected during creel surveys designed to sample salmonid anglers in the summers of 1990 (Zones 2,3,4 and 5), 1991 (Zones 3,4 and 5) and 1992 (Zone 2), and the winters of 1991 (Zones 2,3 and 5) and 1992 (Zones 2,3 and 5) (Chipman 1991, 1992, 1993a, b). The percent of anglers targeting walleye in these creels ranged from 0 to 16% and walleye-targeted harvest rates varied between 0.00 and 0.08 (Table 12).

Harvest rates in Zone 1 (south lake) summer creel surveys were 0.18 walleye per hour in 1976 and 0.05 walleye per hour in 1977 (LaBar and Parren 1983). Zone 1 harvest rates were lower in 1985 (0.05 walleye per hour) and 1991 (0.02 walleye per hour) summer creels (Table 12). However, changes in angling regulations in 1978, 1984 and 1985 (Tables 9 and 10) may have influenced the 1985 and 1991 harvest rates.

In 1978, the daily creel limit was lowered from 10 to 5 walleye, the minimum size limit was raised from 305 mm to 381 mm, and the season was closed in Zone 1 from March 16 to the last Saturday in April. The creel limit remains at 5 walleye per day, but in 1984 the minimum size limit was raised to 457 mm and the Zone 1 season was shortened to the second Saturday in May to March 16th. In 1985, the season for the entire lake was

Table 12. Angler effort, number harvested and harvest rates of walleye from VTF&W Lake Champlain creel surveys.

Year	Season	Lake zone	Effort (hrs)	Estimated harvest (no.)	Catch rate (no./hr.)
1985	summer	1	35,325	1,596	0.05
		2	77,601	1,622	0.02
		3	87,474	1,594	0.02
		4	22,088	291	0.01
1986	summer	3	152,656	902	0.01
1987	summer	5A		22	
		5B		226	
1990	summer	2			0.08 ^a
		3			0.01 ^a
		4			0.04 ^a
		5			0.02 ^a
1991	summer	1	103,135	1,561	0.02
		3			0.02 ^a
		5			0.00
	winter	2		15	
		3		0	
		4		0	
		5		483	
1992	summer	2			0.02 ^a
1992	winter	2		5	
		5		0	

^a estimated harvest rate of anglers specifically targeting walleye

Table 13. 1991 spring (early to late-May) creel survey results (Brian Chipman, VTF&W, unpublished data).

River	Angling Effort (hrs)	Number of Walleye Caught	Number of Walleye Harvested	Number of Walleye Caught per Hour	Average Total Length (N) of Harvested Walleye
Missisquoi River	3,439	151	104	0.040	528 mm (9)
Lamoille River	3,309	2,053	414	0.122	518 mm (29)
Winooski River	24,743	4,075	2,749	0.215	536 mm (48)
Otter Creek	16,180	410	308	0.043	547 mm (40)

changed to begin on the first Saturday in May and continue through March 15. Harvest rates in 1976 and 1977 reflect a longer fishing season and may have included fish that would have been illegal to harvest in the 1985 and 1991 creels.

Harvest rates from Vermont's Lake Champlain creel surveys reflect only daytime fishing and include angling effort not necessarily directed at walleye unless otherwise noted. Colby et al. (1979) reported total catch rates were below 0.05 walleye per angler hour in 43% of over 100 North American walleye waters examined. Catch rates of anglers specifically targeting walleye were somewhat higher: 44% of the lakes had catch rates between 0.06 and 0.15 walleye per hour. Staggs (1989) reviewed 50 creel surveys of walleye lakes in northern Wisconsin and reported an average harvest rate of 0.04 walleye per hour among all anglers, but a 0.104 per hour harvest rate for anglers specifically fishing for walleye.

Anglers specifically targeting walleye in the Missisquoi, Lamoille and Winooski rivers and Otter Creek were surveyed from early to late-May 1991. Catch rates were highest in the Winooski River (0.215 walleye per angler hour) and lowest in the Missisquoi River (0.040 walleye per angler hour) (Table 13). A total of 6,689 walleye were caught in the four rivers, with the majority caught in either the Winooski (4,075) or Lamoille (2,053) rivers. Of those fish caught, 3,575 (53.4%) were harvested. Average length was greatest for walleye harvested from Otter Creek (547 mm) and smallest for Lamoille River fish (518 mm), however, total lengths were based on small sample sizes (9 - 48 fish).

Spring creel surveys of walleye anglers were also conducted on the Missisquoi, Lamoille and Winooski rivers and Otter Creek from 1971 to 1980 (LaBar and Parren 1983). Angling effort (number of hours spent fishing) on the Missisquoi and Lamoille rivers was much lower in 1991 than in previous years (Figures 22 and 23) and there was a significant negative correlation between year and angling effort for the Missisquoi River (Table 14). Thus, springtime angling effort appears to be decreasing on the Missisquoi River. Regression equations modeling the relation between year and number of walleye

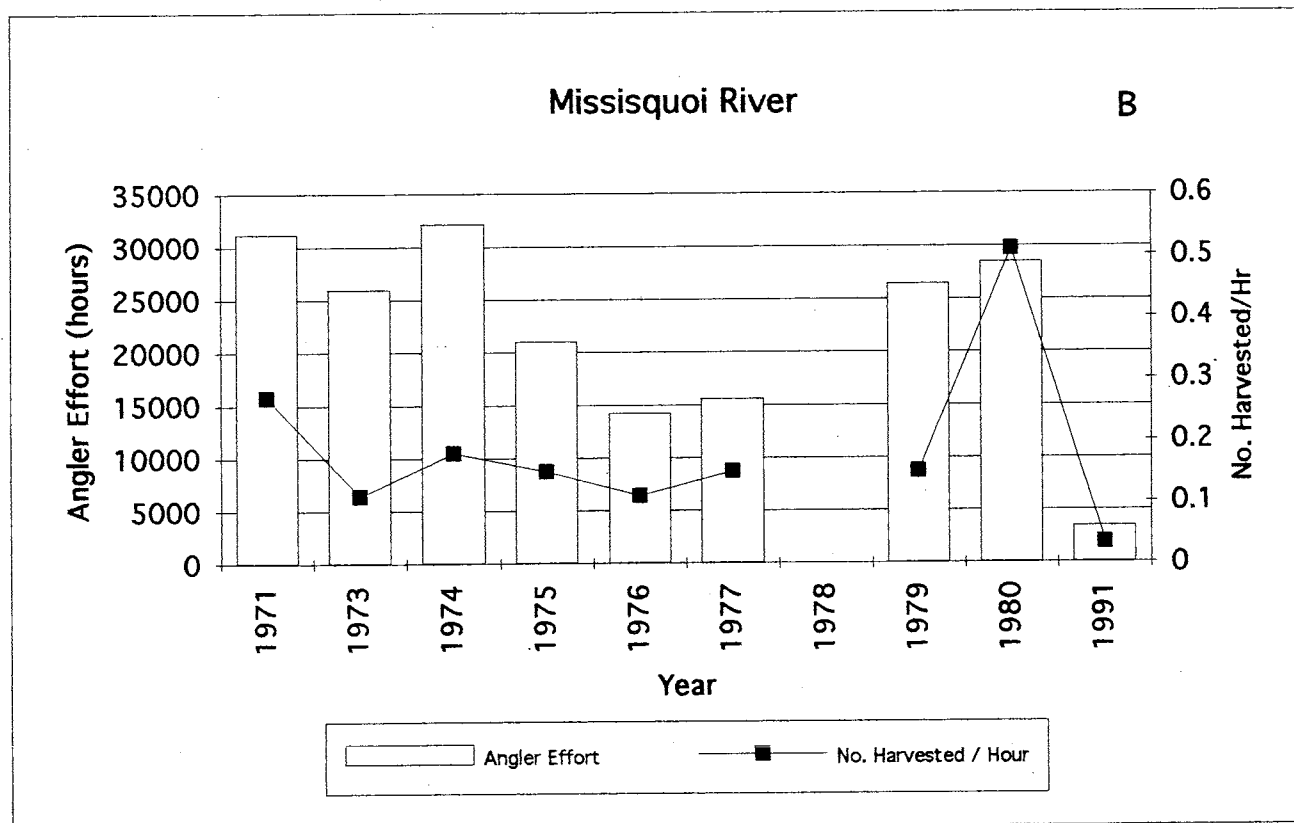
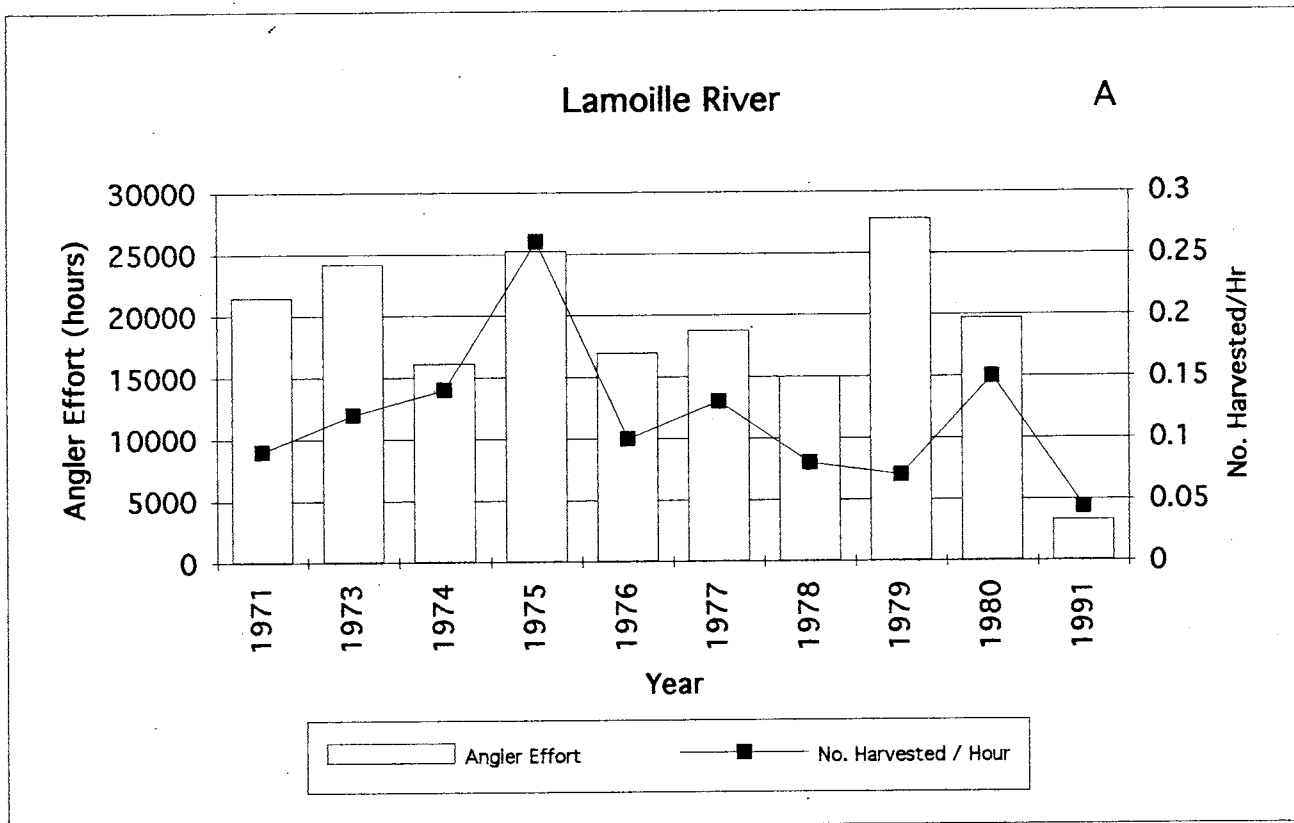


Figure 22. Effort and harvest rates of walleye anglers recorded during spring creel surveys of Lake Champlain tributaries from 1971 to 1991.

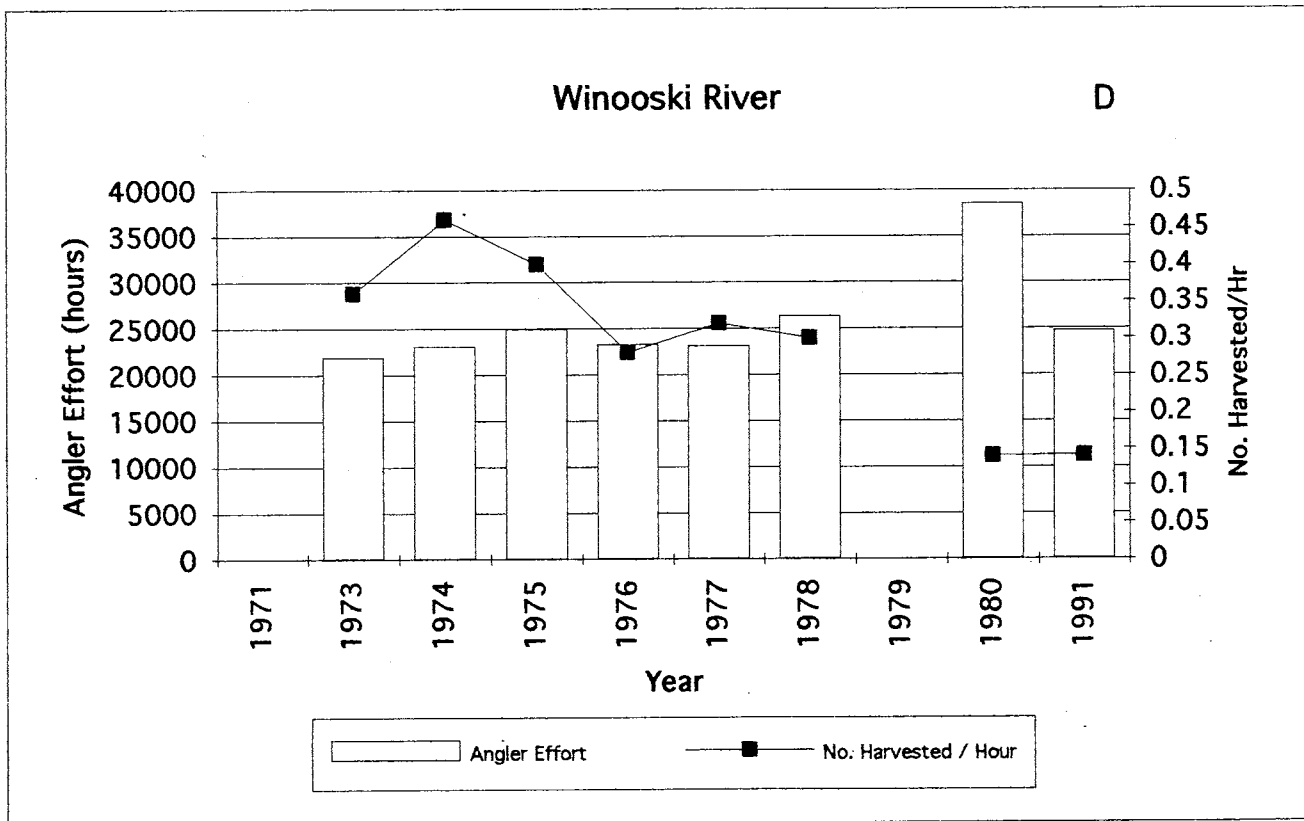
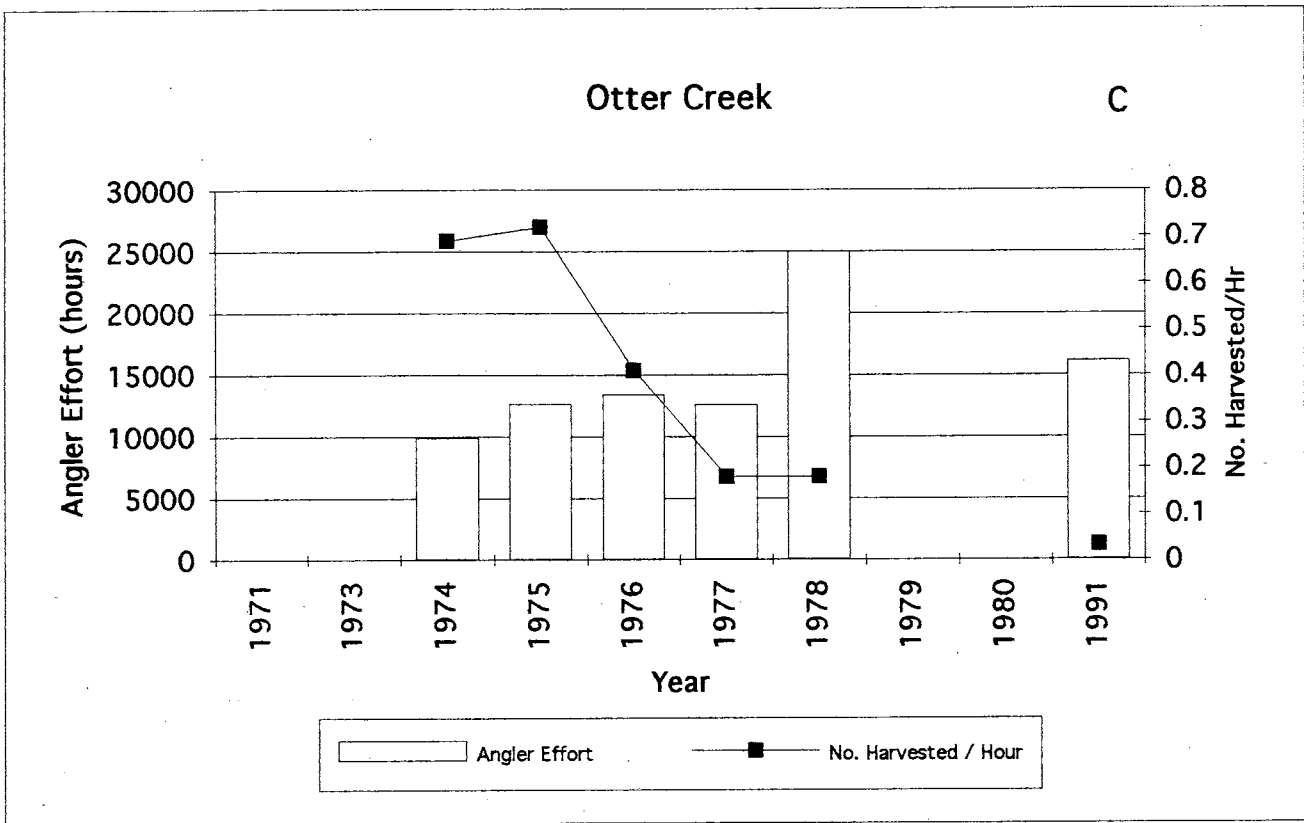


Figure 22 (continued).

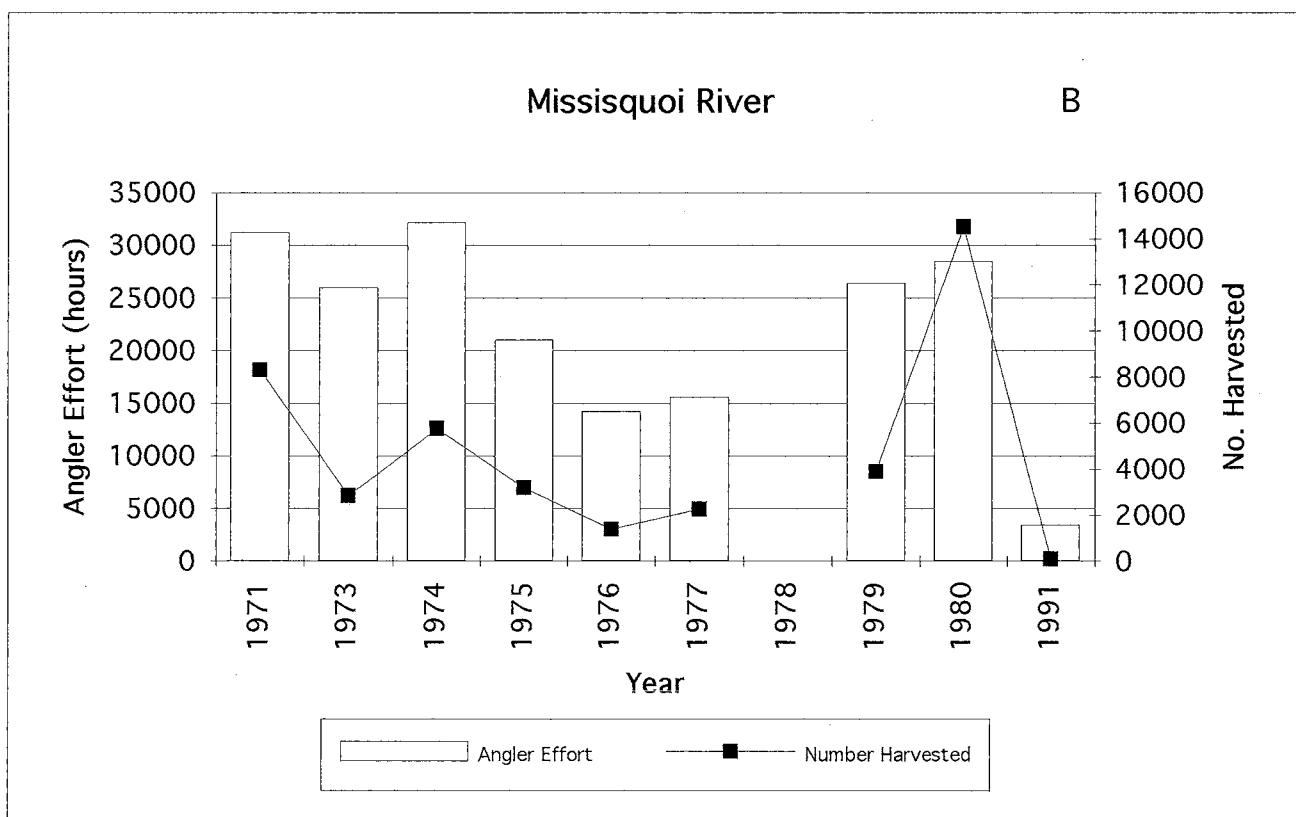
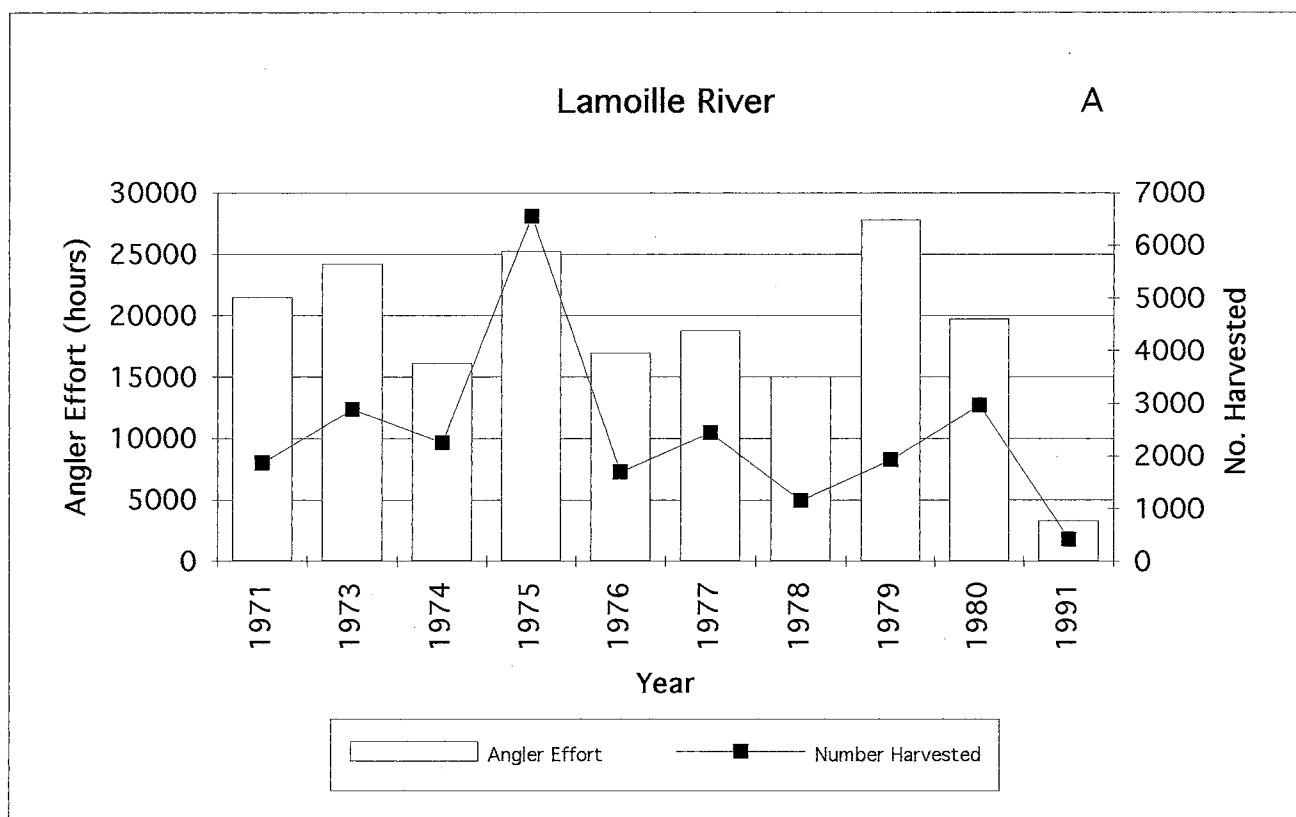


Figure 23. Effort and harvest of walleye anglers recorded during spring creel surveys of Lake Champlain tributaries from 1971 to 1991.

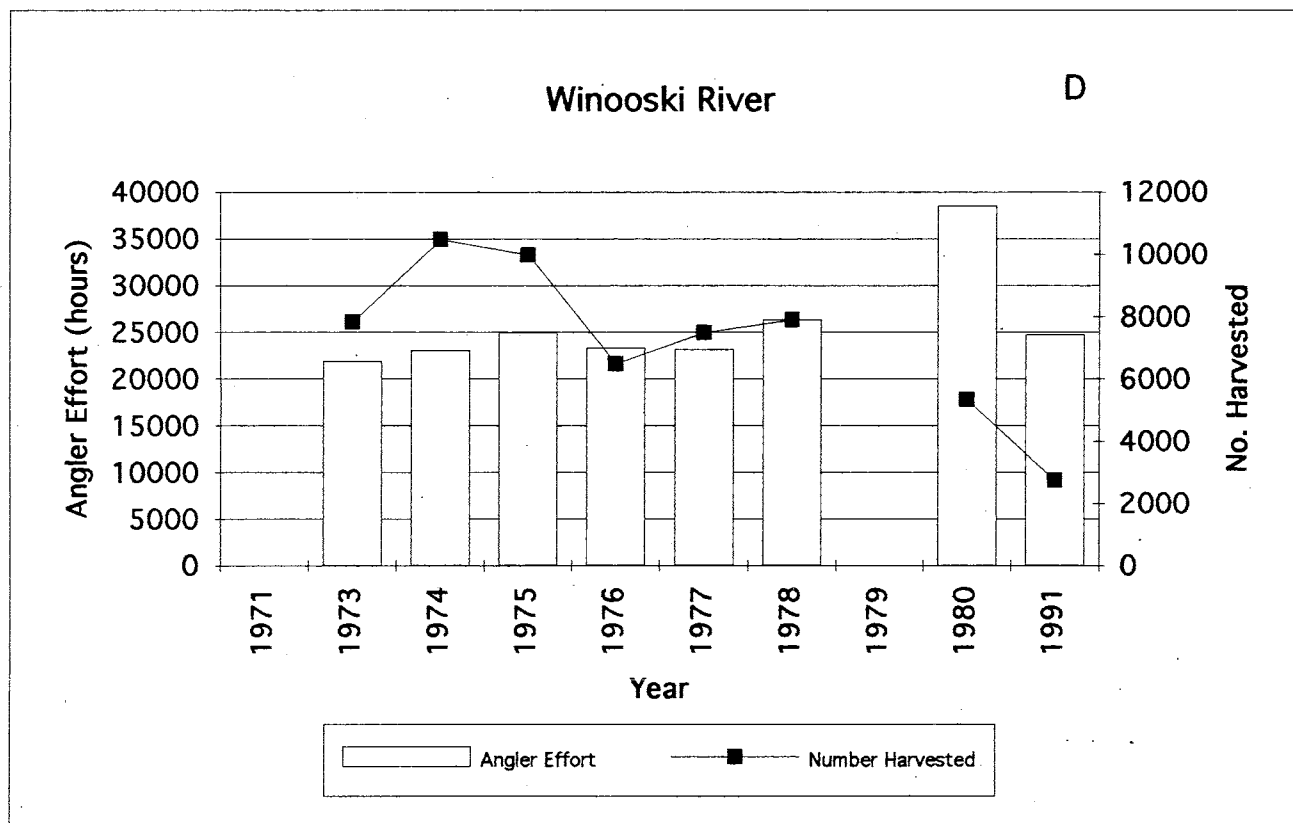
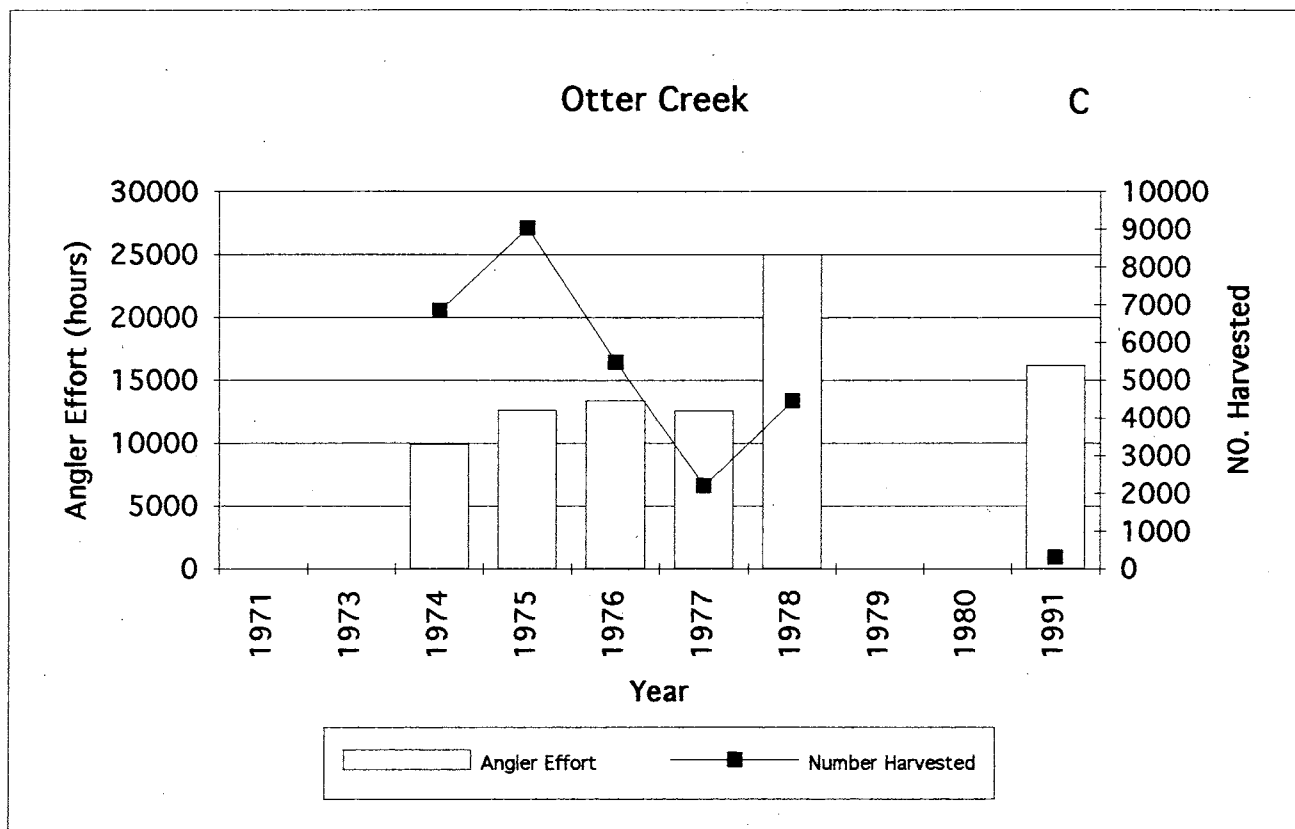


Figure 23 (continued).

Table 14. Correlation coefficients (probability > r) between sampling year, effort (number of hours spent fishing), number harvested and HPUE (harvest per unit of effort) for spring walleye angler creel surveys on Lake Champlain tributaries. Lamoille River anglers surveyed in 1971, 1973 - 1980 and 1991 (N=10 years), Missisquoi River anglers surveyed in 1971, 1973 - 1977, 1979 - 1980 and 1991 (N=9 years), Otter Creek anglers surveyed in 1974 - 1978 and 1991 (N=6 years) and Winooski River anglers surveyed in 1973 - 1978, 1980 and 1991 (N=8 years).

Variables	Tributary			
	Lamoille River	Missisquoi River	Otter Creek	Winooski River
Year - Effort	-0.443 (0.199)	-0.732 (0.025)	0.291 (0.576)	0.246 (0.558)
Year - HPUE	-0.080 (0.826)	-0.197 (0.612)	-0.740 (0.093)	-0.831 (0.011)
Effort - Number Harvested	0.388 (0.267)	0.677 (0.045)	-0.287 (0.581)	-0.339 (0.412)

harvested per hour spent fishing (harvest per unit effort or HPUE) revealed no significant ($p > 0.05$) change in HPUE over time in the Lamoille River, Missisquoi River or Otter Creek, but 1991 harvest rates on the Missisquoi River (Figure 22 panel B) and Otter Creek (Figure 22 panel C) were the lowest recorded during any survey year (Figure 22 panel D). Harvest rates on the Lamoille River in 1991 appeared similar to past harvest rates (Figure 22 panel A). A significant ($p < 0.05$) negative trend in harvest rates was detected for the Winooski River (Table 14). The number of walleye harvested during spring creels (Figure 23) increased with angling effort on the Missisquoi River, but harvest and effort were not correlated on the other three rivers (Table 14).

How changes in minimum size, creel limits and season regulations initiated in 1978, 1984 and 1985 affected spring creel survey statistics is not known. In addition, without data to evaluate the spring walleye fishery during the 1980's, how the 1991 season compares to more recent years is not known.

Anglers fishing for walleye were interviewed on the opening day of walleye season in 1984, 1985 and 1986 at the Lake Champlain New York State Department of Environmental Conservation boat launch site on South Bay. Walleye harvest rates in these surveys declined over the 3 year period: 0.138 in 1984, 0.045 in 1985, 0.030 in 1986 (Nashett 1986). Nashett (1986) speculated that the drop in harvest rates from 1984 to 1985 resulted from shifting opening day from the last Saturday in April in 1984 to the first Saturday in May in 1985 and 1986. Nashett (1986) suggested that post-spawning concentrations of walleye had dispersed by opening day in 1985 and 1986.

Diary Cooperators (refer to Figure 1b for lake zone locations)

To collect additional creel data, members of the Lake Champlain Walleye Association were asked to participate in a cooperator diary program. Volunteers received diary books and instructions on how to collect and record data. The cooperator program began in 1984 and the number of participants submitting usable diaries has varied from

year to year : 36 in 1984, 18 in 1985, 18 in 1986, 38 in 1987, 37 in 1988, 27 in 1989, 39 in 1990 and 46 in 1991 (Anderson 1992). Fishing effort also varied by zone and year and harvest was therefore expressed as the number of walleye harvested per hour (harvest rate).

Mean total length of walleye captured by diary cooperators increased between 1984 and 1991 in all lake zones (Figure 24). This increase in mean total length was significantly correlated with year ($p \leq 0.05$) in Zones 1, 2 and 3, and was marginally correlated ($p = 0.062$) in Zone 5B (Table 15), suggesting that the size of walleye caught by anglers in these zones is increasing over time. The correlation was not significant ($p > 0.10$) in Zones 4 and 5A, however, mean total lengths were not available for 1985 and 1986 in Zone 4, and 1986 and 1989 in Zone 5A. Although anglers may prefer to catch larger walleye, Festa et. al (1987) point out that when the mean size of harvested walleye increases, catch rates often decline.

Anderson (1990a) states that a walleye catch rate of 0.20 per hour would be an acceptable fishery for Lake Champlain. Nighttime harvest rates exceeded 0.20 in the majority of years for which data were available in Zones 2, 3 and 4, and exceeded 0.14 in the majority of years in all zones, except 5B (Table 16, Figures 25 and 26). Daytime harvest rates were lower and did not reach or exceed 0.20 per hour in any year in Zones 3, 4, 5A and 5B (Table 17, Figure 27). How angling success rates of diary cooperators compares to the entire population of walleye anglers is not known, but Culligan et al. (1993) report that angling success of multiple year participants tended to be above average for Lake Erie diary cooperators.

Nighttime harvest rates were often higher than daytime harvest rates (Figure 25). There was no significant correlation between nighttime harvest rates and year in any of the management zones, however, there was a significant negative trend in daytime harvest rates in Zones 2 and 3 (Table 15). Combined day and night harvest rates (Table 18) were significantly correlated to year in Zones 2 and 3, where the trend was negative (Table 15,

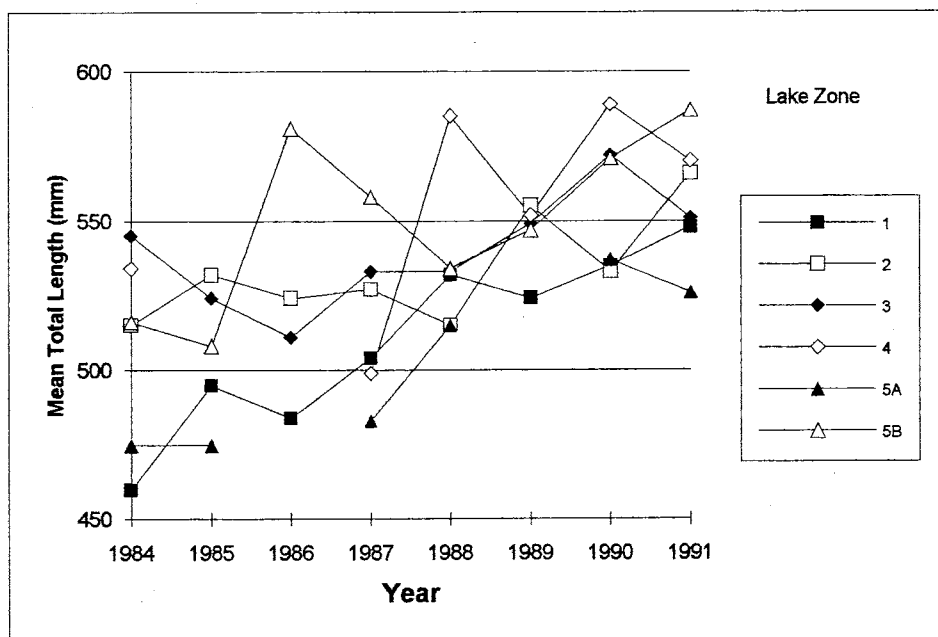


Figure 24. Mean total length of walleye angled from Lake Champlain by diary cooperators from 1984 to 1991.

Table 15. Pearson's correlation coefficients between year (1984 - 1991) and harvest rates (number/hour) and year and mean total length for walleye angled by diary cooperators in six Lake Champlain management zones (p-value in parentheses).

Variables	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5A	Zone 5B
Daytime harvest rate/Year	-0.543 (0.164)	-0.925 (0.001)	-0.791 (0.019)	0.076 (0.886)	0.533 (0.255)	-0.322 (0.437)
Nighttime harvest rate/Year	-0.786 (0.425)	-0.468 (0.242)	-0.571 (0.139)	0.198 (0.707)	-0.481 (0.519)	-0.431 (0.335)
Combined day and night harvest rates /Year	-0.543 (0.164)	-0.925 (0.001)	-0.791 (0.019)	0.076 (0.886)	-0.396 (0.437)	-0.322 (0.437)
Total length / Year	0.946 (0.001)	0.707 (0.050)	0.708 (0.050)	0.556 (0.152)	0.086 (0.840)	0.682 (0.062)

Table 16. Nighttime harvest rates (no. walleye/hour) of diary cooperators.

Zone	Year							
	1984	1985	1986	1987	1988	1989	1990	1991
1			0.16	0.24		0.00		
2	0.45	0.47	0.21	0.17	0.25	0.14	0.50	0.06
3	0.15	0.39	0.31	0.24	0.37	0.07	0.06	0.09
4	0.15			0.27	0.34	0.00	0.33	0.25
5A	0.19		0.00	0.20				
5B	0.06		0.33	0.19	0.19	0.11	0.04	0.03

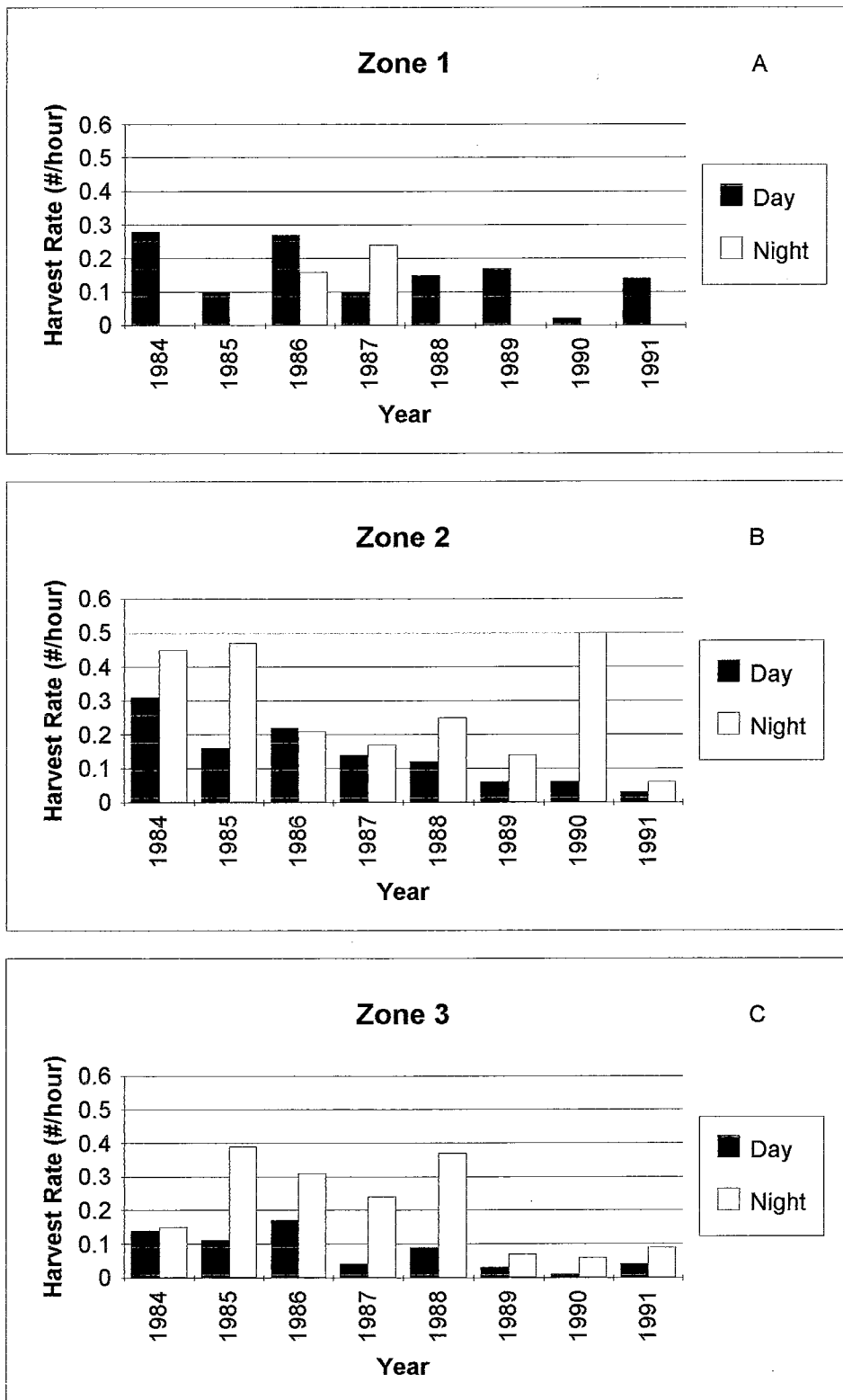


Figure 25. Day and Night walleye harvest rates of diary cooperators on Lake Champlain from 1984 to 1991.

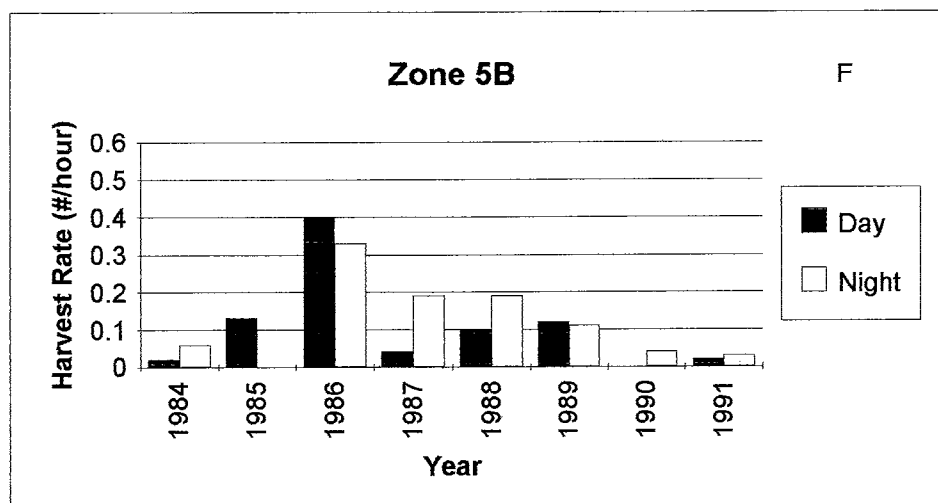
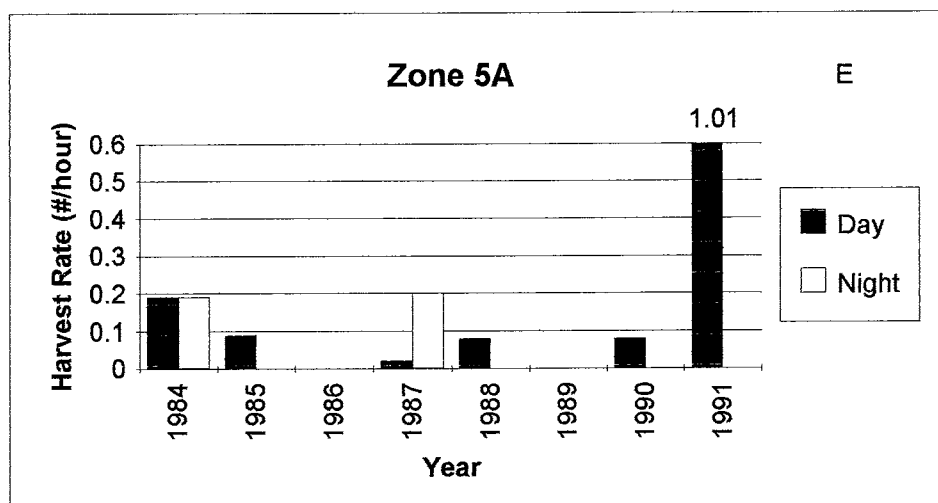
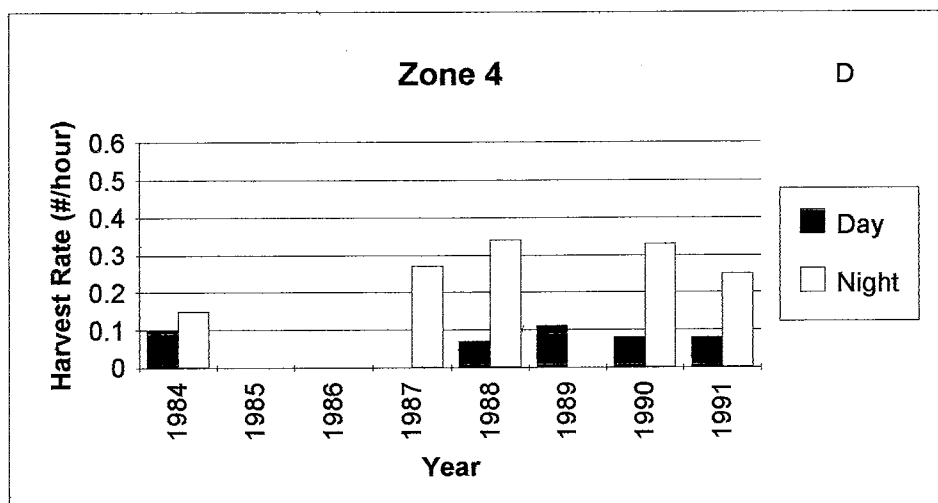


Figure 25 (continued).

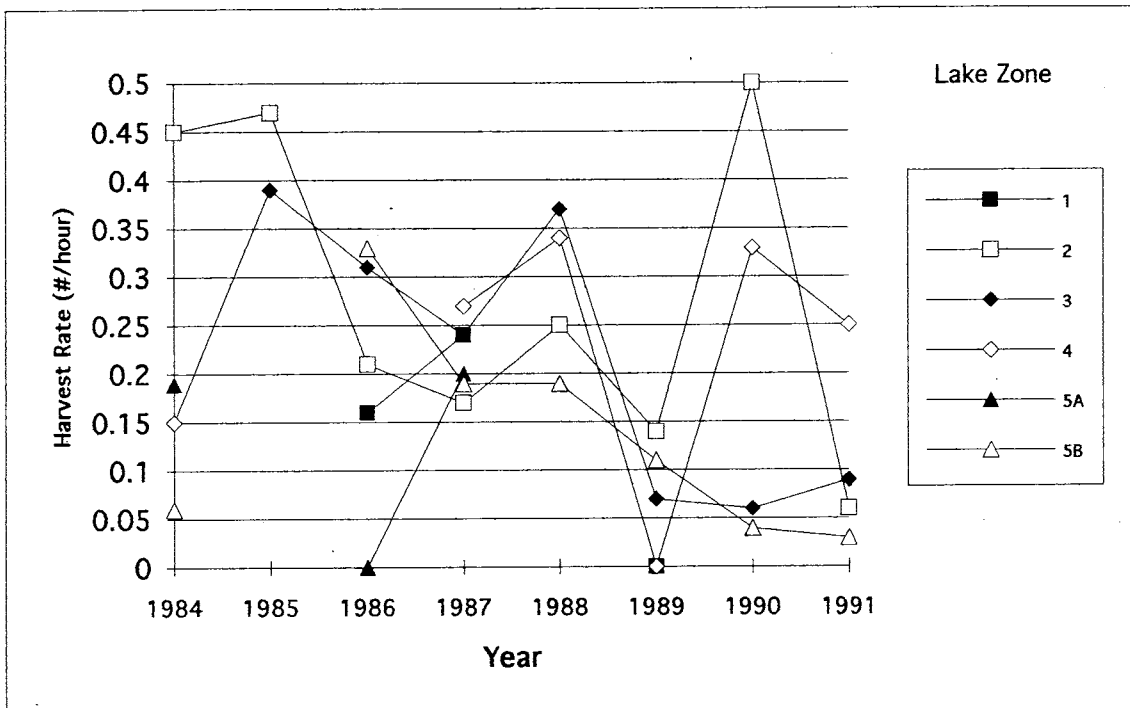


Figure 26. Nighttime walleye harvest rates of diary cooperators on Lake Champlain from 1984 to 1991.

Table 17. Daytime harvest rates (no. walleye/hour) of diary cooperators.

Zone	Year							
	1984	1985	1986	1987	1988	1989	1990	1991
1	0.28	0.10	0.27	0.10	0.15	0.17	0.02	0.14
2	0.31	0.16	0.22	0.14	0.12	0.06	0.06	0.03
3	0.14	0.11	0.17	0.04	0.09	0.02	0.01	0.04
4	0.10			0.00	0.07	0.11	0.08	0.08
5A	0.19	0.09		0.02	0.08		0.08	1.00
5B	0.02	0.13	0.40	0.04	0.10	0.12	0.00	0.02

Table 18. Combined daytime and nighttime harvest rates (no. walleye/hour) of diary cooperators.

Zone	Year							
	1984	1985	1986	1987	1988	1989	1990	1991
1	0.28	0.10	0.26	0.10	0.15	0.15	0.02	0.14
2	0.33	0.20	0.22	0.15	0.13	0.08	0.06	0.04
3	0.14	0.14	0.22	0.11	0.17	0.04	0.02	0.04
4	0.11			0.08	0.15	0.09	0.09	0.09
5A	0.19	0.09	0.00	0.09	0.07		0.08	1.00
5B	0.02	0.13	0.35	0.08	0.13	0.12	0.01	0.02

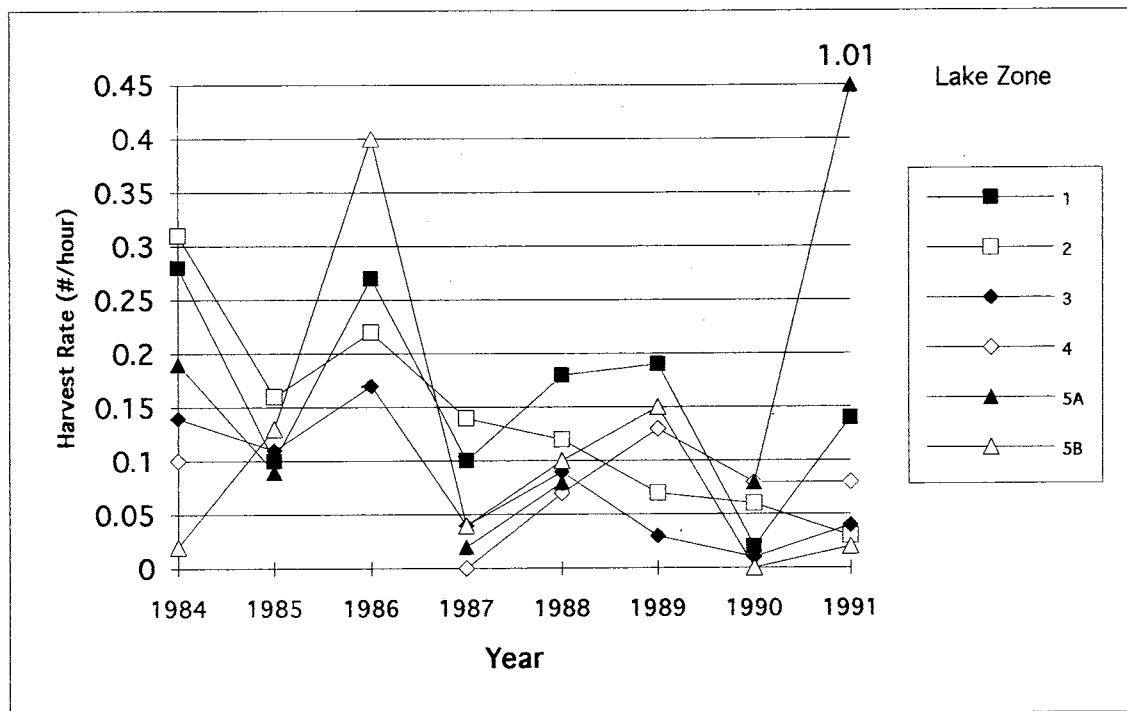


Figure 27. Daytime walleye harvest rates of diary cooperators on Lake Champlain from 1984 to 1991.

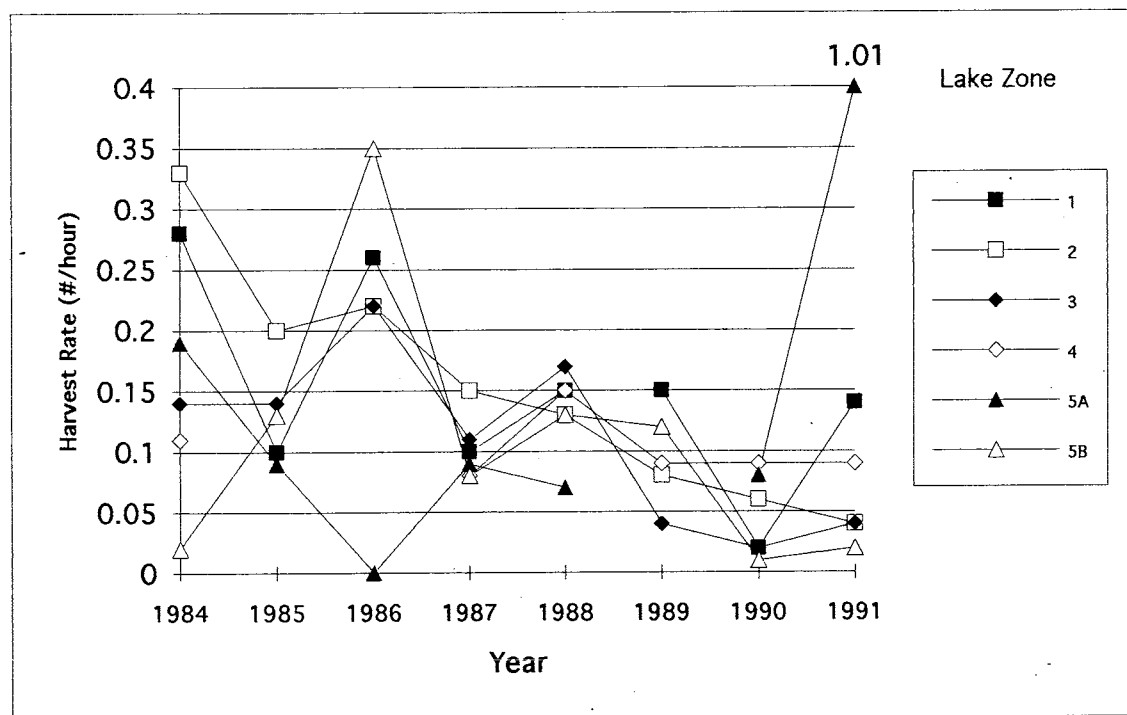


Figure 28. Combined day and night walleye harvest rates of diary cooperators on Lake Champlain from 1984 to 1991.

Figure 28). It should be noted that both day and night harvest rates were available in each year only in Zones 2 and 3.

Genetic characterization

Genetic heterogeneity of walleye collected from the Lamoille, Great Chazy, Missisquoi and Poultney rivers was assessed by Hawley et al. (1991). Observed heterozygosity, a measure of genetic variability, was significantly higher in Lamoille River walleye than in Great Chazy or Missisquoi River walleye. Observed heterozygosity did not differ among other populations, but was relatively high in walleye collected from the Poultney River. Expected heterozygosity was also highest for the Lamoille and Poultney populations. An allele found at low frequencies in Lamoille, Missisquoi and Great Chazy walleye was absent from Poultney River fish. An allele present in the Poultney River population was not found in walleye from the Lamoille and Great Chazy stocks, and was only present at very low frequency in the Missisquoi population. No evidence was found to indicate that inbreeding was reducing levels of genetic variability in the Lake Champlain populations studied.

Hawley et al. (1991) concluded that the Lamoille, Missisquoi and Great Chazy stocks appeared to be genetically very similar, but walleye from the Poultney River were somewhat distinct genetically. However, Gauldie (1991) cautions that temporal variations in allele frequencies within a stock are often as great as variations in allele frequencies between stocks.

Colby and Nepszy (1981) concluded there was little evidence of genotypic discreteness among walleye stocks and that population differences in age class structure, growth rates, fecundity and age of sexual maturity were phenotypic expressions induced by the environment. If environmental influences mask any genetic contribution to these population characteristics, then population differences are not inheritable and can change in response to environmental manipulations such as exploitation rates and habitat modification.

Billington and Herbert (1988) examined differences in the mitochondrial DNA (mtDNA) of ten great lakes walleye populations, but found insufficient variation to be able

to discriminate between spawning stocks. However, they noted the existence of a rare mtDNA variant and suggested the variant could be used as a genetic marker. If large numbers of walleye that carried such a marker could be raised in hatcheries and incorporated into stocking programs, then the survival and reproductive success of these fish and their offspring could be determined by monitoring the frequency of the mtDNA type. Billington and Herbert (1988) further proposed that breeding females of the selected mtDNA type with males from a variety of stocks would maintain the overall genetic diversity of the stocked fish.

Food Habits

During the summers of 1984 and 1985, Kirn (1986) collected 91 adult walleye stomachs from anglers and gill net surveys in Zones 3A and 3B. Over 77% of the guts contained fish and Kirn (1986) concluded that walleye relied heavily on rainbow smelt (Osmerus mordax) for forage. The mean total length of rainbow smelt consumed was 145 mm and 99% of the rainbow smelt were larger than 80 mm. Fewer numbers of cisco (Coregonus artedii), finescale dace (Phoxinus neogaeus), yellow perch (Perca flavescens) and insect prey were also noted. No relation was found between prey length and walleye length.

Gately (1974) found that the major forage species of Lake Champlain adult walleye were yellow perch, rainbow smelt and trout perch (Percopsis omiscomaycus). Hexagenia sp. larvae were an important food item in the diet of walleye from some parts of the lake. All of the stomachs examined by Gately (1974) were collected during the summer, but he speculated that adult walleye probably forage heavily on rainbow smelt during the winter. Hartman and Margraf (1992) found that age-0 walleye from western Lake Erie fed on rainbow smelt in spring and early summer, but switched to shiners in late summer and fall.

In 1993, adult walleye stomachs have been collected for diet analysis as a part of a study addressing the bioenergetics of top predators in Lake Champlain. Preliminary results from this study, which is funded by the Lake Champlain Management Conference, indicates walleye eat primarily rainbow smelt. Information on how walleye diets and biomass are affected by other piscivores that forage heavily on rainbow smelt, such as salmonids, is not available from current data and requires future research.

Knight et al. (1984) reported that age-0 walleye from western Lake Erie were entirely piscivorous after July, feeding primarily on age-0 soft-rayed fishes. They found diets of age-1 and older walleye changed seasonally to reflect shifts in forage-fish availability: walleye ate age-1 emerald shiners (Notropis atherinoides) and spottail shiners

(N. hudsonius) in spring, and age-0 gizzard shad (Dorosoma cepedianum) and alewives (Alosa pseudoharengus) in summer and fall. Knight et al. (1984) interpreted this seasonal change in prey selection as evidence that growth of walleye in western Lake Erie was food-limited.

Hartman and Margraf (1992) likewise concluded that declining growth and delayed age at maturity from 1965 to 1984 indicated that the forage base for walleye from Lake Erie was inadequate. Hartman and Margraf (1992) noted not only seasonal, but year to year changes in the diets of age-0 through age-6 walleye that reflected changes in prey abundances. Walleye consumed mostly gizzard shad and emerald and spottail shiners in years when these prey species were abundant, but fed primarily on white perch (Morone americana) and yellow perch when preferred prey were not available. They hypothesized that increased intraspecific competition for prey created by large walleye year-classes influenced the composition and relative abundances of the prey fish community and led to slower walleye growth rates.

Parasites and Diseases

Sea lamprey (*Petromyzon marinus*)

Sea lamprey wounds were divided into four categories: hits, fresh wounds, healing wounds and scars. Hits, fresh wounds or healing wounds were usually found on fewer than 10% of the fish examined in any given year (Figures 29 - 35). Scars persist for several years and were the most common type of wound. A maximum scarring rate of 25% of fish examined was recorded for female walleye collected from South Bay in 1985 (Figure 29 panel C).

Wounding rates for all wound types combined ranged from 0% for Missisquoi River walleye in 1991 and Lamoille River females in 1991, to 42% in 1985 South Bay females (Figure 35). It should be noted, however, that only 31 female walleye were captured in the Lamoille River in 1991 (Figure 32 panel C). Few fish from either sex exhibited multiple wounds: the maximum number of wounds on an individual fish was seven (Poultney River female, 1990). Sixteen percent of the walleye captured in South Bay in 1985 had more than one lamprey wound, but for most sites and in most years, multiple wounds were observed on fewer than 5% of the fish collected.

Female walleye had higher wounding rates than males (Figure 36). Therefore, differences in total wounding rates between years or sampling sites may be confounded with differences in sex ratios and should be interpreted cautiously.

Information on lamprey wounds was not collected at all sites or in all years, but data are available for the Great Chazy River, South Bay, Poultney River and Lamoille River populations for four or more consecutive years (Figures 37 - 40). The percent of South Bay male walleye with lamprey wounds gradually increased from 9% in 1983 to 17% in 1987 (Figure 36 panel A). Wounding rates for South Bay females, however, reached a peak of 42% in 1985 then declined over the next two years to 32% in 1987 (Figure 36 panel A). No pattern was detected for either gender from the Great Chazy

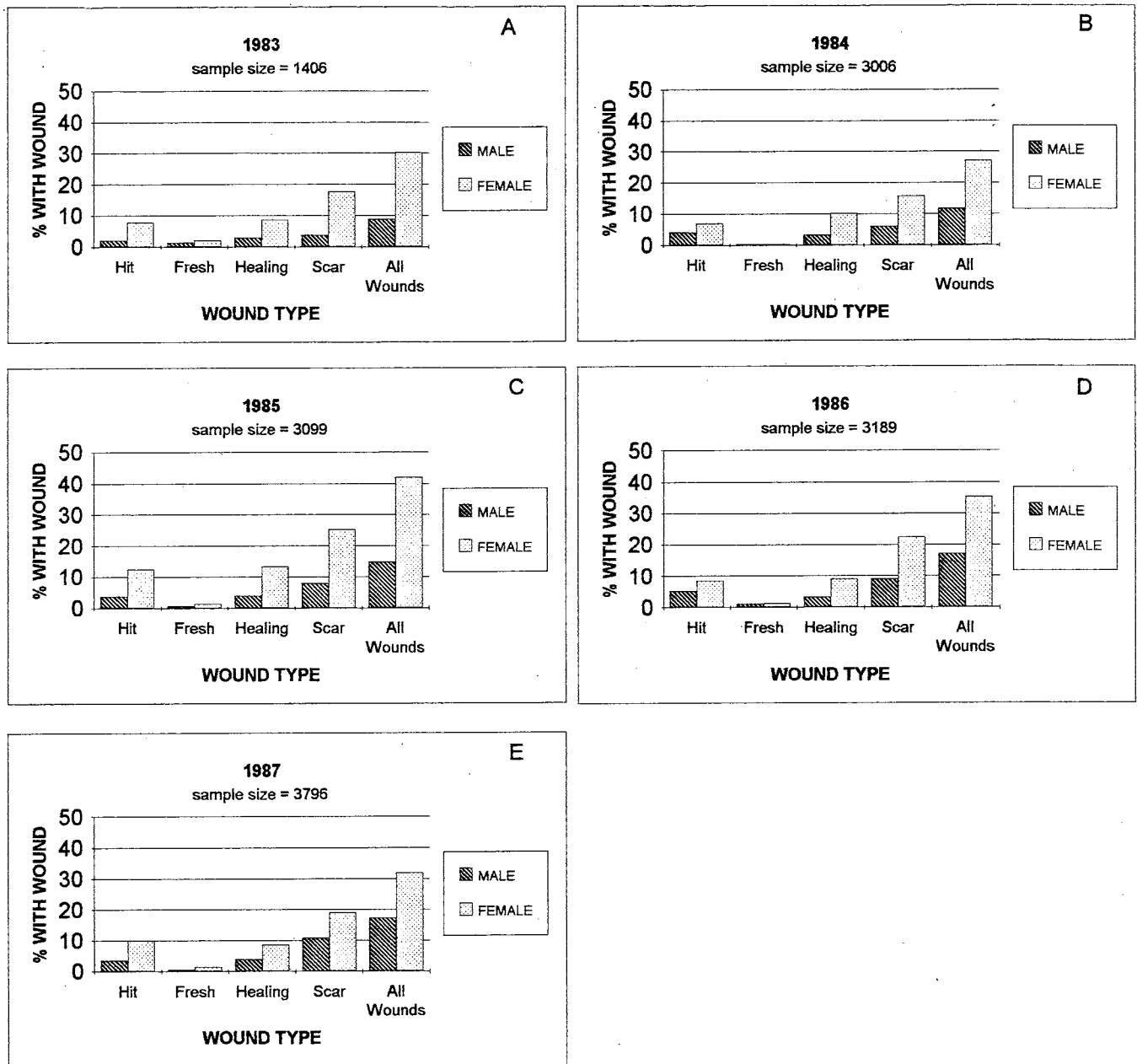


Figure 29. Sea lamprey wounding rates for spawning walleye collected in South Bay from 1983 to 1987. "All Wounds" represents wounding rate of all wound types combined.

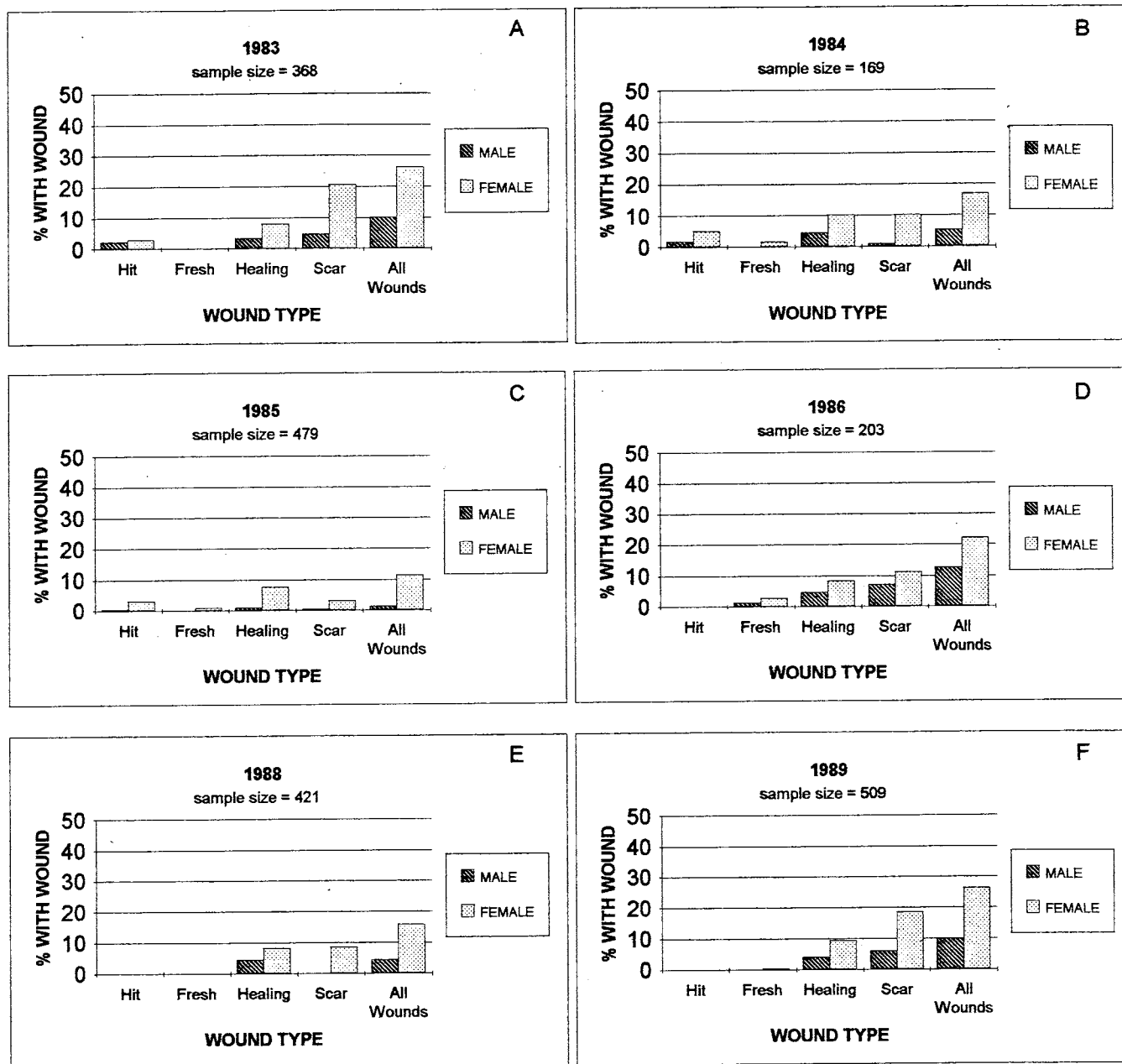


Figure 30. Sea lamprey wounding rates for spawning walleye collected in the Great Chazy River from 1983 to 1989. "All Wounds" represents wounding rate of all wound types combined.

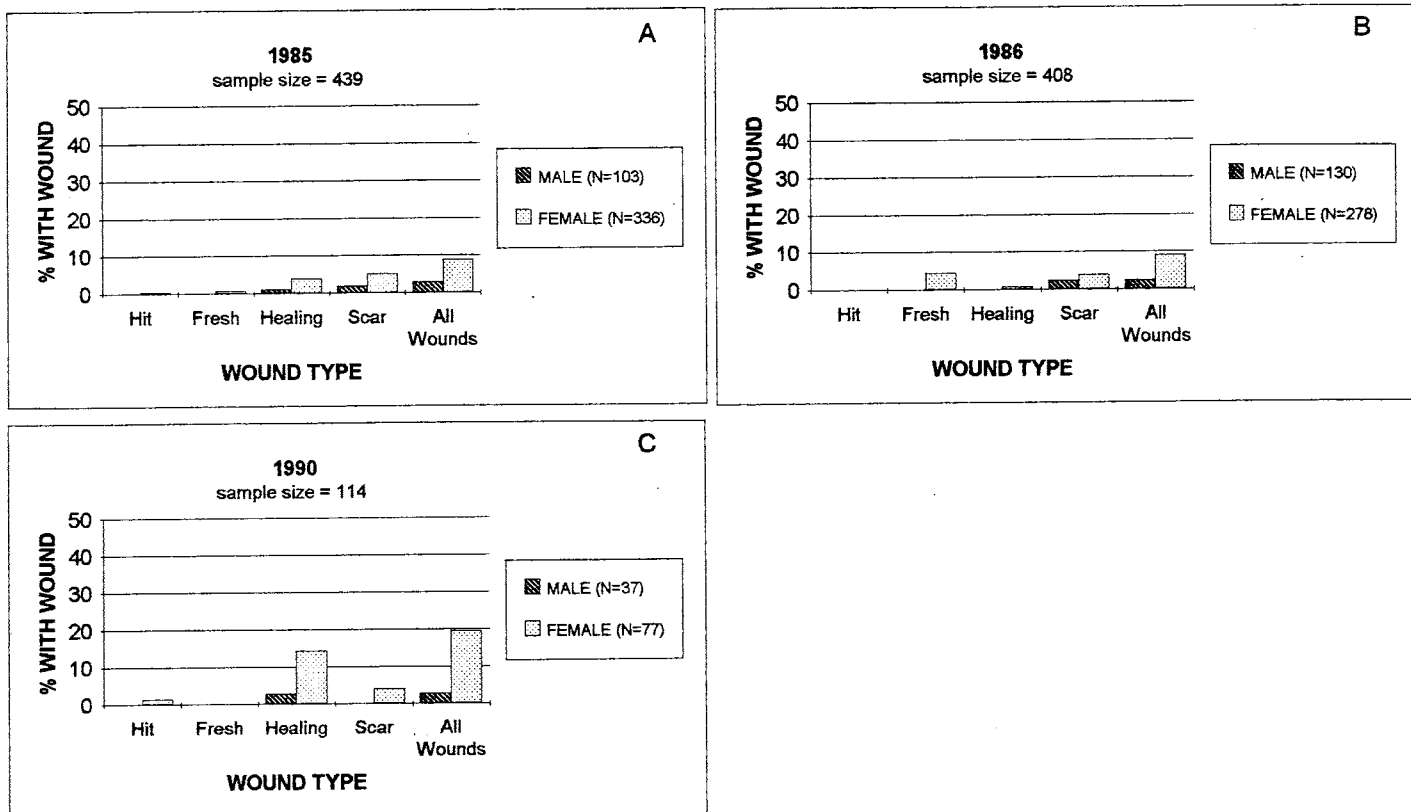


Figure 31. Sea lamprey wounding rates for spawning walleye collected in Missisquoi Bay from 1985 to 1990. "All Wounds" represents wounding rate for all wound types combined.

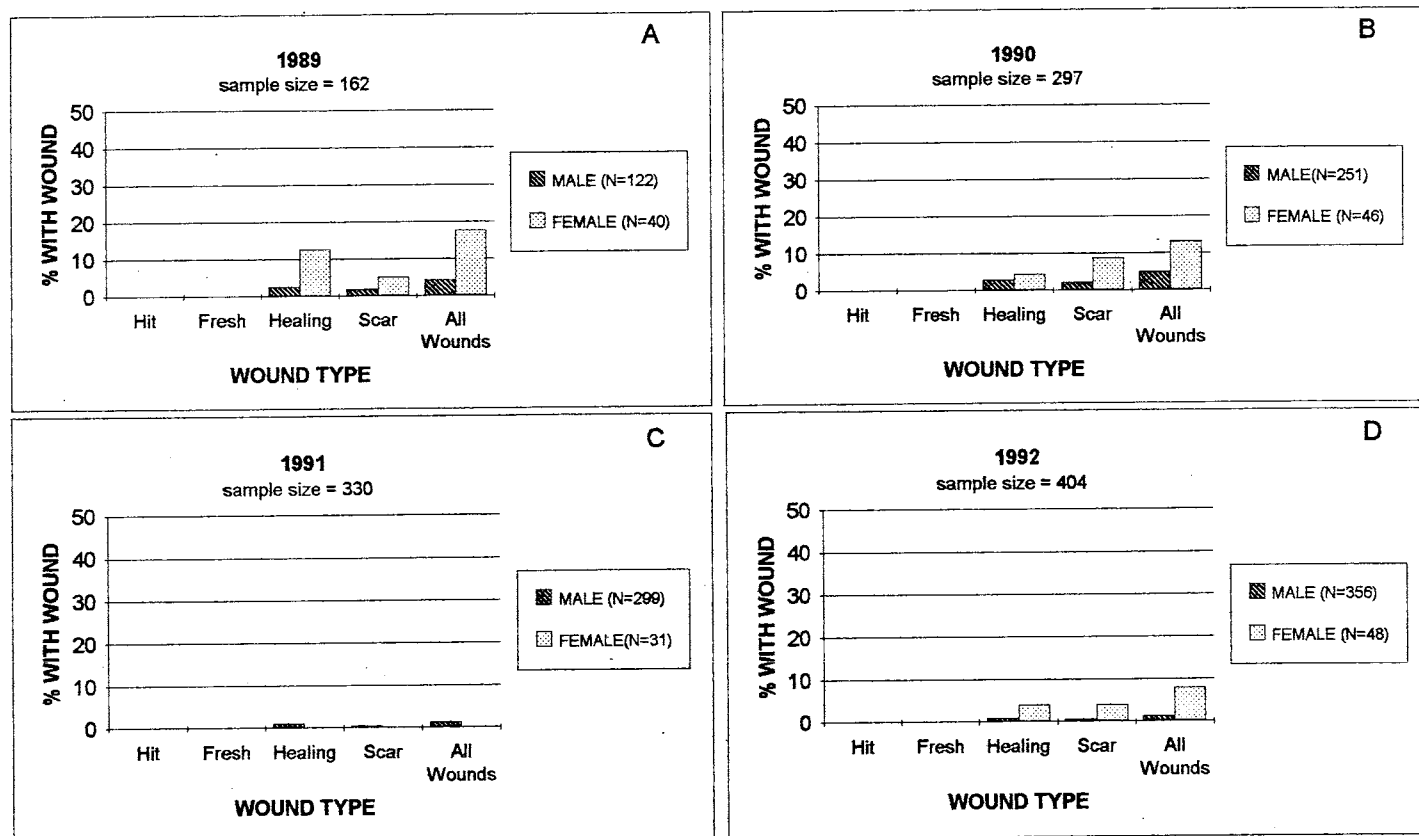


Figure 32. Sea lamprey wounding rates for spawning walleye collected in the Lamoille River from 1989 to 1992. "All Wounds" represents wounding rate for all wound types combined.

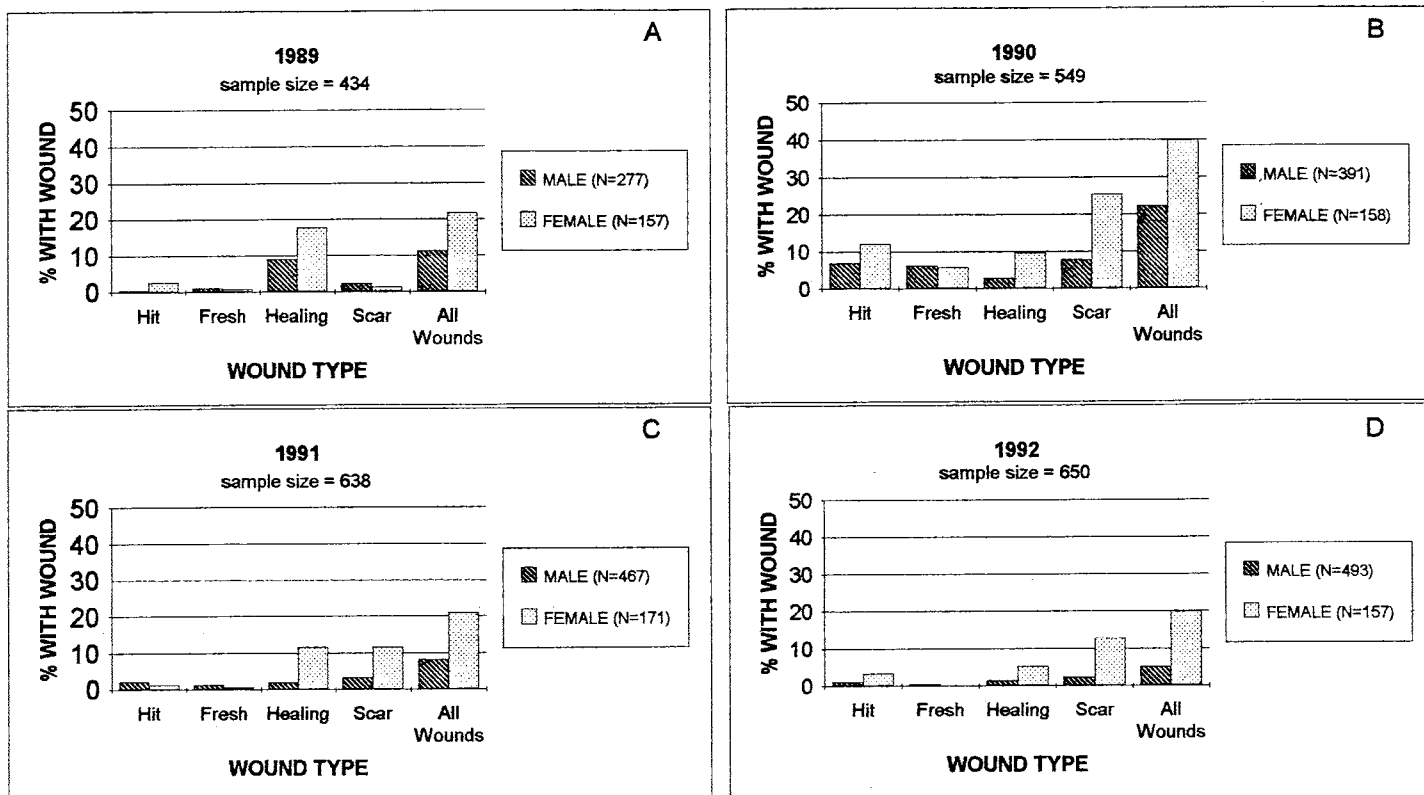


Figure 33. Sea lamprey wounding rates for spawning walleye collected in the Poultney River from 1989 to 1992. "All Wounds" represents wounding rate for all wound types combined.

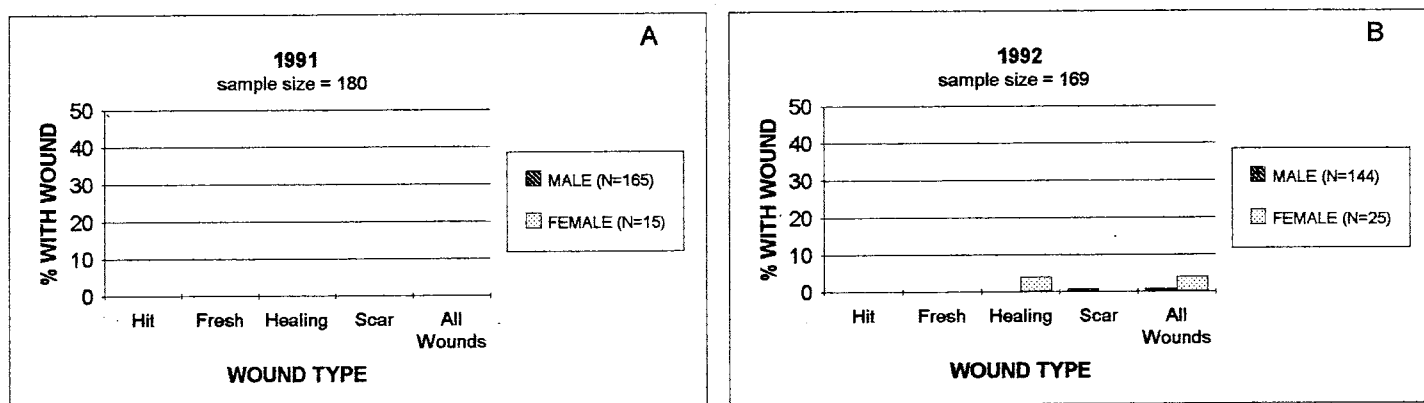


Figure 34. Sea lamprey wounding rates for spawning walleye collected in the Missisquoi River from 1991 to 1992. "All Wounds" represents wounding rate for all wound types combined.

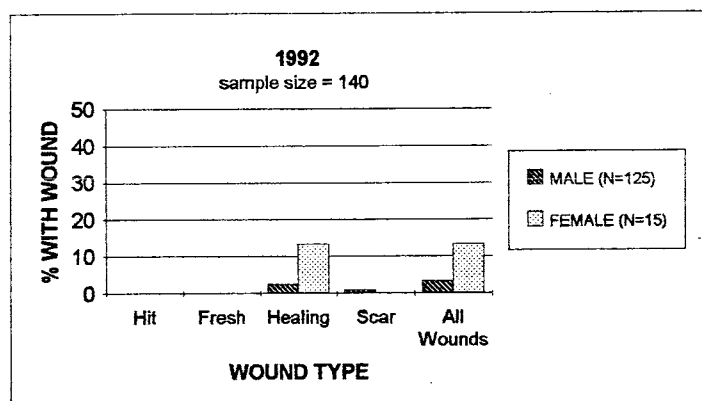


Figure 35. Sea lamprey wounding rates for spawning walleye collected in the Winooski River in 1992. "All Wounds" represents wounding rate for all wound types combined.

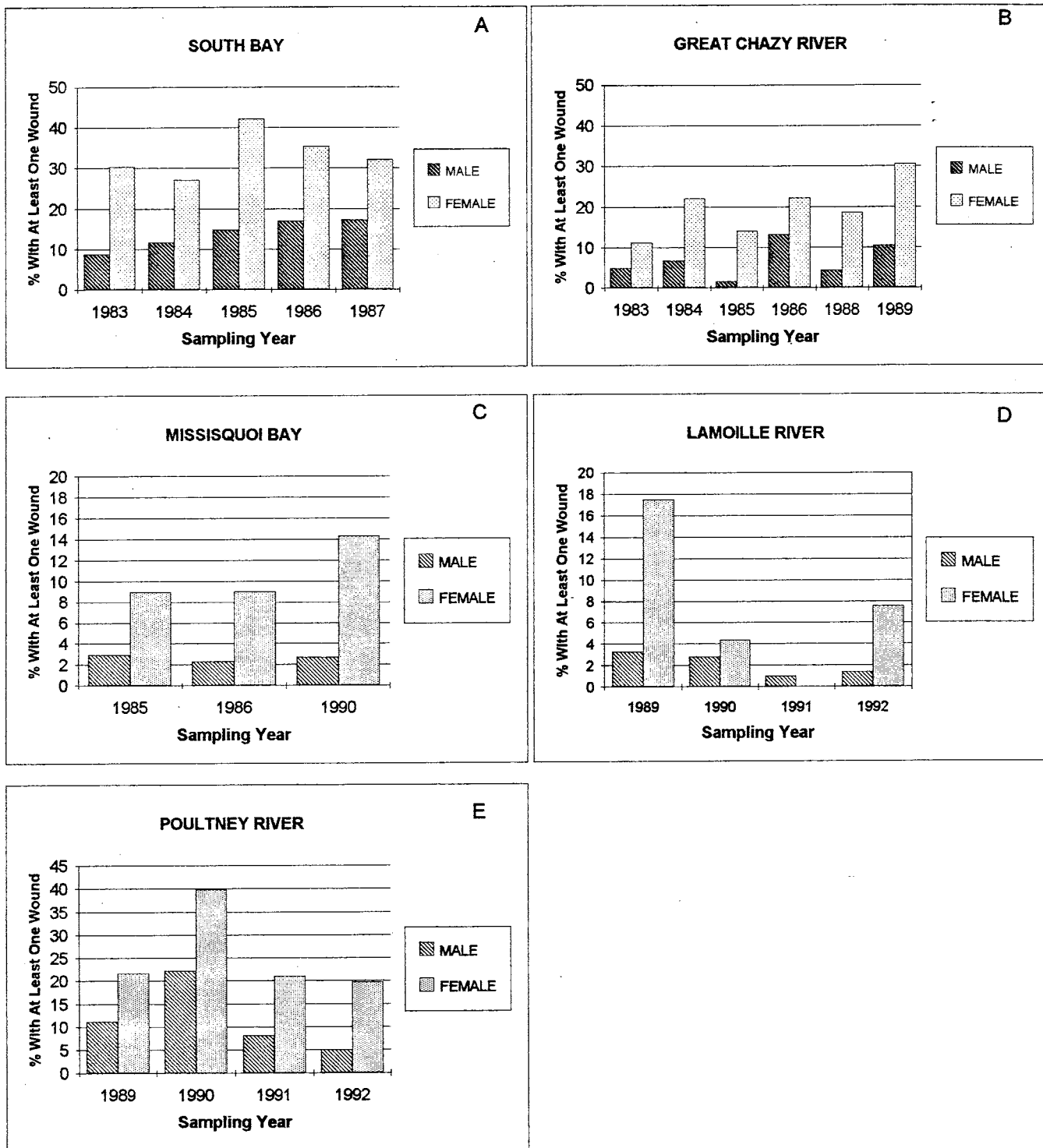


Figure 36. Sea lamprey wounding rates (hits, fresh wounds, healing wounds and scars combined) on spawning walleye collected from Lake Champlain and its tributaries from 1983 to 1992.

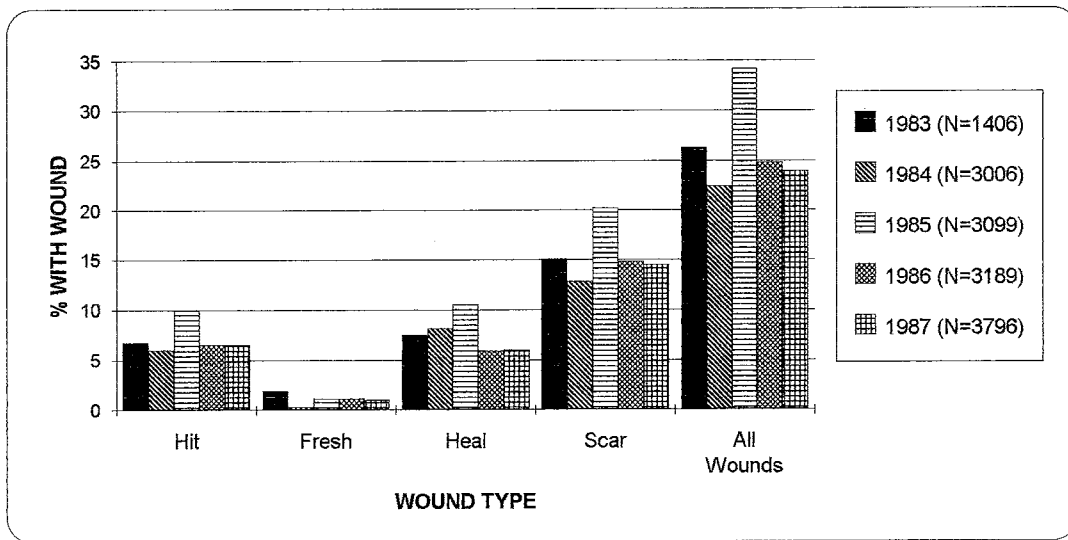


Figure 37. Percent of spawning walleye collected in South Bay from 1983 to 1987 with at least one sea lamprey wound. "All Wounds" represents wounding rate of all wound types combined.

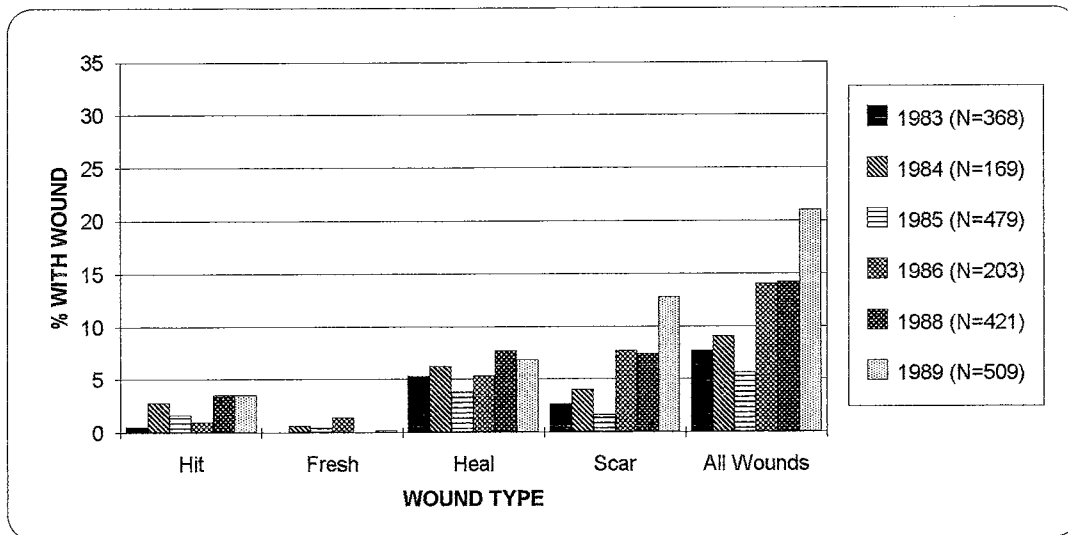


Figure 38. Percent of spawning walleye collected in the Great Chazy River from 1983 to 1989 with at least one sea lamprey wound. "All Wounds" represents wounding rate of all wound types combined.

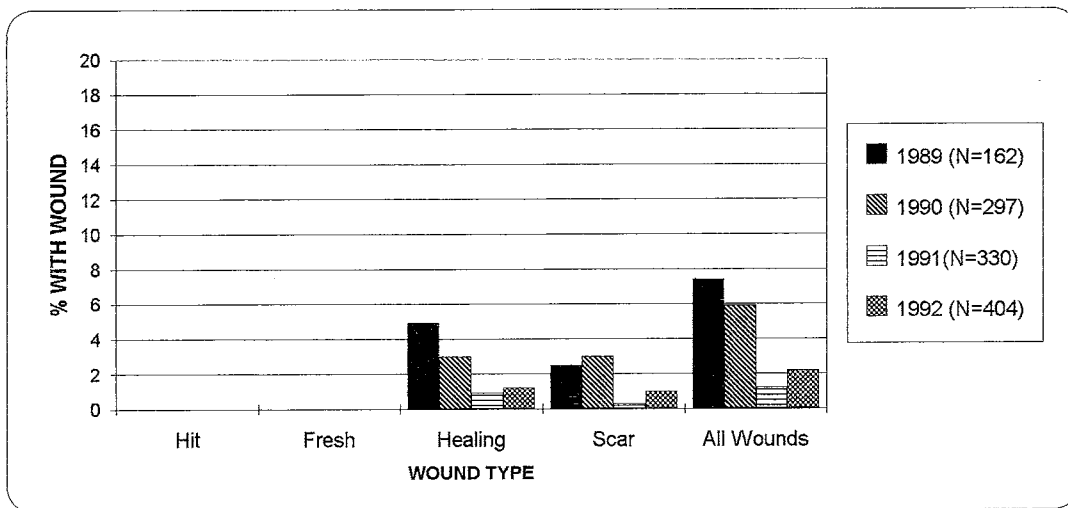


Figure 39. Percent of spawning walleye collected in the Lamoille River from 1989 to 1992 with at least one sea lamprey wound. "All Wounds" represents wounding rate of all wound types combined.

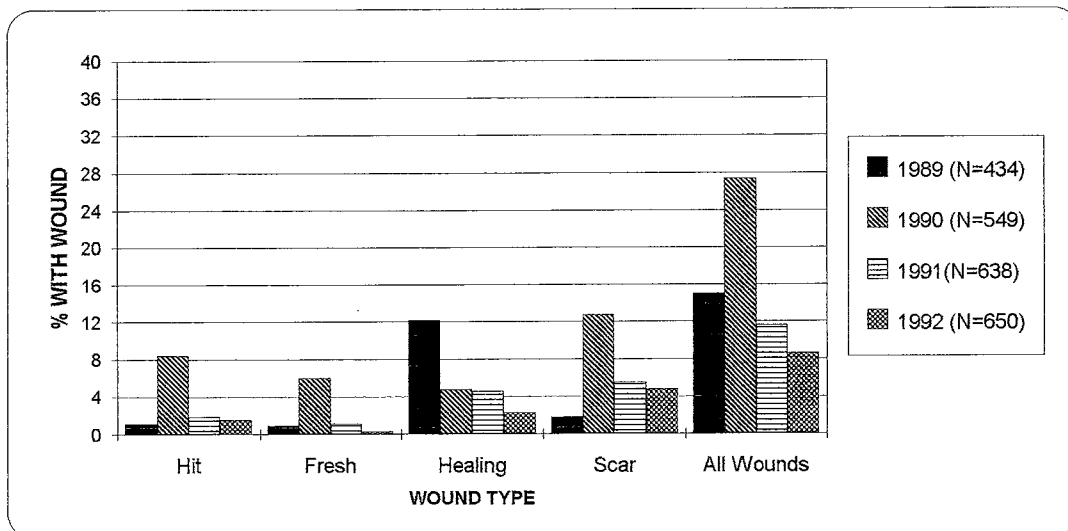


Figure 40. Percent of spawning walleye collected in the Poultney River from 1989 to 1992 with at least one sea lamprey wound. "All Wounds" represents wounding rate of all wound types combined.

River (Figure 36 panel B), but when sexes were combined, a general increase in wounding rates from 7% in 1983 to 21% in 1989 was noted (Figure 38).

Lamprey wounding rates in both the Poultney and Lamoille Rivers showed a general downward trend from 1990 to 1992 (Figures 39 and 40), although a greater percent of Lamoille River females had lamprey wounds in 1992 than in 1990 or 1991 (Figure 36 panel B). In general, walleye from South Bay and the Poultney River appear to have higher wounding rates than fish from more northern populations (Figure 36).

Lamprey wounds were recorded during spring walleye sampling from 1968 to 1971 in the Lamoille, Missisquoi and Winooski rivers (Anderson 1974). The percent of males exhibiting lamprey wounds was very low: 0.8% in the Lamoille, 0.2% in the Missisquoi and 1.3% in the Winooski (Anderson 1974). Wounding rates for female walleye were also low: 0.8% in the Lamoille, 0.7% in the Missisquoi and 1.4% in the Winooski (Anderson 1974).

Other Parasites and Diseases

South Bay and Great Chazy River walleye were examined for externally visible parasites and diseases in all years and 5 types were observed: lymphocystis, black spot, fish leeches, tape worm, and saprolegnia fungus. With the exception of lymphocystis, parasites and diseases infected few walleye (Figures 41 and 42): black spot was second to lymphocystis in prevalence and was noted on a maximum of 4% of the catch (Great Chazy River males 1983). Lymphocystis was the only parasite (except sea lamprey) or disease observed in the last two years of sampling in South Bay (1986, 1987) and the Great Chazy River (1988, 1989).

Systematic records of parasites other than lamprey or lymphocystis were not kept for walleye collected in Vermont waters. However, tape worm infection rates in walleye gillnetted during the 1970's were estimated at 100% (Jon Anderson, VTF&W, personal communication).

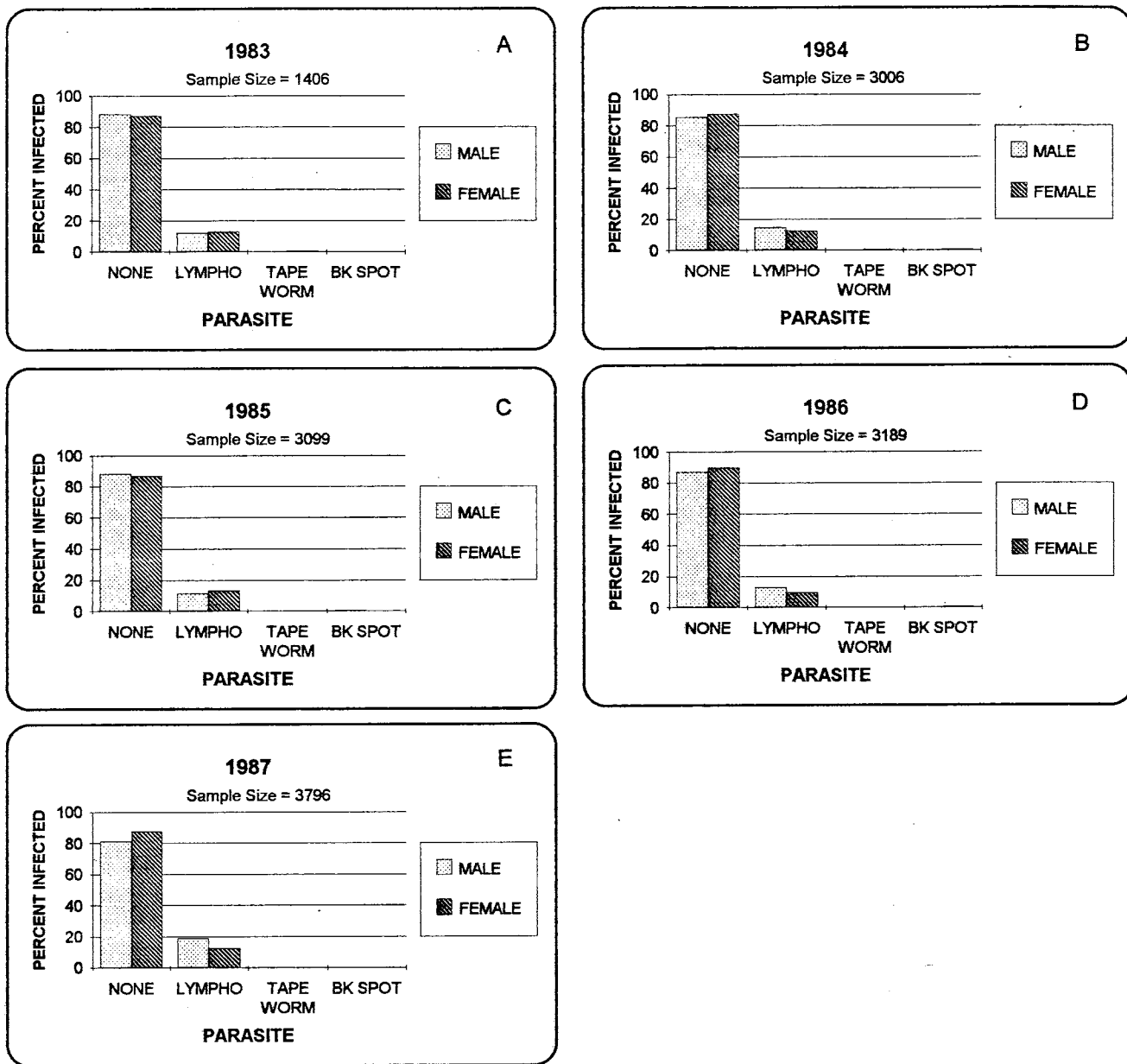


Figure 41. Infection rates of parasites and diseases on spawning walleye collected in South Bay from 1983 to 1987.

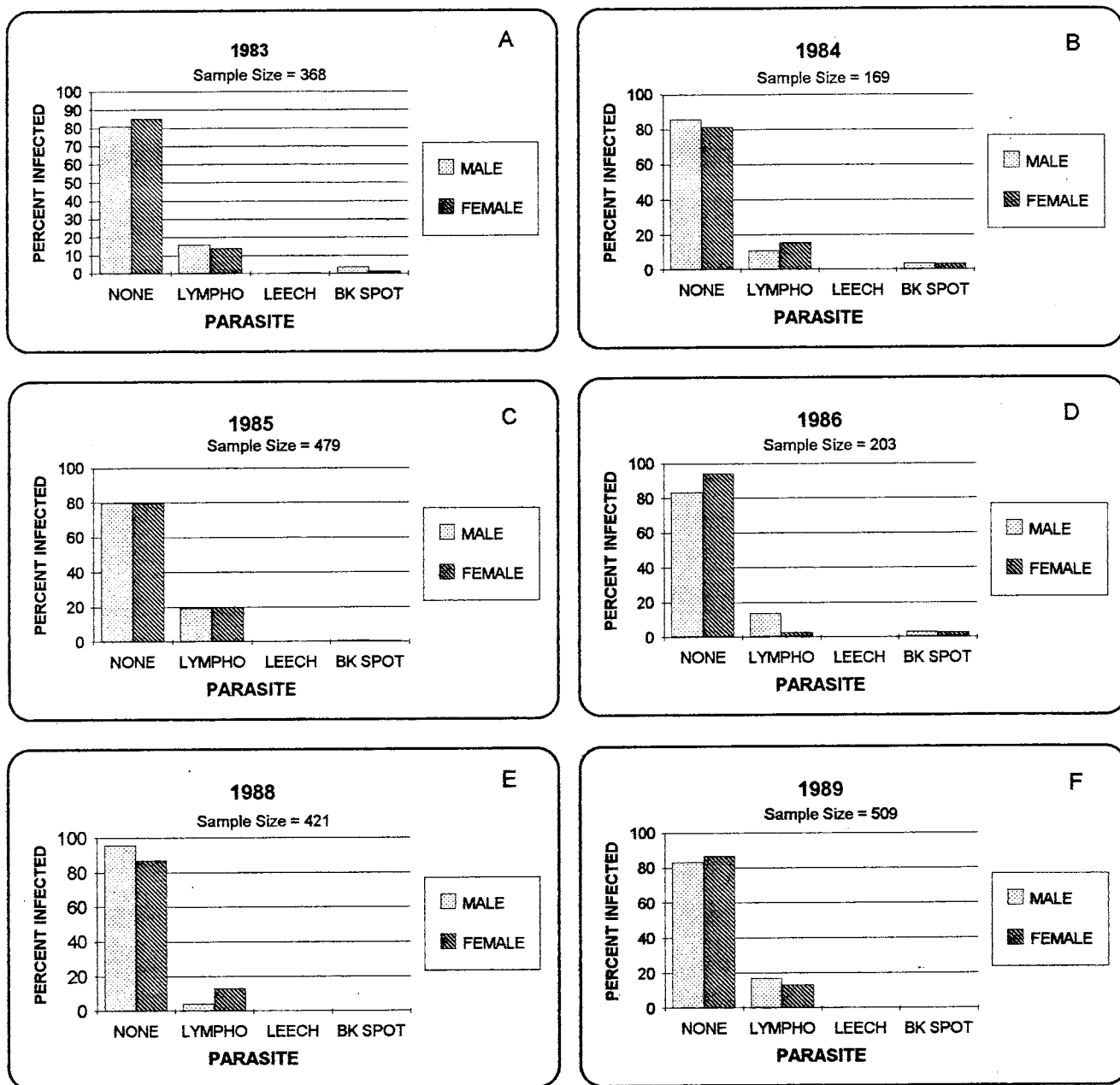


Figure 42. Infection rates of parasites and diseases on spawning walleye collected in the Great Chazy River from 1983 to 1989.

The occurrence of lymphocystis lesions was recorded for walleye collected in the Lamoille, Missisquoi and Winooski rivers in 1992. In addition, walleye collected in the Poultney River on April 12-13, 1989, April 8-9, 1990 and all sampling dates in 1991 were examined for lymphocystis.

Lymphocystis is a chronic, viral disease of connective tissues common in walleye populations (Wolf 1988). Wolf (1988) speculates that the virus spreads by direct contact. Transmission may be enhanced when population density is high and skin abrasions are common (Wolf 1988) and is most prevalent among spawning individuals (Walker 1969). Lesions are most prevalent in the spring, but decrease rapidly following spawning (Ryder 1961). Bowser et al. (1988) describe an inverse relation between temperature and incidence of lymphocystis. The disease is usually described as relatively benign (Wolf 1988), but Margenau et al. (1988) suggest lymphocystis may cause mortality in some populations. Hile (1954) reported that infected walleye from Saginaw Bay, Lake Michigan weighed about 6% less than uninfected individuals.

Less than 10% of Lamoille, Missisquoi and Winooski walleye exhibited lymphocystis lesions (Figure 43 panel A), which is similar to historical infection rates reported by Anderson (1974). Infection rates exceeded 10% in all other populations except Great Chazy females in 1986 and Great Chazy males in 1988 (Figure 43 panels B - D). Maximum percent infected was 19 % in Great Chazy females in 1985 (Figure 43 panel C). In the Nipigon River, Ontario, 30.4% of spawning walleye were infected with lymphocystis (Ryder 1961). 1-5% of spawning walleye were infected in Oneida Lake, New York (Walker 1958).

Bowser et al. (1988) reported a greater abundance of lesions in male than female walleye from Oneida Lake, New York. However, Yamamoto et al. (1976) and Mathias et al. (1985) found the disease to be more prevalent in females from Cren Lake, Saskatchewan, Canada. Lymphocystis infections rates are similar for male and female walleye collected from Lake Champlain (Figure 43).

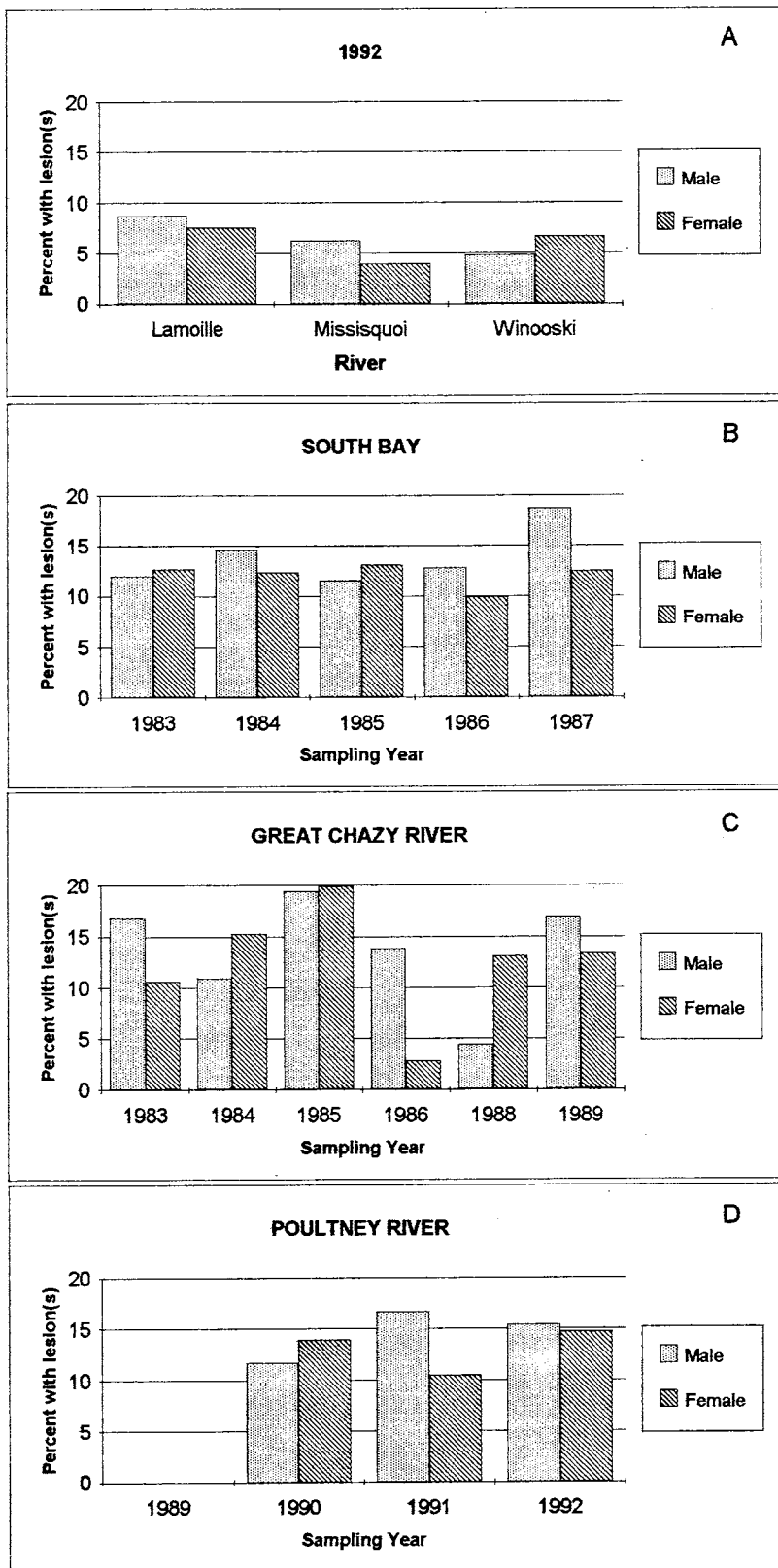


Figure 43. Lymphocystis infection rates in spawning walleye collected from Lake Champlain and its tributaries from 1983 to 1992.

Stocking

Stocking programs to expand, maintain or supplement walleye populations are common, however, the effectiveness of walleye stocking remains controversial. The overriding conclusion of a 1990 symposium on walleye stocks and stocking was that the success of any particular stocking program is largely unpredictable (Ellison and Franzin 1992). Authors of ten studies of stocking effectiveness presented at the symposium reported that 32% of fry stockings, 32% of small fingerling stockings and 50% of large fingerling stockings were considered successful to some degree. Laarman (1978) reviewed walleye stocking programs in 40 North American lakes and reservoirs and concluded that success rates varied with stocking objectives: 48% of programs to establish new walleye populations were successful, 32% of programs to supplement poor natural reproduction were successful and 5% of programs to increase walleye abundance where natural reproduction was already significant met with success. The majority of studies reviewed by Laarman (1978) involved fry stocking.

Since 1986, 1,741,656 walleye have been stocked into the Vermont portion of Lake Champlain and its tributaries by the Lake Champlain Walleye Association and VTF&W (Brian Chipman, VTF&W, personal communication)(Table 19). An additional 10.3 million walleye were stocked by New York's Essex County Fish Hatchery between 1988 and 1992 (Jennie Sausville, NYDEC, personal communication)(Table 20). The vast majority of these walleye (99%) were stocked as fry. Walleye were stocked by the Essex County Fish Hatchery from 1983 to 1987 (Larry Nashett, NYDEC, personal communication), but we had difficulty obtaining reliable stocking records for this period.

Attempts to evaluate the contribution of stocked walleye to the native population have met with limited success. LaBar and Parren (1983) found no evidence indicating that the approximately 1.9 billion (estimated from LaBar and Parren 1983; Figures 15 and 16) walleye stocked into Lake Champlain from 1899 to 1969 contributed to the adult population or the fishery and did not recommend fry stocking for Lake Champlain.

Table 19. Walleye stocked by VTF&W and the Lake Champlain Walleye Association into Lake Champlain and its tributaries from 1986 to 1992.

Tributary	Year	Size (mm)	Number
Lamoille River	1986	51	3,125
Lamoille River	1987	51	15,000
Lamoille River	1988	58	5,000
Poultney River	1988	0	137,000
Lewis Creek	1988	46	3,400
Little Otter Creek	1988	46	7,000
Lamoille River	1989	58	7,500
Poultney River	1989	fry	117,545
Poultney River	1989	58	6,000
Lamoille River	1990	51	19,150
Poultney River	1990	fry	288,050
Poultney River	1990	51 - 76	8,600
Lamoille River	1991	58	7,162
Poultney River	1991	fry	169,560
Poultney River	1991	58	8,024
Missisquoi River	1991	fry	23,000
Missisquoi River	1991	76	216
Poultney River	1992	fry	835,300
Poultney River	1992	56 - 61	4,155
Poultney River	1992	152	22
Missisquoi River	1992	fry	50,000
Missisquoi River	1992	43 - 56	8,469
Missisquoi River	1992	160	681
Otter Creek	1992	56	3,122
Missisquoi Bay	1992	46	14,575
Total			1,741,656

Table 20. Walleye stocked into southern Lake Champlain by New York's Essex County Fish Hatchery from 1988 to 1992.

Area	Year	Size	Number
Crown Point	1988	fry	800,000
Ticonderoga	1988	fry	1,200,000
Champlain Bridge/Bulwagga Bay	1989	fry	727,160
Crown Point	1989	fry	727,160
Crown Point/Ticonderoga	1990	fry	3,500,000
Crown Point/Ticonderoga	1991	fry	2,600,000
Crown Point/Ticonderoga	1991	76 - 102 mm	750
Crown Point	1991	fry	784,500
Total			10,339,570

Stocking practices in many lakes involve the release of both fry and fingerlings. Walleye fry and fingerlings (100 - 150 mm) were stocked into interconnected East and West Okoboji Lakes, Iowa from 1984 to 1989 (McWilliams and Larscheid 1992). Larval walleye were sampled weekly with townets from late April to early June and fall fingerling populations were estimated by electrofishing. Fry mortality consistently exceeded 99% during the first six months following stocking and no correlation was found between fry stocking rates and fall young-of-the-year densities. Fall population estimates of age-0 walleye were positively correlated with fingerling stocking densities. However, overwinter mortality of fish stocked as fingerlings was 2-16 times greater than that of fish stocked as fry. There was no indication of differential survival for the two groups beyond the first year. Therefore, McWilliams and Larscheid (1992) recommended that relative contributions of stocked fry and fingerlings to a fishery be evaluated the year following stocking rather than during the same year because differential overwinter mortality may affect the ultimate contribution of each group to the fishery.

Lajeone et al. (1992) reported similar results for walleye fingerlings (50 - 120 mm) stocked into Pool 14 of the Mississippi River. Although stocked fingerlings comprised 46% of the year class in 1988, by 1989, stocked fish accounted for only 23% of age-1 fish. Lajeone et al. (1992) felt higher over-winter mortality of stocked fish was not responsible for the decline because the length of stocked and naturally spawned individuals were similar in fall samples. None-the-less, the estimated percent contribution of stocked fish to the 1988 year-class declined 50% between the end of the first and second summers following stocking.

Mitzner (1992) evaluated the success of walleye stocking programs in Rathbun Lake, Iowa. From 1984 to 1989, fall population estimates of age-0 fish indicated fish stocked as fry and fish stocked as fingerlings contributed approximately equally to a given year class during the first summer. However, survival during the first winter varied among fingerlings stocked as fry, fingerlings reared in tanks and fingerlings cultured in nursery

lakes. Overwinter survival of fingerlings stocked as fry was superior to those stocked as fingerlings. For stocked fingerlings, survival of tank-reared fish exceeded that of nursery-lake fish in 4 of 5 years. Mitzner (1992) speculated that higher mortality among nursery-reared walleye was related to their smaller size and greater handling and hauling stress. Thus, first winter survival influenced the ultimate contribution of each stocking strategy to a year class. Costs per live age-1 walleye were estimated at \$0.22 for fish stocked as fry, \$1.08 for those stocked as tank-reared fingerlings and \$1.50 for those stocked as nursery-reared fingerlings. However, Mitzner (1992) cautioned that although fry stocking was important in establishing very abundant year-classes and appeared to be the most cost effective strategy, year to year variability in success rates associated with fry stocking would not provide uniform, reliable year-classes if relied upon exclusively.

Mathias et al. (1992) introduced 7.1 million genetically marked walleye fry into Dauphin Lake, Manitoba in 1985. The fish were considered fully recruited to the commercial fishery at age 3. Analysis of the commercial catch in 1988 and 1989 indicated stocked fry comprised only 2.9% of the 1985 year class. However, the relative contribution of stocked fry to a year-class may not be the best measure of the impact those fry have on a fishery because it depends in part on the number of fry produced in natural spawning. For example, in years when natural reproduction is low, stocked fish can form a large proportion of the year-class, without significantly contributing to production. The authors suggest that survival to a specified age and percent of annual harvest are more useful measures of the contribution of stocked fry to a fishery.

Survival of walleye fry and fingerlings introduced into three Iowa rivers was compared by Paragamian and Kingery (1992). Fry survival from early spring to the first fall was almost zero. Fingerlings released into the same rivers accounted for 28 to 100% of the age-0 fish from 1986 to 1989. By age one, the percentages dropped to between 16 and 63%, suggesting either higher mortality of stocked fish than naturally produced walleye or high rates of tag loss. Paragamian and Kingery (1992) concluded that stocked

fingerlings were instrumental in establishing annual year-classes, but recommended that fry stocking be discontinued. Fielder (1992) likewise concluded that walleye fingerlings stocked into lower Lake Oahe, South Dakota enhanced the fall young-of-the-year population, but stocked fry did not. No estimates of stocked fingerling over winter survival or contributions of the stocked fingerlings to the age-1 population were reported.

Mathias et al. (1992) estimated survival to age three was 0.04% for stocked fry and 8-9% for naturally produced fry. These figures are similar to estimates of stocked fry survival in other systems (Carlander and Payne 1977; Schweigert et al. 1977). Survival to age 4 was estimated to be 0.026% of stocked fry. Using these survival figures, Mathias et al. (1992) concluded that the cost-to-benefit ratio of the stocking program was 2.6:1 for the commercial fishery and would be 1.2:1 for a sport fishery. In both types of fisheries, the costs of stocking fry exceeded the economic benefits.

Kayle (1992) sampled young-of-the-year walleye in the fall of 1988 and 1989 in Mosquito Lake, Ohio. He recommended that stocking of walleye fingerlings continue because 65 - 73% of age-0 walleye were stocked fish. However, no estimates of the relative strength of year-classes produced naturally during the study or of first winter survival of stocked fingerlings were made. The ultimate contribution of stocked fish to the fishery is therefore difficult to evaluate.

Few studies have attempted to identify the causes for differential success in stocking practices. Fielder (1992) suggested that fry did not survive because they were stocked before summer zooplankton populations were established. Fingerlings, on the other hand, were stocked later, when zooplankton were most abundant. Lajeone et al. (1992) speculated that the percent of stocked fish present in a given year-class declined over time because of emigration. They estimated that 11% of the individuals stocked into Pool 14 of the Mississippi River in 1988 and 47% of those released in 1989 emigrated from the pool sometime before fall sampling. Paragamian and Kingery (1992) also noted extensive movement of stocked fingerlings between interconnected river systems in north-

central Iowa. In contrast, Fielder (1992) reported minimal emigration of walleye fingerlings from stocked embayments in lower Lake Oahe, South Dakota.

Habitat Degradation and Improvements

Habitat loss or degradation is often cited as a suspected cause of declining walleye populations, but is difficult to quantify. Schneider and Leach (1977) reviewed changes in Great Lakes walleye stocks from 1800 to 1975 and concluded that habitat degradation, in the form of nutrient loading, alteration of spawning habitat, release of toxins and introduction of exotic fish species, was a major contributing factor in the decline of several Great Lakes stocks. They also felt that over exploitation, pollution and exotics could be suppressing the recovery of these stocks.

Rainbow smelt were among the exotics listed by Schneider and Leach (1977), although they concluded that smelt had both positive and negative effects on walleye. Smelt became important in the diets of walleye from western Lake Erie, Bay of Quinte, the North Channel, Georgian Bay and northern Green Bay. Walleye fisheries in Saginaw Bay, eastern Lake Michigan, southern Lake Huron, western and eastern Lake Erie, Bay of Quinte and Black Bay increased after smelt were established in these waters. In contrast, poor walleye recruitment was associated with high smelt abundance in Green Bay and western Lake Erie, but when smelt abundance fell sharply in 1943, strong walleye year-classes were produced. Schneider and Leach (1977) speculated that because smelt are voracious feeders, they could have a severe effect on pelagic larval walleye or their food, particularly where smelt densities are high.

The Missisquoi walleye population has been of particular concern because catch rates have continually declined to a point where the open water fishery in Missisquoi Bay is considered non-existent (Jon Anderson, VTF&W, personal communication). In addition, younger age classes are not well represented in Missisquoi samples (Jon Anderson, VTF&W, personal communication), suggesting walleye recruitment may not be sufficient to maintain the adult population. However, adult walleye have been observed in the Missisquoi River and in Missisquoi Bay during recent spawning seasons and limited

numbers of larval walleye were collected as they left the Missisquoi River in late May, 1993 (D.P. and M.M., unpublished data).

Despite evidence of attempted natural reproduction by the Missisquoi population, survival of larval and juvenile walleye may be low. Rainbow smelt are extremely abundant in the northeast arm of Lake Champlain, where Missisquoi Bay is located (George LaBar, University of Vermont, unpublished data). Schneider and Leach (1977) suggest that rainbow smelt can severely reduce pelagic larval walleye abundance through direct predation or by significantly reducing zooplankton populations on which larval walleye feed. Larval walleye typically begin feeding in the pelagic zone in late May or early June, but zooplankton in Missisquoi Bay may not reach peak abundance until July or August (McIntosh 1992). Holopedium sp. may be abundant in mid to late summer (D.P., unpublished data), but are surrounded by a thick gelatinous sheath and may have little nutritional value. In addition, the yellow perch population in Missisquoi Bay appears to be stunted (Jon Anderson, VTF&W, personal communication) and yellow perch may be feeding on young walleye.

If survival of walleye larvae and fry is low in Missisquoi Bay, then stocked fry are not likely to recruit to the adult population. If fry survival is low because zooplankton prey are not available when fry begin to feed, or because predation on walleye fry by rainbow smelt or yellow perch is excessive, then stocking walleye large enough to avoid predators and late enough to assure abundant zooplankton, may increase the walleye population in Missisquoi Bay.

Sea lamprey were not thought to have had a significant effect on Great Lakes walleye because wounding rates were typically low ($< 3.5\%$), but white perch were implicated in the collapse of the Bay of Quinte stock (Schneider and Leach 1977). Large numbers of spawning white suckers (Catostomus commersoni) have been observed in Lake Champlain tributaries where walleye had recently spawned (Jon Anderson, VTF&W, personal communication). White suckers are known to prey on walleye eggs (Colby et al.

1979), but Corbett and Powles (1986) concluded white sucker and walleye adults did not compete for spawning sites, and larvae of the two species did not compete for food in Apsley Creek, Ontario. How white suckers affect the success of Missisquoi River walleye reproduction is not known.

Walleye spawning habitat was probably lost when a section of the Missisquoi River was rip-rapped for construction of a bridge. Attempts were made to recreate the spawning grounds by adding rubble. The effectiveness of these habitat improvements has not been evaluated, but walleye have been observed in the area during spawning season.

Attempts to increase spawning habitat often involve adding golf ball to baseball size gravel in shallow areas to improve spawning substrate (Colby et al. 1979). Discharge flow rates from control dams can also be regulated to maintain adequate water levels in downstream walleye spawning areas and improve spawning conditions. Improvements in adult walleye habitat are usually related to improving water quality, but attempts to reduce competition by removing rough fish have occasionally been successful in simple fish communities (Rose and Moen 1953; Johnson 1977).

In recent years, growth of Eurasian watermilfoil (Myriophyllum spicatum) and water chestnut (Trapa natans) has reached problematic levels in some areas of Lake Champlain. Festa et al. (1987) reported that of 50 New York water bodies where the dominant sport fishery was for walleye, 54% (N=27) had sparse vegetation, 34% (N=17) had moderately abundant rooted vegetation and only 12% (N=6) had heavy densities of rooted vegetation. We found no studies specifically addressing the effects of dense macrophyte growth on walleye. However, the effects of dense vegetation on predation efficiency of piscivorous fishes is well documented with predatory success generally decreasing with increasing structural complexity (Hall et al. 1970; Ware 1973; Vince et al. 1976; Coul and Wells 1983; Gilinsky 1984; Savino and Stein 1989). Dense plant growth also reduces water movement, leading to siltation of substrates beneath the plants. Such siltation could potentially render lentic walleye spawning sites unusable. Lentic spawning

by Lake Champlain walleye has not been quantified, but Missisquoi Bay is believed to have been an historically important spawning ground, and South Bay remains an active spawning site.

Zebra mussels were first found in Lake Champlain during the summer of 1993. In other systems, zebra mussels have had major affects, including dramatic increases in water clarity. We do not know to what extent this exotic species will affect walleye in Lake Champlain, but we found no reports of significant walleye population declines following zebra mussel invasions. Although zebra mussels are well established in Lake Erie, the 1990 and 1991 walleye year-classes were two of the largest ever recorded (Roger Knight, Ohio Division of Wildlife, personal communication). Also, at the International Zebra Mussel Research Conference held in Toronto, Ontario in February 1992, Canadian investigators (J.D. Fitzsimons, V.W. Cairns, and J. Leach) presented results of a study on the colonization of reefs in Lake Erie by zebra mussels. These researchers concluded that walleye egg survival was not affected by zebra mussels.

Spawning Stream Discharges During Egg and Larval Stages

The Water Resources Division of the U.S. Geological Survey maintains several gauging stations on Lake Champlain tributaries. Mean monthly discharge at stations closest to walleye sampling sites on the Poultney, Lamoille and Missisquoi rivers are presented in Table 21. Discharge from the Great Chazy River was not monitored from 1969 to 1989 (Lloyd Wagner, U.S. Geological Survey, personal communication). Discharge data for 1992 are not yet available. The mean monthly discharge is the arithmetic mean of individual daily mean discharges recorded by continuous recording devices located at each gauging station (Toppin et al. 1992). Stream flow at any given time during the month can vary substantially from the monthly mean.

Reckahn and Thurston (1991) modeled the relation between flow volumes and year-class strength from 1980 to 1987 for several walleye stocks in the Georgian Bay, Lake Huron area. They concluded that in general, spring flow volumes were a major factor regulating year-class strength of river-spawning walleye. However, the strength of the relationship varied among stocks. Two additional variables, maximum mid-winter snow depth and mean April-May air temperatures, improved the models ability to predict year-class size. Rainfall during April and May did not appear to correlate with year-class size. The authors suggested that the biological link between high river flows and good walleye survival was the zooplankton community: high flows flushed more detritus into Georgian Bay resulting in large zooplankton populations for young walleye to feed on. Martin et al. (1981) reported a positive correlation between zooplankton size and diversity and water volumes in the Missouri River.

Based on modeling results, Reckahn and Thurston (1991) predicted strong year-classes were possible when deep snow and warm springs combined to produce high spring run-off volumes. They further speculated that declining year class strength of walleye in the Georgian Bay area could be related to recent weather trends toward low snowfall, mild winters, and the resulting smaller spring run-off volumes.

Table 21. Mean monthly discharge (cubic feet per second) in walleye spawning streams (minimum recorded flow in parentheses). Data adapted from U.S. Geological Survey Water-Data Reports 1988 - 1991 (1992 data not yet available).

Year	Poultney River (below Fair Haven)			Lamoille River (East Georgia)			Missisquoi River (Swanton)		
	March	April	May	March	April	May	March	April	May
1988	456 (107)	352 (145)	294 (164)	1,303 (350)	2,933 (1,050)	1,017 (441)			
1989	274 (110)	560 (187)	573 (132)	1,876 (250)	3,059 (1,200)	2,386 (763)			
1990	754 (183)	629 (295)	660 (169)	2,706 (540)	3,217 (1,200)	1,601 (767)			
1991	582 (127)	407 (283)	209 (53)	2,159 (850)	2,687 (1,020)	1,316 (478)	5,005 (1,700)	3,987 (1,340)	1,917 (730)

Mark-recapture data was used to estimate walleye spawning populations in South Bay, the Great Chazy River and the Poultney River. Poultney River was the only stock for which river discharge data were also available. Unfortunately, the total number of recaptured fish was small (maximum = 54 in 1992), making the number of recaptured fish in any given age class too small to provide reasonable estimates of year class abundance. Therefore, no attempts were made to establish a correlation between stream discharge and year class strength of spawning adults.

Effects of Sewage Treatment Plants on Water Quality

We found no examples of studies explicitly examining the effects of sewage effluent on fish, however, the effects of water quality characteristics typical of sewage discharge have been studied. One of the most critical effects of sewage effluent on fish is a reduction in dissolved oxygen (D.O.); low D.O. can be directly harmful by restricting respiration, or indirectly harmful by increasing the toxicity of other pollutants (Wilber 1969). Oseid and Smith (1971) reported that at low D.O. (2-7 mg/l), hatching of walleye eggs was delayed 1-4 days. Low D.O. is also associated with smaller larval walleye size at hatching and retarded early development (Oseid and Smith 1971; Seifert and Spoor 1974). Domestic sewage often increases levels of organic matter (which can lower D.O.), suspended solids (which can cause siltation of eggs), floating solids, and inorganic salts (Clark et al. 1977). Toxins in sewage which are most likely to reach problem levels include ammonia, zinc, copper and free cyanide (Wilber 1969). However, the toxic effects of many pollutants, such as salts, lead, zinc and nickel, are more pronounced in adult fish than in fish eggs (Jones 1966). We found no studies addressing the effects of chlorine in sewage effluent on fish in the receiving waters.

Heavy Metals and Pesticides

Hazardous materials enter the surface waters of the Lake Champlain basin from a variety of point and non-point sources. Some of these materials are believed to be potentially toxic to fish and other aquatic organisms. Bean and McIntosh (1987) summarized known, potentially toxic pollutants in the Lake Champlain drainage basin. They focused primarily on organic and inorganic contaminants identified by the U.S. Environmental Protection Agency as "priority pollutants", but included additional substances thought to pose potentially significant threats to surface waters. Particular emphasis was placed on pesticides thought to be heavily used in the Lake Champlain watershed. The extent to which pesticides are flushed into Lake Champlain is dependent on the quantity and timing of precipitation and flooding in the basin (Schwartz 1978).

The most commonly used field crop pesticides in the Lake Champlain basin are thought to be alachlor, atrazine, cyanazine, simazine, mancozeb and 2,4-D (Bean and McIntosh 1987). In addition, captan and guthion are the two primary pesticides used in orchards (Bean and McIntosh 1987). Atrazine, cyanazine, simazine and 2,4-D are not acutely toxic to most biota, but may indirectly influence fish through low-level effects on primary producers (Herman et al. 1986). Alachlor, mancozeb and guthion are regarded as moderately to highly toxic to fish, but captan is not thought to be hazardous to fish (Bean and McIntosh 1987). Other pesticides used on crops grown in the Lake Champlain basin (brand names in parentheses) include butylate (Sutan), dicamba, EPTC (Eptam), glyphosate (Round-up), metolachlor (Dual), 2,4-D, cyhexatin (Plictran), dichlone (Phygon), dicofol (Kelthane), fenvalerate (Pydrin), phosmet (Imidan), aldicarb (Temik), and carbaryl (Sevin) (Bean and McIntosh 1987). Historically, methoxychlor and dibrom have been aerially applied to streams to control blackflies and mosquitoes (Bogden 1978). Little information about the ecological effects of these pesticides is available.

Chlorinated hydrocarbon pesticides can be acutely toxic to fish and sublethal effects include reproductive impairment and carcinogenic/teratogenic effects (Connell and

Miller 1984). Hatchability of fish eggs exposed to sediments containing dioxins may be reduced (Bean and McIntosh 1987). Trace elements, including chromium, copper, lead, nickel and zinc, have been found at high levels in sediments of localized areas of Lake Champlain (Hunt 1975). However, with the exception of methylated mercury, accumulation of trace elements by fish is usually limited (Bean and McIntosh 1987).

Levels of chlorinated hydrocarbon pesticides, polychlorinated biphenyls (PCB's) and methylated mercury in the tissues of some Lake Champlain fishes have occasionally exceeded the U.S. Food and Drug Administration's action levels (New York, Vermont and New England River Basin Commission 1979). In particular, levels of mercury in walleye flesh have prompted walleye consumption advisories (Burlington Free Press, 1990).

Point sources of contaminants entering the Lake Champlain system include industrial discharges, wastewater treatment plants, classified hazardous waste sites, and active municipal and private landfills (Tables 22 - 25). In addition, there are 32 landfills within the Lake Champlain basin that have become inactive since 1978 (Bean and McIntosh 1987). Although many wastewater treatment plants do not release priority pollutants, chlorine added during waste treatment can combine with organic compounds present in the receiving waters to create toxic substances (Bogden 1978).

Non-point sources also contribute to pollutants entering Lake Champlain and its tributaries, however little information concerning the quantity or nature of these pollutants is available. Suspected and known non-point sources include urban stormwater runoff, agricultural runoff, boating activity, atmospheric deposition and leaking storage tanks.

How walleye are affected by pollutants found in the Lake Champlain basin is not clear, but it is known that certain toxins, such as DDT, PCB's and mercury can accumulate in walleye flesh. Many pollutants tend to be associated with particulate matter and can become concentrated in areas where sediments accumulate, such as river mouths, bays, and deep-water areas. Bean and McIntosh (1987) report that walleye spawning areas

Table 22. Known pollutants in permitted industrial discharges in each sub-basin of the Lake Champlain drainage basin (adapted from Bean and McIntosh 1987).

Drainage Basin	Industrial Discharge Site	Maximum Permitted Discharge Rate (millions of gallons/day)	Potential Pollutants in Effluent
Winooski River	International Business Machines Champlain Cable Company	5.0 0.125	copper, nickel, lead, zinc copper, zinc, chromium, lead, silver, chloroform
	McNeil Generating Plant	0.50	cadmium, chromium, copper, lead, nickel, zinc
	International Hydronics Corp.	0.02 for 14 days once annually	phenols, oil, grease
Otter Creek	None		
Lamoille River	None		
Missisquoi River	Boise-Cascade Packing Co. Columbia Gas Co. (permit expired March, 1985)	4.5 0.03	zinc arsenic, cadmium, chromium, copper, mercury, lead, nickel, zinc
Poultney River	None		
Lake George	None		
Ausable River	None		
Boquet River	None		
Mettawee River	None		
Chazy River	None		
Saranac River	New York State Electric and Gas Corp. Imperial Paper Co. (Larry Nashett, NYDEC, personal communication)	monitor only	cyanide, lead, zinc, phenol
Lake Zone (within 1 mile of Lake Champlain)	International Paper Co.	12 (winter), 17 (summer)	chloroform, di-n-butyl phthalate, 2,4-dichlorophenol, 2,4,6- trichlorophenol, toluene, pentachlorophenol, nitrobenzene, phthalate esters

Table 23. Known pollutants in effluent of wastewater treatment facilities in each sub-basin of the Lake Champlain drainage basin (adapted from Bean and McIntosh 1987).

Drainage Basin	Number of Facilities	Maximum Combined Discharge (millions of gallons/day)	Known Pollutants in Effluent
Winooski River	14	17.79	phthalate esters, mercury, copper, phenol, methylene chloride, silver, zinc, copper, cyanide
Otter Creek	10	11.25	lead, chromium, nickel, zinc, aluminum
Lamoille River	4	1.10	None
Missisquoi River	5	1.89	None
Poultney River	4	1.48	silver
Lake George	3	3.05	None
Ausable River	2	2.80	None
Boquet River	2	0.38	None
Metawee River	2	0.69	None
Chazy River	1	0.26	benzene, tetrachloroethene, trichloroethylene
Saranac River	4	20.8	phenols, phthalates
Lake Zone (within 1 mile of Lake Champlain)	15	12.83	nickel, cyanide, cadmium, chromium, copper, silver, lead, 1,2 dichloroethane, tetrachloroethane, methyl chloride

Table 24. Known pollutants at hazardous waste sites in each sub-basin of the Lake Champlain drainage basin (adapted from Bean and McIntosh 1987).

Drainage Basin	Number of Hazardous Waste Sites	Known Pollutants at Site
Winooski River	9	polycyclic aromatic hydrocarbons (PAH's), arsenic, cadmium, copper, chromium, lead, nickel, zinc, benzene, toluene, xylene, phenol, bis(2 ethylhexyl) phthalate, di-N-butyl phthalate, 1,1,1 trichloroethane, 1,1 dichloroethane, tetrachloroethene, trichloroethylene, ethylbenzene, carbon tetrachloride, PCB's, 1,2-trans dichloroethylene
Otter Creek	3	information not available
Lamoille River	None	
Missisquoi River	None	
Poultney River	2	mercury
Lake George	None	
Ausable River	None	
Boquet River	2	PCB's
Mettawee River	5	zinc, chromium, nickel, lead, copper, phenols, #2 fuel oil, tetrahydrofuran, cyclohexane, 2-butanone, acetone, xylene, ethylbenzene, PCB's, methylene chloride, trichloroethylene, toluene,
Chazy River	1	toluene, 1,1,1 trichloroethane, 1,1 dichloroethane, ethylbenzene, metaxylene
Saranac River	None	
Lake Zone (within 1 mile of Lake Champlain)	12	PAH's, 2-butanone, xylene, carbon disulfide, acetone, benzene, ethylbenzene, 1,2 dichloroethane, carbontetrachloride, trichloroethylene, methyl chloride, chlorobenzene, 1,2 dichloropropane, PCB's, pesticides, chromium, nickel, zinc, lead

Table 25. Known pollutants in leachate from active landfills within sub-basins of the Lake Champlain drainage basin (adapted from Bean and McIntosh 1987).

Drainage Basin	Number of Active Landfills	Known Pollutants in Leachate
Winooski River	13	zinc, toluene, 1,2 dichloroethene, benzene, carbon tetrachloride, 1,1 dichloroethene, ethylbenzene, arsenic, cadmium, copper, chromium, lead, nickel, xylene, phenol, bis(2 ethylhexyl) phthalate, perchloroethylene, trichloroethene, trans 1,2 dichloroethene
Otter Creek	10	1,2 dichloropropane, toluene, 1,3 dichloroethene xylenes, lead, copper, 1,1,1 trichloroethane, methylene chloride
Lamoille River	8	lead, zinc, copper, toluene, tetrahydrofuran
Missisquoi River	2	zinc, lead, toluene
Poultney River	None	
Lake George	5	None
Ausable River	5	zinc, lead, phenols, toluene, xylene
Boquet River	6	None
Mettawee River	6	zinc, chromium, nickel, lead, copper, phenols, #2 fuel oil, tetrahydrofuran, cyclohexane, PCB's
Chazy River	1	zinc, phenol
Saranac River	5	zinc, lead, phenols,
Lake Zone (within 1 mile of Lake Champlain)	3	None

often overlap with areas predicted to accumulate sediment-associated toxins. If early fish life stages are exposed to sediments contaminated with, for example, trace elements or PCB's, decreased hatchability or fry survival may occur (Bean and McIntosh 1987).

Management Plans and Strategies

Walleye management plans from a variety of agencies were reviewed to determine general strategies employed on other water bodies. Particular emphasis was placed on locating recent plans for large, temperate-zone systems. Information contained in the plans ranged from simple statements of general goals to specific modeling equations used to establish exact harvest recommendations. In general, management strategies tended to avoid recommending specific yield targets, but instead focused on the number of angler days provided per year as a measure of success of the fishery. Catch rates were also a common means to evaluate angler success.

Specific goals outlined in management plans from Wisconsin, Minnesota, New York, Ohio and the Great Lakes Fishery Commission are presented in Table 26. Of these plans, that of the Lake Erie Walleye Task Group to the Great Lake Fisheries commission (Knight et al. 1993) contains the most detailed description of procedures to manage the walleye resource. To set commercial and sport fisheries recommended allowable harvest (RAH) levels, the Lake Erie Walleye Task Group relies on two centralized databases: 1). gill net surveys providing biological sample data and 2). sport and commercial catch/effort data. Catch-at-age-analysis (CAGEAN) is applied to these databases to estimate stock size. October gill net catches of age-1 walleye are regressed against the number of age-2 fish estimated by CAGEAN to create an index for using the age-1 gill net data to predict recruitment to age-2 in the next year. This index, together with observed survival of age-2 and older fish is used to project age-3 and older standing stock size. Once standing stock has been projected, estimated yield at the optimum fishing rate (F-opt) is used to set the RAH for a given year.

In its state-wide management plan, the Wisconsin Department of Natural Resources recommended surveying walleye waters to obtain population estimates, mortality rates and age and growth data (Steve Hewett, Wisconsin Department of Natural Resources, personal

Table 26. Walleye management goals set by various agencies.

State/agency	Waters	Year	Goal / Objective
Wisconsin	State-wide	early 1980's	Maintain 8.5 million angler days through 1985. Provide potential harvest of 2.6 million walleye/yr. Improve potential harvest of fish > 380 mm by 10% in selected waters by 1985.
Minnesota	State-wide	1987	Provide 13 million angler days of walleye fishing/yr.
New York	186 waters state-wide	1987	Provide average of 3.4 kg/hectare/yr and/or catch rates exceeding 0.20/angler hour for anglers targeting walleye.
Ohio	Lake Erie	circa 1989	Provide minimum of 1.5 million angler days/yr. Provide harvest rate of 0.40 - 0.60 walleye/angler hour.
Great Lakes Fishery Commission	Lake Erie	1993	Recommended allowable harvest (RAH) for commercial and sport fisheries determined annually. 1992 RAH set at 12.203 million walleye or 9,901 tonnes.

communication). A need to evaluate the effectiveness of stocking programs and angling regulations was also identified. The Minnesota Department of Natural Resources likewise recommended evaluating the effects of walleye stocking in its state-wide plan (Minnesota Department of Natural Resources 1987) and listed several other issues of concern: inadequate habitat protection, heavy fishing pressure on some lakes, limited data on population dynamics, stock structure and the economic value of walleye sport fisheries, and the need for increased communication with other governing agencies and the angling public. The majority of recommendations made by Festa et al. (1987) to restore and enhance New York's walleye fisheries involved expanding stocking programs, although increasing stock assessment programs and angler access facilities, providing information to the public and maintaining the quantity and quality of walleye habitat were also suggested.

Fish population surveys tend to be very expensive and should be designed to provide the most useful information at the least cost. Beginning in 1993, agencies responsible for managing the walleye resource of Lake Erie standardized sampling methods to increase analytical power, and improve sampling efficiency and design (Culligan et al. 1993). A similar cooperative approach between agencies managing Lake Champlain walleye could increase the amount of information available on the status of walleye throughout the lake. Where possible, standardization of sampling designs both among populations and among years would increase the value of this data set for detecting long-term trends in the Lake Champlain walleye resource.

Recommendations

Based on the data summary and literature review contained in this report, and discussions held with the Fisheries Management Subcommittee of the Lake Champlain Fish and Wildlife Management Cooperative, John Forney (Cornell University), Brett Johnson (Colorado State University) and Roger Knight (Ohio Department of Natural Resources), we make the following recommendations for **potential** use in a Lake Champlain walleye management plan (order of recommendations does not indicate priority):

(1). Creel survey

Information concerning the Lake Champlain walleye sport fishery and the characteristics of harvested walleye is currently limited. We recommend a lake-wide creel survey of anglers specifically targeting walleye to estimate the age distribution of harvested walleye and total angler harvest. Together with natural mortality estimates, these data can then be used in a CAGEAN (catch-at-age analysis) or GIFSIM (generalized inland fisheries simulator) model to estimate harvestable stock size. A critical step in modeling harvestable stock is to design the creel survey specifically to estimate model input variables. Because year to year variability in creel data is normally very high, multi-year creel surveys are necessary to account for that variability and provide reliable estimates. Ten years of creel data are preferable, but a minimum of five years are needed before reasonable stock size estimates are possible (Roger Knight, Ohio Department of Natural Resources, personal communication). Data from more limited creel surveys can provide information on growth, spatial and temporal distribution, diet, catch rates and exploitation rates.

(2). Diary cooperator program

The walleye angler diary cooperator program has the potential to provide valuable harvest and biological data. We recommend expanding the program. Annual workshops should be conducted to train cooperators to accurately collect catch per unit effort information, length measurements and scale or spine samples for aging.

(3). Standardized sampling

Attempts to sample walleye outside of spawning grounds have met with mixed success. Researchers and managers need to jointly identify a variety of sampling techniques for efficiently and accurately assessing Lake Champlain walleye populations throughout the year. Other agencies typically rely on fall shoreline seining and electrofishing to collect juvenile walleye and fall gill netting to collect both adults and juveniles. After research has established guidelines for quantitatively sampling particular subsets of Lake Champlain walleye, we recommend management agencies standardize sampling designs and protocols to increase efficiency and improve analytical power. In addition, coordination of data storage formats would facilitate data sharing.

(4). Juvenile survival

Survival of Lake Champlain adult walleye appears good, but no data on survival to spawning age are available. If abundances of adult walleye are limited by low survival of pre-adults, research to identify life stages with high mortality becomes critical to managing the population. We recommend research to quantify survival of each walleye life stage from egg to juvenile and identify variables influencing pre-adult survival. Catch per unit of effort estimates of age-0 or age-1 walleye can also be used to create an index for predicting year-class strength.

(5). Species interactions

Lake Champlain is a large, complex system and walleye are likely to interact with a diversity of other fish species. Salmonids stocked through the Lake Champlain salmonid restoration program have the potential to consume juvenile walleye and compete with adult walleye for forage. Research is needed to assess interactions between walleye and salmonids to allow predictions of potential effects of efforts to enhance the abundance of one top predator on the others. Substantial numbers of spawning white suckers (*Catostomus commersoni*) have consistently been observed on walleye spawning grounds at times when walleye larvae are hatching and beginning to drift toward Lake Champlain. Potential impacts of white suckers on walleye eggs and larvae should be researched. Rainbow smelt are extremely abundant in the northeast arm of Lake Champlain, where the walleye fishery has recently declined. We recommend researching the effect of large rainbow smelt populations on larval walleye survival.

(6). Stocking evaluation

The success of any particular stocking program is largely unpredictable. Given that considerable resources are allocated to walleye stocking in Lake Champlain, we recommend conducting research to evaluate the effectiveness of walleye stocking programs. Reliable methods for estimating stocked fish survival will need to be developed before the absolute and relative contributions of stocked walleye fry and fingerlings to the adult population and the fishery can be assessed.

(7). Harvest regulations

Based on available data, we cannot recommend changes in angling regulations. However, if regulations are changed, both the direct effects on walleye, and the indirect effects on other species, especially rainbow smelt, produced by such changes should be assessed using bioenergetics models.

(8). Habitat

Walleye habitat in Lake Champlain has not been assessed. Because adult growth rates appear to be good, we assume adequate adult habitat and forage are available. To address the possibility of increasing the abundance of walleye in Lake Champlain through natural reproduction, spawning habitat needs to be quantified. If quality spawning areas are limited, habitat improvement techniques, including flow regulation, may expand available spawning beds.

(9). Measures of success

After total population size and harvest rates have been estimated (minimum of five years of data), measures of success can be established to help management agencies evaluate the effectiveness of various management strategies.

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