IDENTIFICATION, MOVEMENT, GROWTH, MORTALITY, AND EXPLOITATION OF WALLEYE STOCKS IN LAKE ST. CLAIR AND THE WESTERN BASIN OF LAKE ERIE[1]

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ABSTRACT

The harvest of walleye by sport and commercial fisheries in lakes St. Clair and Erie is under a cooperative management program involving several states and two countries. In this report we present the results of a long-term tag-recapture study as well as corroborative evidence of stock discreteness from studies of population characteristics such as growth and allelic frequencies of walleye in these waters. Walleye were tagged in the spring from 1975-87 in lakes St. Clair and Erie. Tag-recapture data indicate a general tendency for walleye to move northward after tagging. Walleye tagged in Lake St. Clair had higher recovery rates and lower survival rates than walleye tagged in Lake Erie. A reward-tag study in Lake St. Clair provided an estimate of a non-reporting rate of approximately 33% which is comparable to rates in the literature for other species. Data from the Ontario commercial (gill-net) fishery, Michigan Department of Natural Resources trap-net surveys, and sport fisheries from western Lake Erie and Lake St. Clair were analyzed with a catch-at-age model which permitted estimation of population abundance (12.2 to 34.5 million fish), fishing mortality rate (0.19 to 0.37), and annual survival rate (0.57 to 0.68). It appears that exploitation rates for the sport fishery in the western basin exceeded those of the commercial fishery from 1978-82. In recent years (1983-87), exploitation rates were comparable. Average abundance and catch of walleye in the western basin were 12.2 and 3.4 million fish in 1978-82; average abundance and catch in 1983-87 were 34.5 and 5.2 million fish. We found good agreement between the estimate of the harvest from creel surveys and that from the catch-at-age model for Lake Erie. Walleye abundance and harvest in Lake St. Clair were 10% of the values for the western basin of Lake Erie. Two discrete stocks were delineated by analysis of allelic frequencies of samples from Lake St. Clair and Lake Erie spawning populations. These two stocks are the western basin of Lake Erie and Lake St. Clair stocks. No further subdivision of stocks was possible based on the genetic analysis of 21 loci. These genetically different stocks intermix in the northern waters of this system. Based on a consideration of the results of the genetic analysis, catch-at-age analysis, and tag-recapture study we recommend independent but coordinated management of the walleye populations in Lake St. Clair and Lake Erie.

INTRODUCTION

From 1900–50 the walleye (*Stizostedion vitreum*) was one of the most valuable sport and commercial species in the lower Great Lakes; however, their abundance declined, apparently due to cultural and biological stresses, and reached an all-time low during the early 1960's (Regier et al. 1969). In the late 1960's fishery managers on Lake St. Clair and Lake Erie initiated a cooperative management program for Lake Erie resources. Since 1976, walleye in western Lake Erie have been managed under an interagency quota system. The Michigan Department of Natural Resources (MDNR) began a study of the Lake St. Clair walleye population in 1975 and the western Lake Erie population in 1978. This study covers the period 1975–87. Extensive sport fisheries were active on Lake St. Clair and Lake Erie during that period but no commercial walleye harvest was permitted in Lake St. Clair or in the Michigan and Ohio waters of western Lake Erie.

Extensive walleye harvests occur each year throughout the St. Clair-Detroit River system and western Lake Erie. Harvest methods are restricted to angling except in the Ontario waters of southern Lake Huron and Lake Erie. Estimates of the walleye harvest for the entire area are not available; however, the annual harvest in western Lake Erie averaged 6,873,800 fish from 1985–87 (Lake Erie Committee, Great Lakes Fishery Commission, unpublished data). This level of harvest was roughly equal to the highest commercial harvest from Lake Erie (7,000 tons) taken in 1956 just prior to the walleye population collapse (Nepszy 1977). The commercial harvest of walleye from Lake St. Clair during the period 1870–1965 averaged about 50 tons (Johnston 1977). Commercial harvest of walleye in Michigan's and Ontario's waters of Lake St. Clair has been banned since 1919 and 1970, respectively. The annual walleye angler harvest in Michigan's waters of the St. Clair River, Lake St. Clair, and Detroit River in 1983 and 1984 averaged 134,143, 132,454, and 163,828 fish, respectively (Haas et al. 1985). The average walleye harvest from Ontario waters of Lake St. Clair was 109,000 fish from 1977–87 (D. MacLennan, Ontario Ministry of Natural Resources, unpublished data). The creel survey estimates for the St. Clair and Detroit rivers probably reflect about half the daytime walleye catch since there is an equally intense sport fishery in Ontario's half of these waters. In addition, the night-time harvest of walleye by anglers from the St. Clair and Detroit rivers is thought to be substantial but has not been measured.

Efficient utilization and allocation of the walleye resource requires knowledge of population distribution and abundance. The size of the walleye populations in Lake St. Clair and the western basin of Lake Erie, and the number of Lake Erie walleye that migrate into Lake St. Clair (where they are exploited under a different regime) are critical questions for quota management.

Early tagging studies showed that walleye moved within and between Lake St. Clair and Lake Erie (Wolfert 1963; Ferguson and Derksen 1971; VanVooren 1978). The tagging evidence

for migration between these waters and the decline in commercial stocks in some areas (Schneider and Leach 1977) suggested the existence of two or more genetic stocks. This prompted management agencies to examine stock structure and migration pattern, and to determine the feasibility of management based on the genetic stock concept.

Appropriately designed tag-recapture experiments provide information on survival rates and the spatial and temporal distribution of individual fish. These distribution patterns through time are indicators of population movements and mixing. Survival and exploitation rates are estimated by noting relationships between number of individuals tagged and number of tagged individuals recaptured (see e.g., Ricker 1975). In this study, we investigated non-reporting in the walleye fishery through a reward-tag experiment.

Differences in population parameters such as growth rate, recruitment, or mortality rate may be used to delineate stocks (Ihssen et al. 1981). These parameters reflect population responses to different environments and thus are not necessarily indicative of reproductive isolation (i.e., genetic stocks). However, the population parameter approach may permit delineation of stocks for management purposes and may provide corroborative evidence of stock discreteness. In this study, we examined growth rates of Lake Erie and Lake St. Clair walleye.

We also examined biochemical genetic differentiation among walleye using electrophoretic techniques and supplemented information on stock discreteness with data from a tag-recapture study. A preliminary mixed-stock sample of walleye collected during fall, 1980, in Lake Erie (Figure 1A) was screened for genetic variation at 84 enzyme loci. Ten of the resolved loci were polymorphic and the mean heterozygosity for the sample was 0.057 (J. Seeb, L. Wishard, and P. Abersold, Pacific Fisheries Research, Seattle, Washington, unpublished data). We were encouraged by the relatively high genetic variability which might allow estimation of stock structure. We collected data from spawning walleye at eight locations in Lake St. Clair and Lake Erie and examined these data for stock differences using electrophoretic and growth information.

Study area

The study area comprises 862 km of Great Lakes waterways bounded by Lake Huron and Lake Erie (Figure 1A). We have divided it from north to south into five geographical units: southern Lake Huron, the St. Clair River, Lake St. Clair, the Detroit River, and Lake Erie. Lake Huron, the fifth largest lake in the world, is 330 km long and has a surface area of 59,674 km². The St. Clair River is 63 km long, has an approximate flow of 5,300 m³/s, and falls 1.5 m over its course (Direcki 1984a). The upper half of the river is characterized by a narrow channel with very little littoral area. Lake St. Clair is approximately 30 km long and has a surface area of 1,100 km². The Detroit River is 51 km long, has an approximate flow of

5,400 m³/s, and falls 0.9 m over its length (Direcki 1984b). The St. Clair River has an approximate surface area of 65 km²; 58% is deeper than 6.4 m. The Detroit River has a surface area of 86 km²; 48% is deeper than 6.4 m (D. Schloesser, U. S. Fish and Wildlife Service, personal communication). The Michigan-Ontario boundary roughly divides the St. Clair-Detroit River system in half. The western basin of Lake Erie has a surface area of 3,276 km². Major walleye spawning tributaries have been identified: Ontario's Thames River on Lake St. Clair (Ferguson and Derksen 1971) and Ohio's Maumee River on Lake Erie (VanVooren 1978; Figure 1A). There are no walleye spawning grounds in Michigan's waters of Lake St. Clair or Lake Erie where successful reproduction has been verified in recent times. Lake St. Clair is characterized by a diverse plant and invertebrate animal community which, compared to Lake Erie, has shown relatively little evidence of negative impacts of enrichment (B. Manny, U. S. Fish and Wildlife Service, personal communication).

METHODS

Net samples

Trap nets set in the spring in Lake St. Clair and Lake Erie provided abundance data on age 2 and older walleye. Gill nets set in the fall in Lake Erie provided data on abundance of yearling and older fish. Gill nets typically provide indices of relative year-class strength (Willis 1987). Impoundment gear (trap net) is generally considered to be superior for relative abundance studies (Yeh 1977; Craig 1980); however, traps must be fished for extended time periods which is expensive. We examined the relative year-class strength indices from the two gear types for Lake Erie because gear selectivity influences the size distribution of the sample.

Trap nets were used to capture fish for tagging and to provide an index of relative abundance, catch per unit of effort (CPUE; number caught per 24 hours). This assumes that CPUE is linearly related to fish abundance and that a percent change in CPUE will reflect the same percent change in abundance (Bannerot and Austin 1983). We captured walleye during spring in Lake St. Clair and Lake Erie with 6-foot-deep trap nets fished at the same locations each year (Figure 1B). Five nets were fished throughout each sample period and were normally tended on all weekdays, weather permitting. We tried to obtain a minimum of 50 net lifts for each period. The Lake St. Clair surveys were carried out from 1975–85 and the Lake Erie surveys from 1978–87. The average Lake Erie sampling period began on April 17 and lasted 20 days; the average Lake St. Clair sampling began on May 23 and lasted 29 days.

The entire catch from each trap net was identified and enumerated. Growth data and age samples (scales) were collected from walleye and other species. The maximum time between net lifts was 72 hours; the majority was lifted after 24 hours. We compared the fish communities of Lake St. Clair and western Lake Erie with the Shannon-Weiner diversity index

(Vandermeer 1981) calculated from the trap-net data. This index measures the evenness of the distribution of individuals within species. The Shannon-Weiner function is given by:

$$H = \sum P_i \ln(P_i)$$

where P_i is the fraction of all individuals in the community contained in species i (Vandermeer 1981). The value of H is largest when the number of species is greatest and when individuals are apportioned most evenly among species.

We fished multi-filament, graded-mesh gill nets at two stations in Lake Erie (Figure 1B) in October from 1978–87 as part of the interagency yearling-walleye index program. Replicate sets were made each year with gangs of nets, 1.83 m deep, each consisting of seven 30.48 m long panels that ranged from 51 to 127 mm stretched mesh measure by 13 mm intervals. All walleye captured in gill nets each year were sampled for age and growth data.

Tag-recapture study

Walleye were tagged by MDNR personnel during the spring trap-net surveys in Lake St. Clair and western Lake Erie. We did not consider these tagged populations as spawning stocks because fish were tagged after spawning had occurred; none of the known walleye spawning grounds were located in Michigan's waters. The Lake St. Clair tagging station was located approximately 47 km northwest of Ontario's Thames River spawning ground and 129 km north of the Maumee River spawning ground (Figure 1B). The Lake Erie tagging station was located near Monroe, Michigan, 24 km north of Ohio's Maumee River spawning site.

Fish were removed from the trap nets and immediately placed in an on-board live tank equipped with continuously circulating lake water. Fish were removed individually from the live tank and tagged without anesthesia before release at the net location. Total length measurements were made on all tagged fish, while total weight measurements and scale samples were taken from portions each year varying from 36% to 100% of the total number tagged. When scale samples were taken, all fish from that trap net were processed. Net lifts were sampled throughout the survey period for age data. All fish were tagged with size 10 or size 12 monel metal strap tags affixed by overlapping the tag snugly around the dentary bone. The tags were inscribed with the local MDNR address and individual tag number. Tag-recapture data were solicited from anglers and commercial fishermen on a voluntary basis.

We tagged 11,876 walleye at the Anchor Bay site, Lake St. Clair, from 1975–85 and 17,957 walleye at the Monroe site, Lake Erie from 1978–87.

The time of tagging was an important variable in defining the movement of the two stocks and the rate of mixing. The Lake Erie tagging was carried out in April each year; most fish were captured immediately after spawning. The Lake St. Clair tagging followed; most fish

were tagged during the last week of May and first week of June. The average Lake Erie walleye was tagged about 36 days earlier than the average Lake St. Clair fish. Walleye tagged in Lake Erie were most likely all Lake Erie stock primarily from the Maumee River because of the proximity of tagging date to spawning times; other stocks would not have had time to migrate that far. However, the walleye tagged in Lake St. Clair might have been either Lake St. Clair or Lake Erie stock since ample time was available for migration and mixing.

Tag-recovery data were summarized by location and Julian date. Dates of tagging and tag recovery for recaptured walleye were coded by the Julian calendar and thus were independent of the calendar year. This permitted calculation of the extent of dispersal from the tag sites and time-at-large. Numbers of tags from each tag site, recovered within a specific area, were compared to provide estimates of stock mixing. Nonparametric statistics were used to test for differences between median recapture dates.

Recently, a generalized stochastic model (and sophisticated computer algorithm) became available for the analysis of data from tagging experiments (Brownie et al. 1985). This model (hereafter referred to as the BROWNIE model) provides maximum likelihood estimates of recovery and survival rates which are unbiased. Total mortality rate (natural logarithm of survival rate) may be partitioned into fishing and natural mortality rates if an estimate of the tag reporting rate is available (Horsted 1963). This is because tag recovery rate is a product of the exploitation rate and the reporting rate (Krementz et al. 1987). (Brownie et al. [1985] refer to the recovery rate as the reported exploitation rate.)

The BROWNIE model was used to analyze the results of the tag-recapture experiments in Lake St. Clair and Lake Erie. We estimated mean annual survival, recovery, and adult life span and these values were compared statistically using the recommended z test (Brownie et al. 1985).

In many studies the reporting rate is assumed to be 100%, that is, all of the tags recovered by the fisheries are seen and subsequently reported. If 100% reporting is assumed, then the recovery rate is an estimate of the exploitation rate. More likely, reporting rate is less than 100% and may vary over time (Rawstron 1971), space (Chadwick 1968; Henny and Burnham 1976; Reeves 1979; Green et al. 1983), or other factors (Rawstron 1971; Green et al. 1983).

If an estimate of the exploitation rate is available, then fishing mortality rate may be estimated. However, fishing mortality rate is underestimated whenever the assumption of complete reporting is violated. As reporting rate decreases, the relative error of the recovery rate (and hence, the relative error of the exploitation rate) increases (Conroy and Williams 1981; Figure 2). For example, if 80% of the tags are recognized and reported, the relative error of the recovery rate is 25%. Clearly, estimation of the exploitation and fishing mortality rates will be most reliable when reporting rates are high.

High reporting rates are difficult to ensure. Rewards, ranging from money to books to chances in a lottery, have been offered for the return of tags. Presumably the monetary reward or prize is a further incentive to the angler or commercial fisherman to report the catch. Holt (1963) suggested "planting" of marked fish in the catch of commercial fishing vessels as a way to estimate non-reporting. Margetts (1963) used this method to study non-reporting in the British cod fishery in the Barents Sea. Green et al. (1983) inserted (used) internal anchor tags in the catch of marine recreational anglers in Texas to examine non-reporting for seven species.

A reward-tag study was carried out on Lake St. Clair in 1981, 1982, and 1983 to provide an estimate of the non-reporting rate for traditional non-reward tags. Funds to pay rewards were solicited from local conservation organizations. Reward tags of four denominations, $2.00, $4.00, $6.00, and $8.00, carried a reward inscription, such as "Reward $8.00", and returns from these tags were used to examine the effect of monetary value on angler cooperation. Every third walleye received a reward tag. The different reward denominations were applied in repeating sequence from $2.00 through $8.00 so that no denomination bias was introduced.

Relative abundance

Relative year-class strength for Lake Erie walleye was calculated by estimation of the mean CPUE for ages 1 to 5 for 1977–82 year classes. (All five age groups were not represented in years prior to 1977 and after 1982.) Catch of age 6 and older fish was low and did not significantly contribute to the overall catch for a particular year. Gill-net and trap-net indices were compared with a nonparametric test of association (Hotelling-Pabst test for significance of Spearman's rho). This test does not require assumption of bivariate normality (Conover 1980). The null hypothesis tested was that gill-net and trap-net indices for 1977–82 year classes are mutually independent, i.e., the two gear types do not provide similar estimates of relative abundance.

We used the catch-at-age model, CAGEAN (Deriso et al. 1985), to estimate current and historical walleye stock sizes in Lake St. Clair and the western basin of Lake Erie. This model uses fishing mortality and catch-at-age data to arrive at stable and reliable estimates of current stock size. It is an improvement of the traditional virtual population analysis since multiple gear types and auxiliary information on fishing effort are explicitly considered in the model. The Marquadt algorithm is used to solve a system of nonlinear equations and to provide least-square estimates of model parameters. We used the IBM personal computer (PC) version of CAGEAN; this "reads in" gear-specific catch-at-age, fishing effort, and weight data and estimates age-specific abundance, catch, fishing mortality, selectivity, and catchability (CAGEAN-PC User Manual 1987).

We felt this age-structured program would be useful because it calculates stock abundance estimates from historical catch and effort data (including auxiliary survey data) as well as estimates of mortality and exploitation rates. We compared CAGEAN-derived estimates of mortality with estimates from tag analyses. Angler catch and effort data from creel surveys were combined with the trap-net survey data to produce comparable catch and stock abundance estimates for Lake St. Clair and Lake Erie walleye.

Growth

The western basin population has undergone significant change during the past 15 years generally from low to high abundance. There is evidence that growth has responded to increased density by decreasing in recent years. The western basin population is also under the most critical management program because it is shared by at least two states and one Canadian province and is sought by expanding sport fisheries and efficient commercial gill-net fisheries.

Some of the walleye collected by trap net were sampled for scales with the intention of age determination and subsequent growth analyses. Mean length-at-age was estimated for Lake St. Clair and Lake Erie walleye sampled from 1975–87. Because growth of Lake Erie walleye was suspected to differ before and after 1982, mean lengths-at-age were computed for the periods 1978–82 and 1983–87. Growth was described by the von Bertalanffy model,

$$L_t = L_{max} [1 - exp \{-k (t-t_0)\}]$$

fit to mean length data for age 1–9. Model parameters were estimated with a nonlinear least squares method (FISHPARM, Prager et al. 1987), the preferred method of fitting this model (Vaughan and Kanciruk 1982).

We examined the relationship between length and age with regression analysis for Lake Erie and Lake St. Clair walleye. Because we found different relationships for the two groups (see Results section) we did not use the regression model for size-at-age comparisons. Instead, comparisons of mean length-at-age were made with a t-test.

Growth differences of year classes were examined by computing relative growth indices:

$$RGI_j = \sum_{i=1}^{k} [\overline{L(t)}_j - \overline{L(t)}]$$

where

$$RGI_j = \text{the relative growth index of jth year class}$$

$$k = \text{number of age groups}$$

$$\overline{L(t)} = \text{mean length-at-age over all year classes}$$

$$\overline{L(t)}_j = \text{mean length-at-age of jth year class}$$

The purpose was to relate relative growth of a year class with its year-class strength (as measured by the rank transform of trap-net CPUE).

Genetic analysis

Walleye were collected during spawning at six sites in Lake Erie and two in Lake St. Clair (Figure 1A) with gill nets or by electrofishing. Mixed-stock samples of approximately 200 fish each were collected with gill nets from Anchor Bay, Lake St. Clair, in November 1983 and 1984. Whole fish were placed on ice immediately and taken to the laboratory where they were kept frozen at $-20\,°C$. Fish were thawed in the lab to extract muscle and liver tissues. Tissues were then refrozen at $-80\,°C$ for later electrophoretic analyses. Total length, total weight, gonad weight, age, sex, and maturity were collected from all walleye sampled for genetic information. Somatic weight was calculated by subtraction of gonad weight from total weight.

Horizontal starch-gel electrophoresis was employed to separate the various enzymes. The staining procedures were modified from Allendorf et al. (1977) and Harris and Hopkinson (1977). Stains with agar overlays were made according to Todd (1983); we used the nomenclature for allelic variants suggested by Allendorf and Utter (1979).

BIOSYS-1, a FORTRAN program by Swofford and Selander (1981) was used to analyze the allelic frequency data. Measures of genetic variability include allelic frequencies and mean heterozygosity. Polymorphic loci were tested for conformance to Hardy-Weinberg expectations of random mating and inter-populational heterogeneity of allelic frequencies by means of Chi-square tests. Stock composition of the fall samples from Lake St. Clair was obtained by an iterative procedure which calculated suspected genotypic frequencies from the observed allelic frequencies of the Lake St. Clair and Lake Erie samples.

RESULTS

Net samples

Trap-net catches indicated the fish communities in Lake St. Clair and western Lake Erie were similar with respect to kind and number of species (see Appendices 1, 2, and 3 for a species list and annual trap-net CPUE). The Shannon-Weiner index value calculated from the Lake St. Clair trap-net data was 2.10 and from the Lake Erie trap-net samples, 1.24. Since the number of species was nearly identical (Lake St. Clair, 39 species; Lake Erie, 40 species), the rather large difference observed was most likely due to the relatively uneven distribution of individuals within species in the Lake Erie samples. Mean trap-net CPUE values for 20 of the most prevalent species in Lake St. Clair and Lake Erie are shown in Figure 3. Trap nets in Lake Erie sampled 3.34 times as many fish; however, those individuals were mostly yellow perch, which had a CPUE 50 times greater than in Lake St. Clair. We feel that the Lake Erie fish community is unbalanced relative to that in Lake St. Clair; this may have implications for walleye growth and year-class success in Lake Erie (see Discussion section).

Trap nets captured considerably more walleye in Lake Erie (mean CPUE was 22.9) than in Lake St. Clair (mean CPUE was 8.5). The Lake St. Clair and Lake Erie trap-net CPUE of walleye age groups for each sample with corresponding effort data are given in Appendices 4 and 5. It is important to note that Lake Erie walleye were almost fully recruited to the trap nets at age 2, while the Lake St. Clair walleye were not fully recruited until age 3. The fall gill-net CPUE for walleye by age group for each season in Lake Erie is given in Appendix 6.

The Hotelling-Pabst test of the null hypothesis of no association between gill-net and trap-net abundance indices (Table 1) indicated that the association was significant ($r_s=0.899$, $N=6$, $P<0.01$). Thus, the relative year-class composition of the walleye population was well represented in the trap-net samples taken for the tag-recapture study. A similar analysis of ages 2–5 from 1976–82 indicated that gill-net and trap-net samples yielded similar relative abundance estimates ($r_s=0.964$, $N=7$, $P=0.001$). Inclusion of age 1 in the mean catch per unit effort decreased the strength of the association, but not significantly. Graded-mesh gill nets, designed to capture small fish, provided more efficient samples of age-1 fish than did trap nets.

Growth

The von Bertalanffy model was a reasonable description of growth for Lake St. Clair and Lake Erie walleye (Figure 4). Growth constants were similar (k=0.104, Lake St. Clair; k=0.102, Lake Erie) although the asymptotic length values were not; Lake Erie walleye growth is characterized by a higher asymptotic length (L_{max} =902 mm) than growth of Lake St. Clair

walleye (L_{max} = 854 mm) (Figure 4). Von Bertalanffy model parameters fit to two data sets from Lake Erie (1978–82 and 1983–87) indicate greater asymptotic lengths in the second period (689 mm versus 781 mm). There is some indication, then, that growth of Lake Erie walleye changed from the period 1978–82 to 1983–87.

Linear models were employed to describe length-at-age for Lake Erie (N = 12,312) and Lake St. Clair (N = 7,237) walleye taken by trap net. The two-parameter models investigated were:

$$(\text{I}) \ \text{Length} = a \bullet (\text{age}) + b$$
$$(\text{II}) \ \text{Log(Length)} = a \bullet (\text{age}) + b$$

Although both regressions were significant, Model I exhibited the best fit as determined by r-square values (Model I r^2 = 0.78 and 0.80 for Lake Erie and Lake St. Clair; Model II r^2 = 0.75 and 0.77). This linear model accounted for the greatest amount of variability in observed length. The slopes of the Model I regressions for Lake Erie and Lake St. Clair walleye were significantly different (F = 888.0, df = 1, 19,548; P < 0.01; F-statistic for difference in slopes, Sokal and Rohlf 1981), implying that for a given age, total lengths are significantly different. Mean lengths for age 2 to age 10 were compared with a t-test (Table 2). At ages 3, 4, 5, 6, and 8 walleye from Lake Erie were significantly larger than the same age fish from Lake St. Clair. Lake St. Clair walleye were significantly larger than those from Lake Erie only at age 2, although this difference was small and biologically insignificant (340 versus 337 mm).

For Lake Erie walleye (1972–84) the 1972 year class exhibited the highest overall relative growth (189.4); the 1977 and 1978 year classes had the lowest (–115.5 and –120.7, respectively) (Table 3). The trap-net index of relative abundance for the fast-growing 1972 year class was low; the slow-growing 1977 year class had the second highest relative abundance index. However, this apparent inverse relationship between year-class strength and relative growth was not consistent for all year classes (Figure 5). The linear relationship accounted for only 36% of the variation in the relative growth index (r = 0.597, P < 0.05). For Lake St. Clair walleye (1964–82), the lowest relative growth index was –61.8 (1978 year class, rank = 12th highest of 19 year classes) (Table 4; Figure 6). The 1969 year class exhibited the greatest relative growth index (255.0) and was 14th in rank abundance. The linear relationship of relative growth to rank abundance was not significant, i.e., the correlation coefficient was not significantly different from zero (r = 0.241, P > 0.05). The variation in observed relative growth could not be adequately modeled with rank abundance.

The abundance of a particular year class may influence growth of subsequent year classes. Therefore, we examined the cumulative effects of year classes on growth by computing 3-year and 2-year running averages of trap-net CPUE. There was no significant linear relationship between 3-year or 2-year running averages of CPUE with relative growth in Lake

Erie walleye (3-year average: $r=0.238$, $P>0.05$; 2-year average: $r=0.339$, $P>0.05$). This attempt to relate relative growth to 3- and 2-year running averages accounted for 34% (3-year average) and 24% (2-year average) of the variation in relative growth of Lake St. Clair walleye. Variability in growth of walleye year classes was best modeled by cumulative effects of year-class abundances in Lake St. Clair populations whereas, the variability in growth of walleye year classes in Lake Erie is better described by the relative abundance of individual year classes.

Tag-recapture study

A total of 1,333 Lake St. Clair tags and 1,159 Lake Erie tags were eventually recovered by fishermen and voluntarily reported. The lower reporting rate for the Lake Erie tags probably reflects a lower exploitation rate compared to Lake St. Clair, instead of poorer cooperation from Lake Erie fishermen.

The major portion of the tag recoveries were reported by anglers; 10% of tag returns were from commercial fishermen. There appears to be ample angling harvest throughout the area to provide enough voluntary tag recoveries to adequately monitor movements of the tagged stocks.

The areal distribution of all recaptures of Lake St. Clair and Lake Erie tags are summarized by recovery area in Figure 7. This figure shows the distribution of recoveries expressed as percent of total recovered within each lake. Lake Erie walleye show a consistent and relatively strong tendency to move northward into the Detroit River, Lake St. Clair, and as far north as Saginaw Bay, Lake Huron (170 km). Lake St. Clair walleye also show a strong tendency to migrate northward (Figure 7). Only 3% of the Lake St. Clair tags were recovered in Lake Erie indicating a very low rate of movement southward. There is also some evidence to suggest that Lake Erie recoveries of walleye tagged in Lake St. Clair tend to be walleye of Lake Erie origin that had originally migrated to Lake St. Clair early enough to be intercepted by the Lake St. Clair tagging effort. The evidence was obtained from comparison of the mean Julian date of recapture in Lake Erie of fish tagged in Lake St. Clair with the mean date of recapture in Lake Erie for all Lake Erie tagged walleye.

Twenty-nine percent of all recoveries of Lake Erie tags were reported from the Detroit River and north (Table 5). This ratio did not vary between years in spite of dramatic increases in Lake Erie angling harvest and walleye abundance.

The monthly distribution of tag returns from Lake St. Clair and Lake Erie are shown in Figures 8 and 9. On-site creel surveys of the angler catch indicated that tag recovery patterns were similar to patterns of harvest. Over 78% of the walleye tagged in Lake St. Clair were recovered from Lake St. Clair in May through August. Data from a creel survey of Michigan waters of Lake St. Clair in 1983 and 1984 indicated that 88% of the boat harvest of walleye occurred during that same period (Haas et al. 1985). Eighty-one percent of the Lake Erie tags

were reported from Lake Erie waters in May to July. Creel surveys of Michigan waters of Lake Erie showed that 96% of annual walleye harvest in 1986 and 1987 was taken in May to July (G. Rakoczy, Michigan Department of Natural Resources, unpublished data).

Recapture dates within specific lake areas provided some of the most useful information for stock management purposes. We had postulated that tagged walleye returned to their natal spawning grounds (a behavior referred to as homing) and that individual fish repeated their migration route each year in a circular pattern. Peak walleye spawning activity has been observed around April 3 in the Thames River (D. MacLennan, Ontario Ministry of Natural Resources, personal communication) and around April 1 in the Maumee River (C. Baker, Ohio Department of Natural Resources, personal communication). Most of our Lake Erie walleye were tagged within 3 weeks of peak spawning so they probably were part of the Maumee River stock. Since tagging was protracted in Lake St. Clair, those fish might have originated from either the Lake St. Clair or the Lake Erie stock.

We analyzed tag data according to the postulate that any particular tagged walleye would return to the same location on a particular Julian day; for example, back at the original tag site on subsequent tagging anniversaries. With this postulate in mind, we grouped the date information by lake of tagging and lake of recapture and made comparisons of median Julian days using the Mann-Whitney U and Wilcoxon two-sample tests. Nonparametric statistics were used because we found that variances were not homogeneous. Median Julian dates for all possible combinations of tagging and recovery are shown in Table 6. Walleye tagged in Lake St. Clair were recovered on day 155 (median recovery day) in Lake Erie; this was significantly earlier ($P=0.003$) than recovery day 180 for walleye tagged and recovered in Lake Erie. This indicated that some of the walleye tagged in Lake St. Clair and subsequently recaptured in Lake Erie may have originated from the Lake Erie stock. We postulate that their period of vulnerability to capture in Lake Erie was much shorter and earlier in the year as they were migrating to and from their natal Lake Erie spawning grounds. Apparently, very few tagged walleye from Lake St. Clair migrated to Lake Erie since the median recovery date in Lake Erie should have been the same as, or later than, the median recovery date of the Lake Erie stock. In other words, if numerous walleye tagged in Lake St. Clair had subsequently migrated to Lake Erie, then their median angler recovery day in Lake Erie should have been June 29 (day 180) or later, consistent with their probable vulnerability to fishing in Lake Erie.

Recovery data from the north half of the St. Clair River were evaluated for estimates of the rate of mixing of the Lake St. Clair and Lake Erie stocks. We chose this recovery site because the narrow river is characterized by substantial and consistent angling pressure, and angler exploitation of walleye and other species is higher in this area than elsewhere in the system. An estimate of the average annual daytime harvest of walleye in Michigan waters of the upper St. Clair River from 1983–84 was 120,000 fish (Haas et al. 1985). Seventeen percent

of all recoveries of Lake St. Clair tags and 6% of all recoveries of Lake Erie tags were reported from this area.

We compared the distribution of recovery dates in the upper St. Clair River for the Lake St. Clair and Lake Erie stocks to see if they were similar. The monthly distribution, as percent tags recovered in the upper St. Clair River, is shown in Figure 10. Both stocks showed the highest recovery rates in June and July with Lake Erie walleye slightly skewed toward earlier recaptures. The distributions of Julian recovery dates for the two groups of tagged fish were identical (Mann-Whitney U-test; $P=0.33$).

The overall ratio of Lake Erie tags to Lake St. Clair tags recovered in the upper St. Clair River was 68:226. We feel this ratio represents the best estimate of stock mixing: 23.1% of the upper St. Clair River walleye population was Lake Erie stock. This estimate agrees favorably with the estimate derived from genetic analysis of walleye sampled from Lake St. Clair (see section on Mixed-fishery analysis, below). This consistency invites speculation on the use of tag-recovery data for estimation of stock contributions. While it is true that there are many assumptions (e.g., equal distribution of fishing pressure throughout the study area for a particular period of time, equal non-reporting bias, equal catchability, complete mixing of the tagged group of fish with non-tagged individuals, etc.), in general, tag recovery ratios may provide a preliminary assessment of the extent of stock mixing. We calculated these ratios for Lake Erie, Lake St. Clair, and the Detroit River from total tag returns for the period 1975–87 and thus these estimates represent annual average stock contributions. The Lake Erie stock comprised approximately 23%, 8%, 95%, and 70% of the walleye populations in upper St. Clair River, Lake St. Clair, Lake Erie, and the Detroit River (Appendix 7).

Walleye survival rate estimates were generated from non-reward tag-recovery data using the IBM mainframe computer version of the BROWNIE model. The mean survival and tag recovery rate estimates for Lake St. Clair and Lake Erie are shown in Table 7. These estimates were compared using the z test which indicated that the survival rate was significantly greater for Lake Erie walleye than for walleye from Lake St. Clair ($z=2.911$, $P<0.002$). The mean life span for adult walleyes in Lake Erie was significantly longer ($z=2.817$, $P<0.002$). The mean recovery rate for Lake Erie tagged walleye was also significantly less ($z=7.803$, $P<0.001$) than the estimated recovery rate for the Lake St. Clair walleye; however, this comparison is valid if angler reporting behavior, which is unknown, is the same for both lakes.

Reward-tag study

A reward-tag study on walleye was carried out on Lake St. Clair from 1981–83 to provide an estimate of the frequency of non-reporting, i.e., tag recovery not followed by tag reporting. There were 909 walleye tagged with reward tags and 2,043 tagged with non-reward tags during the 3-year reward study on Lake St. Clair. The number of walleye tagged with non-reward

tags and the number tagged with each reward denomination from 1981–83 are listed in Appendix 8. The numbers reported to MDNR by fishermen from time of tagging through 1987 are also given.

There was an overall ratio of 1.6 walleye reward tags reported for every non-reward tag. These data were examined further to determine whether the recovery frequency for reward tags was significantly greater than the non-reward tags. The recovery data derived from the three tagging years were combined for each of five sequential recovery seasons, without regard to calendar year, since the ratio of one reward to two non-reward tags was maintained throughout the 3-year tagging period. This resulted in five sequential recovery periods for each tagged cohort; 5 years was essentially the maximum survival period for any tagged fish. The percent of walleye with reward and non-reward tags recovered each season is shown in Figure 11. The observed recovery frequency of non-reward tags was used to calculate the expected values for the reward tags and frequencies of reward recoveries were higher than non-reward frequencies during all recovery seasons. The reporting frequency of walleye reward tags was different from the frequency of non-reward tags ($\chi^2 = 47.2$, $P < 0.005$).

The reporting rate for walleye reward tags may be related to the monetary value of tags. The frequencies of recovery of $2.00 tags was compared to the frequencies for each of the larger denominations. The recoveries of the $4.00 (20.0%), $6.00 (19.1%), and $8.00 (21.0%) tags were slightly higher than the $2.00 (15.6%) tags but did not vary among themselves. None of the larger denominations showed a significantly higher recovery rate compared to the $2.00 tags ($4.00 $\chi^2 = 4.1$, $P > 0.10$; $6.00 $\chi^2 = 2.8$, $P > 0.10$; $8.00 $\chi^2 = 4.5$, $P > 0.10$).

Although reward tags of four denominations ($2.00, $4.00, $6.00, and $8.00) were used in this study, there was no clear indication that an increase in reward was associated with an increase in reporting rate. Therefore, all recapture data were pooled across reward denominations. Rawstron (1972) found no difference in reporting of $1.00 and $5.00 reward tags from largemouth bass. Furthermore, he interviewed anglers and found that a $5.00 reward was insufficient inducement (Rawstron 1971). Our results indicate that there was no appreciable difference in reporting of tags, irrespective of the value. Recovery rates were significantly different for reward (0.189) and standard or non-reward (0.120) tags pooled across years (two-tailed t-test for significant difference in ratios, Cochran 1977; $t = 21.805$, df = 2, $P < 0.05$). Reward tags were recovered at a significantly higher rate (approximately 7% higher) than the standard tags.

Unbiased estimates of survival rate from the tag-recapture model (Brownie et al. 1985) may be used to estimate fishing mortality rate if the reporting rate is known. A single estimate of the reporting rate, the ratio of reward-tag to standard-tag return rate, is needed. This ratio may be highly variable for a given year after tagging as well as for a given cohort of tags (Table 8). We examined these ratios over time and between cohorts of tags (1981 versus 1982,

e.g.). The difference in reporting rate in the first and second years (first year is year of tagging) is significant for reward and standard tags ($t=19.021$, year 1, df$=2$; $t=5.463$, year 2, df$=2$; $P<0.05$). These differences were not significant in the third, fourth, or fifth years. This implies that reporting rates are essentially the same in later years regardless of the type of tag (reward or standard). However, the rate of return of standard tags is significantly less than the rate of return of reward tags for the first and second years; therefore, tag recovery data are biased by non-reporting in the first 2 years, but generally not thereafter. Variation in recovery rates, due to reporting rate or other factors, does not bias the survival rate estimates from the tag-recapture model when survival rates are constant for all individuals (BROWNIE Model 1) (Pollock and Raveling 1982).

The 95% confidence interval for the ratio of reward-tag to standard-tag return rate in the year of tagging is 0.88 to 2.34. In the following year it is 0.91 to 1.59 (95% confidence interval for ratio of two ratios, Cochran 1977). These two estimates are not significantly different and a combined estimate for the ratio is 1.48 (ratio of reward-tag return rate to standard-tag return rate). The reporting rate is estimated by the inverse of this ratio, i.e., it is the ratio of the standard-tag to reward-tag return rate. Assuming all the reward tags are reported, the reporting rate for the walleye fishery in Lake Erie-Lake St. Clair is 0.674 (non-reporting rate is $1 - 0.674 = 0.326$). If the assumption of 100% reporting does not hold, then this estimate is biased. For example, if 80% of the reward tags were reported, the bias would be 25% or 0.169 (reporting rate may range from 0.505 to 0.843). Clearly, the accuracy of the reporting rate is contingent upon the 100% reporting assumption. However, numerous tagging studies indicate that this assumption may not be valid (e.g., Mullan 1959, Paulik 1963, Rawstron 1971, Green et al. 1983). Non-reporting rates vary from 15% to 77% in fish tagging studies and from 50% to 60% in waterfowl and bird banding studies (Table 9). Our estimate of 33% is within the range of published non-reporting rates.

Genetic analysis

Of 21 loci assayed, only four exhibited polymorphisms such that the frequency of the most common allele did not exceed 0.95 in any one population (Tables 10 and 11). These loci were ADH-1, GMP-3, IDH-1, and MDH-3. Mean heterozygosity ranged from 0.076 with standard error (SE) of 0.035 in the Kelley's Island sample to 0.081 (SE$=0.037$) in the Sandusky River sample with most of the others at 0.080 (SE$=0.037$). None of the samples differed significantly for this measurement. The several stocks examined in this study were similar in the amount of genetic variability measured and in shared polymorphisms.

Within-lake heterogeneity

Walleye stocks in Lake Erie did not appear to have significant genetic heterogeneity and thus, individual stocks could not be delineated (Table 10). However, analyses of the pooled data from the six Lake Erie localities revealed significant departures from random mating expectations at IDH-1 and MDH-3 (Table 11). These were due to excess heterozygotes which suggest that more than one spawning stock was represented in the pooled sample.

Spawning walleye from the Clinton and Thames rivers in Lake St. Clair appeared to be genetically identical to one another (Table 12). In addition, there was no significant heterogeneity between year classes from these two rivers which was corroborated by pair-wise contingency Chi-square analyses at all loci (Table 12). Based on genetic data, there seems to be no evidence to support the hypothesis of separate stocks in the Clinton and Thames rivers.

Between-lake variability

We found significant stock differentiation between the Lake Erie and Lake St. Clair walleye based on three loci (Table 11). Only ADH-1 exhibited no significant heterogeneity among the four most polymorphic loci. The dendrogram based on Nei's (1978) minimum genetic distance was significant at the level separating the Lake St. Clair populations from those of Lake Erie (Figure 12). We concluded that the Lake St. Clair and Lake Erie walleye stocks represent distinct gene pools and that a measure of the extent of mixing would be feasible.

Mixed-fishery analysis

The stability of the allelic frequencies and the magnitude of the genetic differences between Lake Erie and Lake St. Clair walleye stocks permitted measurement of the proportional contribution to mixed-stock samples taken in Lake St. Clair in the fall. In 1983, the mixture was estimated to contain 92.1% Lake St. Clair fish and 7.9% Lake Erie fish ($N=217$; standard deviation (SD) $=19.5$). In 1984, the mixture was estimated to contain 68% Lake St. Clair fish and 32% Lake Erie fish ($N=253$; SD $=19.8$). Simulations of mixed salmon fishery data have shown that the actual proportion was contained within one standard deviation for sample sizes of 200 or more fish (Milner et al. 1983). Therefore, a reasonable expectation is that Lake Erie fish made up 0.0% to 27.4% of the November 1983 sample and 12.2% to 51.8% of the November 1984 sample. The overlap of the confidence intervals for the two estimates suggests that stock composition in the 2 years was similar; therefore, a combined estimate was calculated: 76.9% Lake St. Clair fish and 23.1% Lake Erie ($N=470$; SD $=14.1$). These were the

same proportions estimated from analyses of tag-recapture data from the northern half of the St. Clair River.

Total length and somatic weight data from the Thames River and Maumee River samples used in the genetic analysis were compared for differences in population growth to further investigate stock structure. The data were analyzed by single age/sex categories to eliminate the potential for bias. Three cohorts contributed individuals to each age/sex group. Growth differences between year classes were probably not a significant factor since the same 3 years of sampling contributed data to both sites. The two-sample t-test was used to compare population means and a significant t-statistic ($P<0.05$) indicated that the two means were not identical. Mean length and somatic weight for the Maumee River population were significantly greater than the Thames River population in most of the comparisons (Tables 13 and 14). All of the comparisons with large sample sizes indicated that the Maumee River stock had significantly ($P<0.01$) greater growth, in terms of both length and somatic weight. Regression analyses were used to examine differences in the length-weight relationships for males and females from the two sampling sites. Linear regressions of $\log_e$ length (mm) versus $\log_e$ somatic weight (g) for the two spawning samples were significantly different for males ($F=26.8$, $P<0.01$) and females ($F=22.3$, $P<0.01$). Maumee River walleye had significantly heavier bodies at a given length compared to the Thames River fish. Analyses of the growth data suggest that the Lake St. Clair and Lake Erie walleye belong to distinct stocks, and this conclusion corroborated the genetic evidence.

Abundance estimates: CAGEAN model

Abundance of walleye in the western basin of Lake Erie was estimated with the CAGEAN catch-at-age model (Deriso et al. 1985). We used the CAGEAN three-gear catch-at-age model which allows survey data to be combined with data from multiple gear fisheries. Deriso et al. (1985) found that bias was substantially reduced when auxiliary information, such as effort data and survey catches, was included in the analyses. We combined western basin walleye catch and effort data from the commercial and sport fisheries for 1978–87 (unpublished Ontario and Ohio fishery data obtained through the Walleye Task Group, Lake Erie Committee, Great Lakes Fishery Commission) with MDNR spring trap-net data. Walleye growth decreased during the 10-year period, such that recruitment to the survey trap nets was delayed by 1 year for some year classes. The data were somewhat arbitrarily grouped into two time periods, 1978–82 and 1983–87, because we speculated that the decrease in growth may have affected catchability coefficients and age-specific selectivities. Similar changes in recruitment probably took place in the sport and commercial fisheries. We set the full recruitment age to three for the sport and commercial fisheries during the early period, and to four during the later period. The full recruitment age was 1 year less for the trap-net samples. We set natural

mortality to 0.2; there were no data to produce a reliable estimate. The analyses of tag recovery data suggest, however, that natural mortality has been higher than 0.2 since tag reporting rate has been quite low.

The CAGEAN estimates of mean instantaneous fishing mortality, annual survival, commercial and angler exploitation, total abundance and catch for each year are presented in Appendix 9. Average parameter values during the early period (1978–82) were: survival, 0.57; instantaneous fishing mortality, 0.37; commercial exploitation, 0.07; and angler exploitation, 0.22. Average abundance and catch were 12.2 and 3.4 million fish, respectively. Average parameter values during the second period were 0.68, 0.19, 0.06, and 0.10; while, average abundance and catch were 34.5 and 5.2 million fish. Commercial exploitation has been a relatively small part of the fishery in the western basin of Lake Erie during the entire period. The abundance and catch estimates and the observed catch for the western basin during the entire 10-year period are given in Figure 13. The CAGEAN results show increased walleye abundance and catch following recruitment of the strong 1982 year class with fairly good agreement between observed and estimated catch.

The CAGEAN program was also used to analyze subsets of data from Lake St. Clair and western Lake Erie to permit generalized comparisons of walleye abundance between the two areas. The period from 1978–85 was selected because catch and effort data from two gear types, angling and trap-net samples, were available for Lake St. Clair during that period. Lake St. Clair angler harvest data (Table 15) were available from Ontario's waters for the entire period (D. MacLennan, Ontario Ministry of Natural Resources, unpublished data) and from Michigan's waters for 1983 and 1984 only (Haas et al. 1985). We assumed that the relationship between the Ontario and Michigan sport fishery was constant during this 8-year period. Ontario effort and harvest estimates for all years except 1983 and 1984 were used to estimate Michigan effort and harvest with the ratio of the Michigan to Ontario effort and harvest in those 2 years. CAGEAN estimates of walleye abundance and harvest for Lake St. Clair and western Lake Erie are shown in Figures 14 and 15. Similar trends in abundance and catch were apparent in the two lakes with more obvious deviations in harvest.

The CAGEAN estimates of abundance and harvest in Lake St. Clair were roughly 10% of the western Lake Erie values. Lake St. Clair is approximately one third as large as the western basin of Lake Erie. The ratio of lake size to estimated walleye abundance was 3.3 which suggested that walleye density was considerably lower in Lake St. Clair. These results are consistent with the grand mean trap-net CPUE values for walleye which were 22.9 in Lake Erie and 8.5 in Lake St. Clair (ratio = 2.7) (Appendices 4 and 5). The CAGEAN estimates are not independent of the trap-net CPUE values since they were part of the input data; however, the angler effort and catch data (used by the CAGEAN model) were more influential in determining abundance estimates. The average angler CPUE was 0.13 in Lake St. Clair and

0.46 in Lake Erie. The temporal pattern of angler tag reporting shows that Lake St. Clair walleye were exploited over a longer period of the year (Figures 8 and 9). The higher tag reporting rate for Lake St. Clair walleye (Table 7) suggests that exploitation was slightly higher. The Lake St. Clair anglers sought a wider variety of fish species compared to Lake Erie anglers (R. Haas, personal observation); and the Lake St. Clair fish community, with its greater species evenness, provided a wider variety of species that were abundant enough to support fisheries.

CAGEAN estimates of harvest were compared to the creel survey harvest estimates which were used as observed inputs to the model (Figures 16 and 17). There was good agreement between the observed and estimated values except for the early years in Lake St. Clair for which the CAGEAN estimates were substantially lower than the creel estimates. We have no explanation for this.

DISCUSSION

Net samples, growth, and abundance

The comparison of relative year-class strengths as measured by the trap-net and gill-net samples in Lake Erie indicates that these gear types provide similar information. Trends or changes in the relative abundance of year classes are apparent from examinations of the CPUE data from either sample.

It is apparent from the growth analyses that growth regimes differ in Lake Erie and Lake St. Clair. In general, mean total length-at-age is greater for Lake Erie than for Lake St. Clair walleye. In addition, a change in growth may have occurred in Lake Erie walleye (1978–82 versus 1983–87)

If there is a relationship between year-class abundance and year-class relative growth, it appears to be stronger among Lake Erie walleye than among Lake St. Clair walleye. Year-class specific growth variations in Lake St. Clair walleye are not linearly related to year-class abundance, whereas growth variations in Lake Erie walleye are. Variations in relative growth in Lake St. Clair walleye seem to be influenced by the relative abundance of two or three older age classes.

These observed differences in relative growth and abundance may be examined in light of feeding studies. The abundance of walleye is greater in Lake Erie (higher values of CPUE) where competition for food resources may be high. Age-0 walleye from western Lake Erie prey mainly on shiners (*Notropis atherinoides* and *Notropis hudsonius*) and young-of-the-year clupeids (*Dorosoma cepedianum* and *Alosa pseudoharengus*) (Knight et al. 1984). Thus, fluctuations in recruitment of prey may affect year-class strength of walleye in Lake Erie (Knight et al. 1984). No diet studies are available for Lake St. Clair walleye.

The high Shannon-Weiner index for Lake St. Clair suggests that individual prey fishes may be spread more evenly among species so that alternate prey species may be more available. Invertebrates in Lake St. Clair may provide an additional source of food items and may broaden the food base, thereby relaxing competition for fish species. For example, *Hexagenia*, which are abundant in Lake St. Clair, but rarely found in Lake Erie, may constitute a significant portion of the diet of Lake St. Clair walleye. A broad food base which includes invertebrates may provide a more stable resource when recruitment variability of forage fish is high.

Population modeling of the Lake Erie walleye in the western basin using the CAGEAN model suggests that average abundance during the past 10 years has been about 23 million fish with an upward trend; walleye abundance may have been about 40 million fish since 1984. Hernandez (1988) modeled the western basin fish community and predicted that walleye abundance would eventually reach equilibrium at about 40 million fish under predator-prey conditions that existed in the western basin of Lake Erie during the 1970's and early 1980's.

Tag-recapture study

Extensive tag recovery data demonstrated that the Lake St. Clair and Lake Erie walleye have a much stronger tendency to move upstream than downstream following spawning activity. Apparently, very few Lake St. Clair walleye migrate to Lake Erie. The temporal pattern of Lake St. Clair tag recoveries from Lake Erie indicated that many were probably Lake Erie fish that had already migrated to Lake St. Clair before capture and tagging. However, there was substantial migration of Lake Erie walleye into Lake St. Clair and the St. Clair and Detroit rivers where they contributed to the angler harvest. Angler recoveries during subsequent spawning seasons indicate that the Thames River in Lake St. Clair and the Maumee River in Lake Erie provide spawning habitat for the majority of walleye present at our tag sites during spring. Analyses of tag reports from the upper half of the St. Clair River showed that 23% were from Lake Erie. We cannot determine the reliability (e.g., with confidence limits) of the stock composition estimates derived from tag recovery ratios and we caution their strict interpretation. However, it should be noted that although the estimate for Lake St. Clair (8% Lake Erie walleye) is lower than the reported combined estimate from genetic analysis (23%), it equals the estimate from the same analysis for the sample collected in November 1983. Tag recovery ratios provide an additional set of stock composition estimators. Almost all of the walleye harvested in Lake Erie (95%) and the majority (70%) harvested in the Detroit River come from the Lake Erie population. The Lake St. Clair stock contributes greatly to the angler fishery in Lake St. Clair and the northern section of the St. Clair River (approximately 92% and 77% of the walleye harvested in these areas were Lake St. Clair fish). The Lake St. Clair stock contributed a modest percentage (30%) to the walleye harvest in the Detroit River. These

estimates in conjunction with estimates of the average annual harvest may be used to examine the pattern of exploitation for a particular stock. For example, an average of approximately 263,000 Lake St. Clair walleye were harvested annually from the Lake St. Clair-Lake Erie system by anglers in recent years (see Appendix 7). Forty-six percent were taken from Lake St. Clair, 35% from the northern St. Clair River, and 19% from the Detroit River. This suggests that management measures for the Lake St. Clair stock must not be geographically confined to Lake St. Clair; substantial harvest of this stock occurs in the northern St. Clair River. A similar analysis of the exploitation pattern for the Lake Erie stock indicates that the harvest of this stock outside of Lake Erie is negligible, on the order of 150,000 fish compared to 7 million in Lake Erie proper.

Reward tags ranging from $2.00 to $8.00 provide similar return rates from the fishery and these return rates are higher than those from standard tags. An increase in the size of the reward (say, $100.00) may increase the number of tags reported and permit a less biased estimate of non-reporting. The reward should be of sufficient amount to approach 100% reporting; i.e., as long as the reward tag is seen, it is a good assumption that it will be reported. Paulik (1963) cautions that a change in the value of the reward may not be the sole factor to account for an increase in reporting rate. For example, we noted an increase in the percent of tags returned during the first year from 1981–83 for both reward and non-reward tags. A follow-up reward tag study should parallel the first study (1981–83) as closely as possible to ensure that targeted fish populations and patterns of exploitation remain similar.

The recovery rates for reward tags were highly variable and similar to recovery rates of standard tags in the third, fourth, and fifth years. Chadwick (1968) found similar results in a 4-year study of the California striped bass fishery. After the first year, differences in returns from reward tags and standard tags could not be attributed to a true difference in nonresponse (Chadwick 1968). Recovery rates for reward-tagged fish and standard-tagged fish are low beginning in the second year; reward tag returns ranged from 0 to 5 fish (Chadwick 1968). Thus, sample size is an important factor in determining the observed variability in recovery rates in later years. Studies of long duration of populations with high average survival rates are prone to negatively biased estimates of recovery rates in the middle of the study if tagged individuals have varying survival and recovery rates (Pollock and Raveling 1982).

The estimated non-reporting rate for walleye, 33%, seems average relative to those for other species (Table 9). Because the return incentives were low, we feel that the assumption of 100% reporting of reward tags is unjustified and partitioning of total mortality rate into fishing and natural mortality components is unwarranted. Green et al. (1983) caution that fishing mortality rates are underestimated if tag recovery data are adjusted with a biased reporting rate ratio. Although we cannot be sure of 100% reporting, the reward tag study does indicate that a

monetary reward improves reporting rate. Even a small amount can improve reporting rate by approximately one and one-half times.

Genetic analysis

The lack of significant genetic structuring within Lake Erie populations suggests that considerable gene flow does occur. The absence of significant genetic heterogeneity between samples from the Clinton and Thames rivers on Lake St. Clair supports the conclusion that these two localities represent the same gene pool. In fact, a number of walleye tagged during the spawning season in the Clinton River were recovered during subsequent spawning runs in the Thames River (R. Haas, Michigan Department of Natural Resources, unpublished data). However, there is evidence among the Lake Erie samples that the western basin fish do not represent a single, panmictic population. It is possible that the period of low walleye abundance in Lake Erie, during the late 1950's to early 1960's, encouraged interbreeding by otherwise discrete spawning populations.

The genetic differentiation of Lake St. Clair walleye from those of Lake Erie suggest that fry hatched in a spawning area return to that same area to spawn as adults. This conclusion is consistent with the results of this study because the observed genetic structure would not be maintained if young, maturing walleye chose spawning sites at random. Analyses of fall samples from Lake St. Clair corroborated the results of the tag study that significant numbers of Lake Erie walleye mix with the Lake St. Clair population during non-spawning times.

The ability to examine the mitochondrial genome (i.e., mtDNA) in fish has provided researchers with another tool potentially useful for stock delineation (Chapman and Powers 1984; Avise 1987). Mitochondrial DNA is not inherited according to principles of Mendelian genetics; rather, it is transferred from the female parent to her offspring (see e.g., Avise and Lansman 1983). Thus, the term clone has been used to identify unique mtDNA polymorphisms among groups of related conspecifics. This technique, recently applied to Great Lakes walleye populations, supported the existence of two groups of walleye (Billington and Hebert 1988). One group predominates in the eastern Great Lakes (Lake Ontario, Lake Simcoe) and was postulated to be derived from colonization from the Atlantic refugium. Another group predominated in the west (Muskegon, Tittabawassee, and Thames rivers, Lake St. Clair, and western Lake Erie) and was associated with the Mississippi refugium (Billington and Hebert 1988). The greatest clonal diversity was found among walleye from Lake St. Clair and western Lake Erie. However, no particular clones could be associated with individual spawning sites, i.e., no further stock delineation was supported by these data. These results are coincident with our observation that spawning groups associated with any particular river or reef (in Lake Erie) appear to interbreed with groups spawning at adjacent sites. Hence, we

could delineate only two major groups. In addition, both studies report a high level of polymorphisms among walleye from Lake Erie. Despite these similarities, Billington and Hebert (1988) could not separate groups from Lake St. Clair and Lake Erie. We suggest that part of the difficulty may have been due to the nature of their samples; approximately 18% of the Lake St. Clair and 23% of the Lake Erie walleye examined were collected in October, a time we found characterized by mixing of stocks.

RECOMMENDATIONS

Walleye management in Lake St. Clair should not necessarily proceed from the same premises as management in Lake Erie because the two lakes have demonstrably different populations. Management of the Lake Erie and Lake St. Clair populations are complicated by the probable large-scale movement of Lake Erie walleye into Lake St. Clair. Haas et al. (1985) estimated that the average annual sportfishing effort in 1983 and 1984 in Michigan's waters of the St. Clair River was 810,000 angler hours; Lake St. Clair, 2,000,000 angler hours; and in waters of the Detroit River, 1,409,000 angler hours. If we assume that angling effort in the Ontario waters of these two rivers occurs at a similar level, then total fishing effort in the Lake St. Clair system exceeds angling effort in the western basin of Lake Erie (5,600,000 angler hours; Walleye Task Group, Great Lakes Fishery Commission). We recommend that effective angler effort for walleye harvest be measured every year for Lake St. Clair and the St. Clair and Detroit rivers, as well as for western Lake Erie. Knowledge of angler exploitation rates from southern Lake Huron to western Lake Erie will be a key to effective management of walleye stocks. Although Lake Erie supports a greater population of walleye, exploitation is concentrated in other areas. The fishing pressure on individual stocks cannot be determined without an accurate assessment of stock contribution and angler exploitation rate by area.

We also recommend reward-tag studies on Lake Erie and Lake St. Clair walleye, using large enough reward denominations ($100.00), so that walleye exploitation can be measured with acceptable accuracy. Estimates from the catch-at-age (CAGEAN) model indicate that angler exploitation rates are approximately three times commercial exploitation rates for western Lake Erie walleye (range: 1 to 7 times). Because the angler harvest is a major portion of the total harvest, estimates of exploitation rates are necessary to calculate fishing mortality rates. Walleye managers need improved, consistent measures of sportfishing effort and catch in the St. Clair-Detroit River system; they need to know the level of walleye exploitation in Lake St. Clair and Lake Erie; and they need to understand the impact of St. Clair-Detroit River system harvests of walleye originating from Lake Erie populations. Finally, we recommend that walleye diet studies be conducted on Lake St. Clair, presumably a richer food community, where growth rate and relative abundance do not appear to be causally related.

ACKNOWLEDGMENTS

SPRING SPAWNING SAMPLES

(1) Clinton River   (4) Sandusky River

(2) Thames River   (5) Niagara Reef

(3) Maumee River   (6) Kelleys Island

(7) Pt. Pelee

FALL MIXED-STOCK SAMPLES

(8) Western Basin - Lake Erie

(9) Anchor Bay - Lake St. Clair

(10) Monroe - Lake Erie
(Preliminary)

LAKE HURON

ST. CLAIR RIVER

CLINTON RIVER (9) (1)

LAKE ST. CLAIR

THAMES RIVER (2)

DETROIT RIVER

-N-

0 8 16
Km

(8)

RAISIN RIVER

(7)

(10)

LAKE ERIE

(5)

(3)

(6)

MAUMEE RIVER

(4)
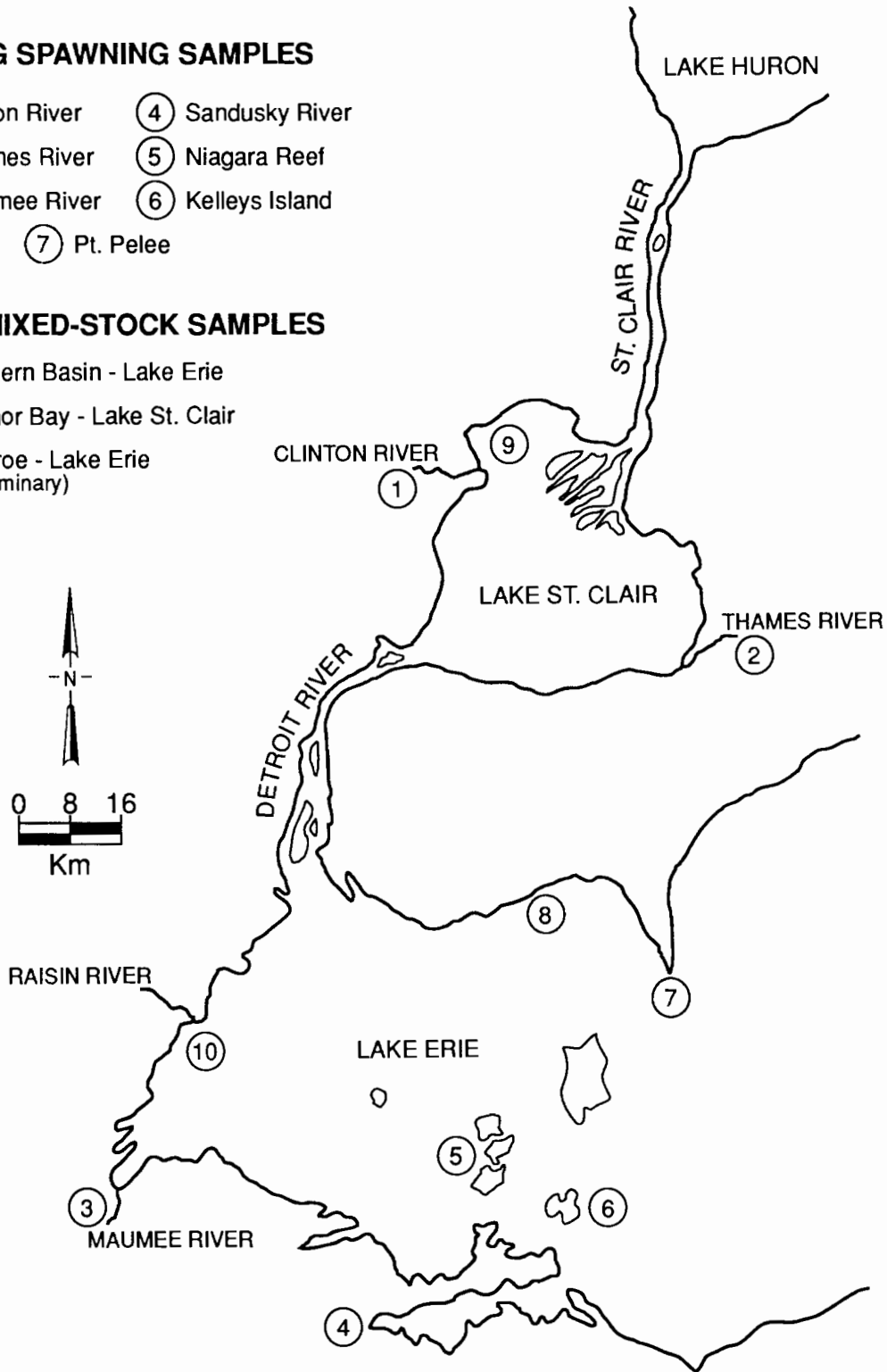
Figure 1A. Location of capture sites for spawning walleye in the St. Clair-Detroit River system and western Lake Erie. Also indicated are sampling sites for the fall mixed-stock analysis.

TRAP-NET SITES

(1) Lake St. Clair

(2) Lake Erie

GILL-NET SITES

▲ Lake Erie

LAKE HURON

ST. CLAIR RIVER

CLINTON RIVER

(1)

LAKE ST. CLAIR

THAMES RIVER

−N−

0 8 16
Km

DETROIT RIVER

RAISIN RIVER

▲

(2)

LAKE ERIE

▲

MAUMEE RIVER
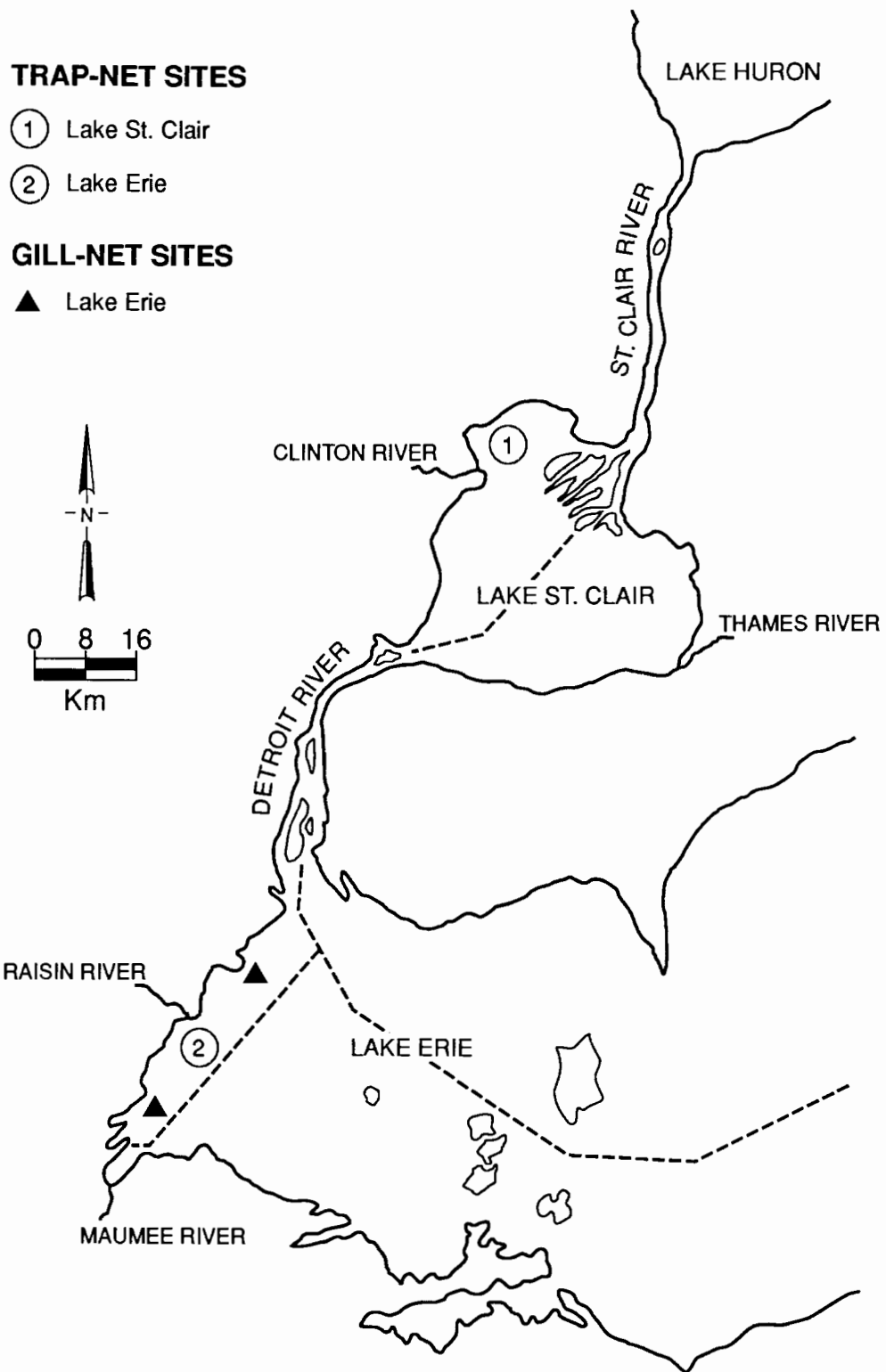
Figure 1B. Map of study area and location of trap-net and gill-net stations.
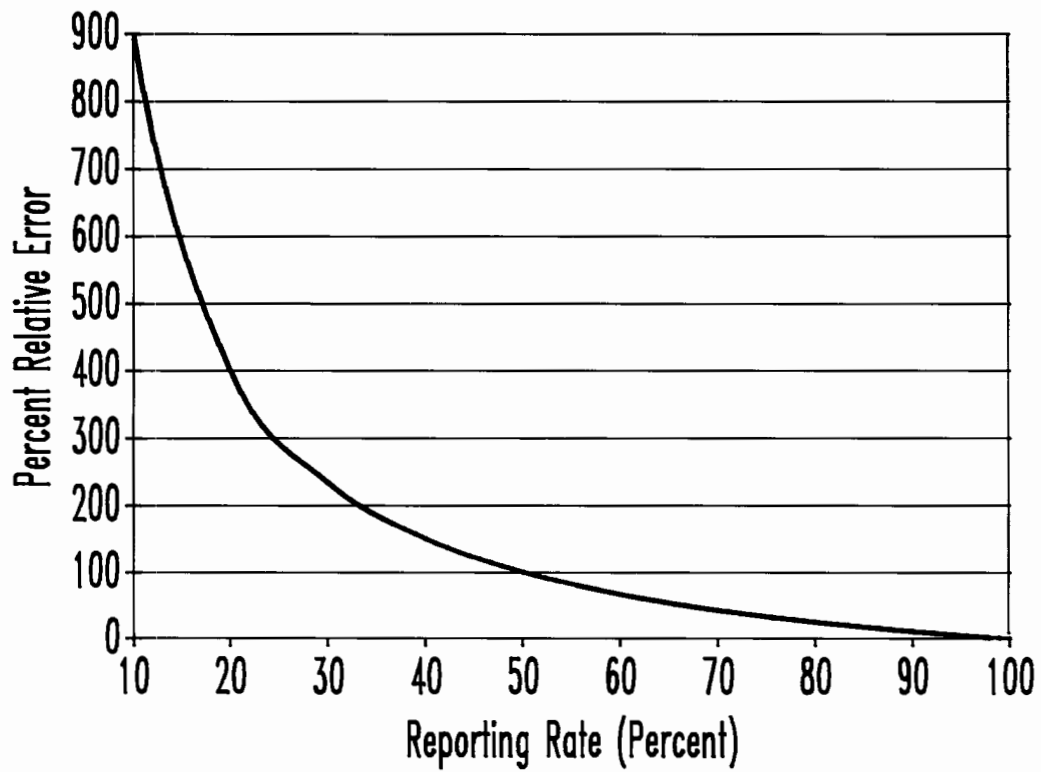
Figure 2. Relationship between relative error (bias) of the exploitation rate, $E(\lambda)$, and the reporting rate, α, of reward tags. The line is defined by $E(\lambda) = (1/\alpha) - 1$ (Conroy and Williams 1981).
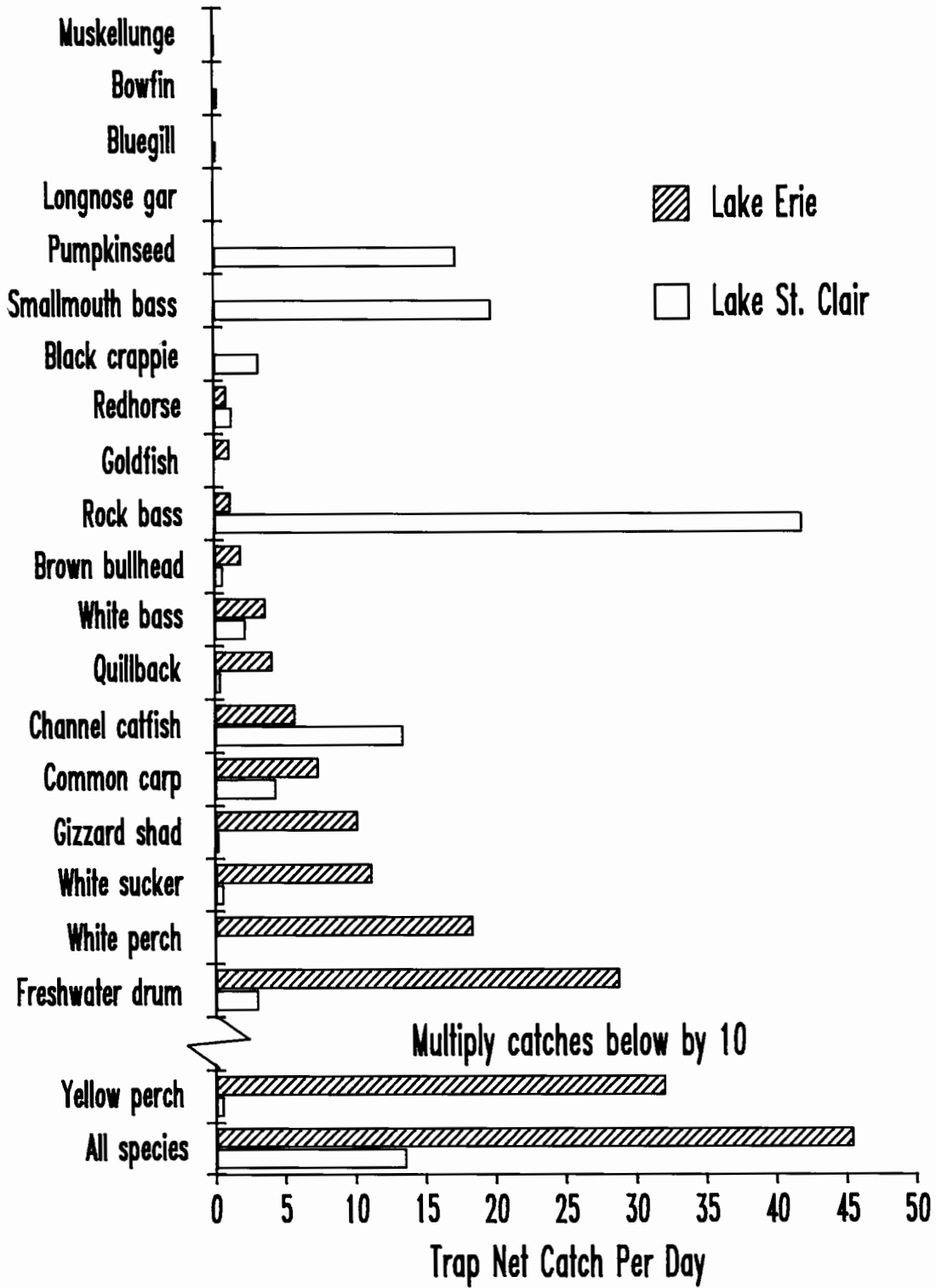
Figure 3. Mean trap-net CPUE for 20 species and all species combined in Lake St. Clair and Lake Erie.
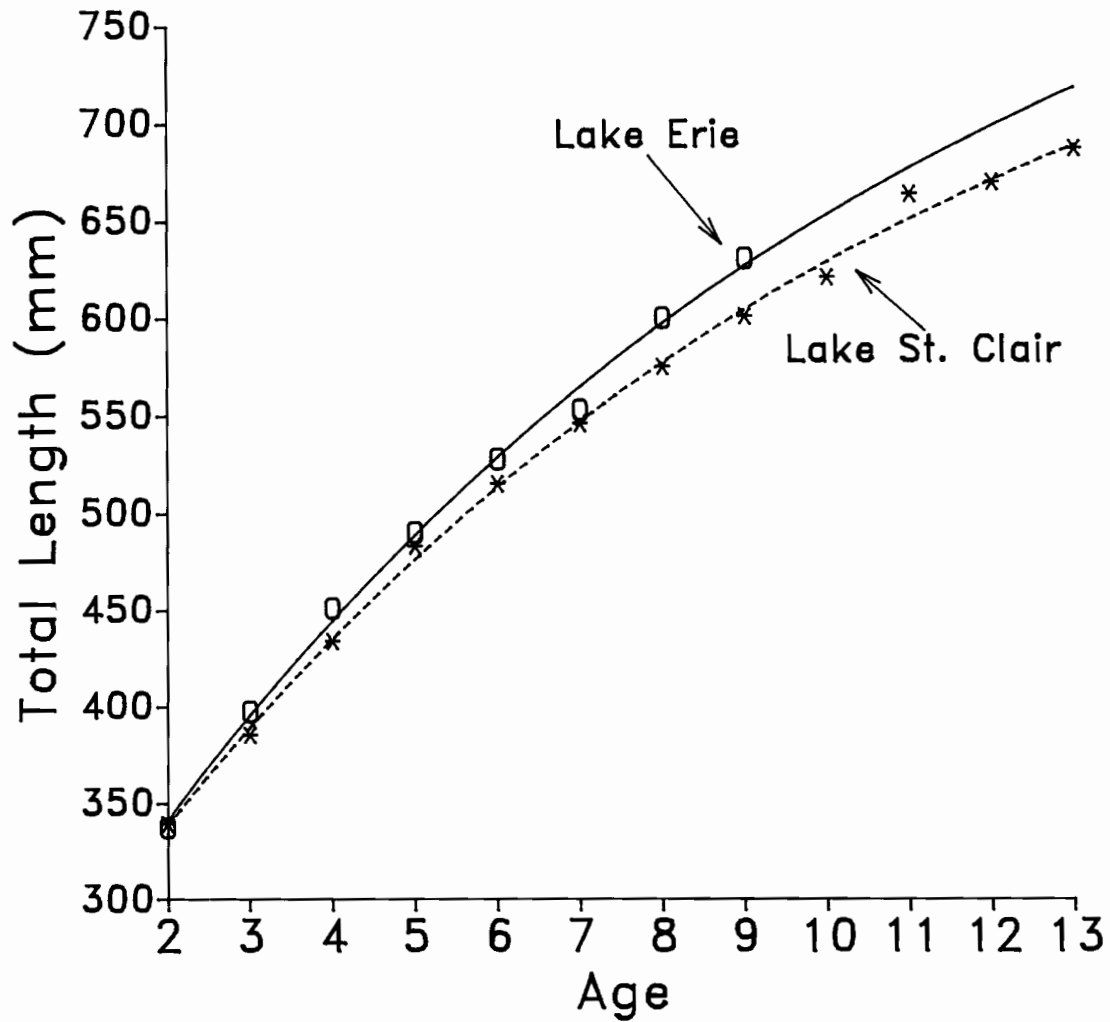
Figure 4. Von Bertalanffy growth model for Lake St. Clair (dashed line) and Lake Erie (solid line) walleye. Mean length-at-age values for Lake St. Clair (*) walleye and Lake Erie (0) walleye were estimated from the 1972-85 and 1978-85 trap-net samples.
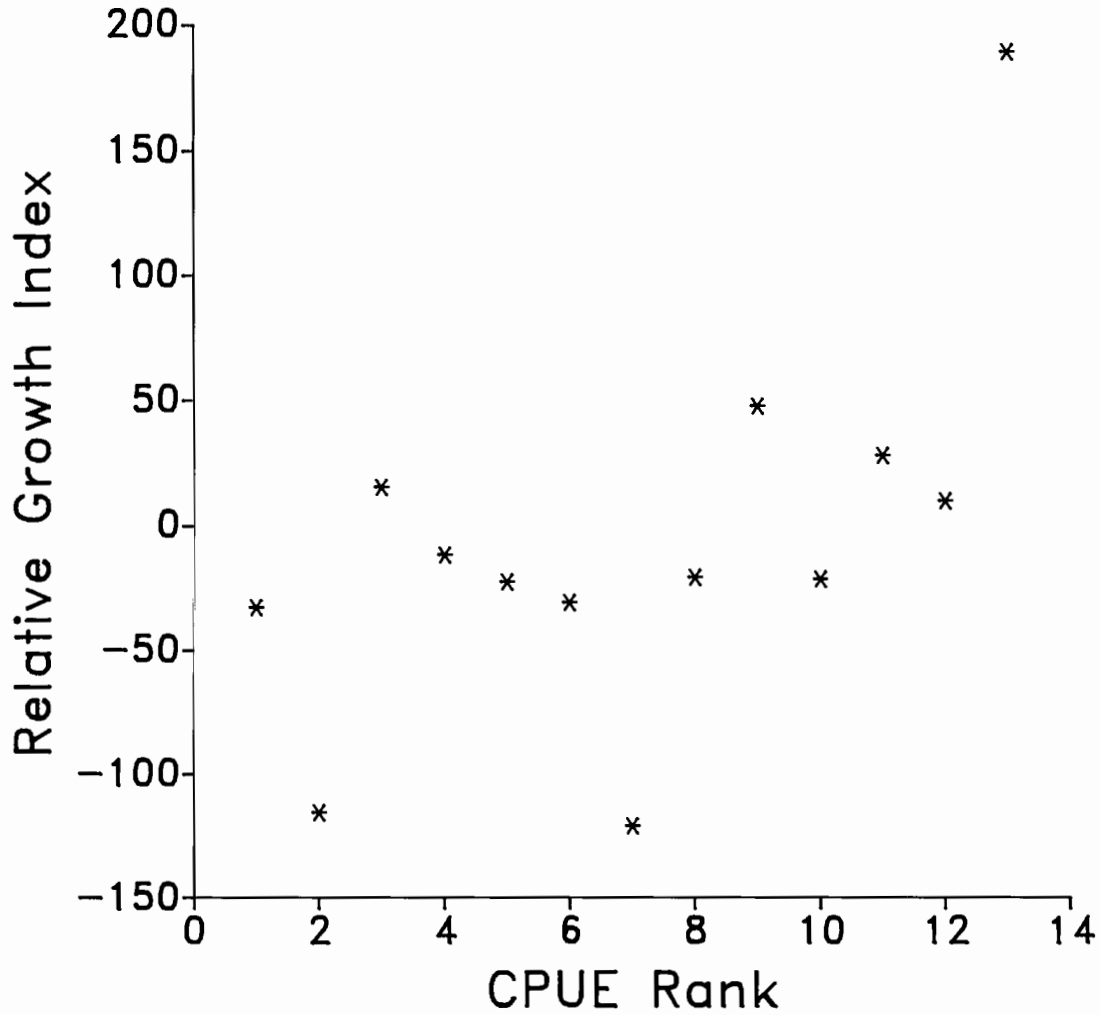
Figure 5. Relationship between relative growth index of Lake Erie walleye and rank transformation of the mean catch per unit effort (CPUE rank) for the 1972–84 year classes. Each point on the graph represents one year class. See text for method of calculation of the relative growth index; CPUE data are from trap-net samples.
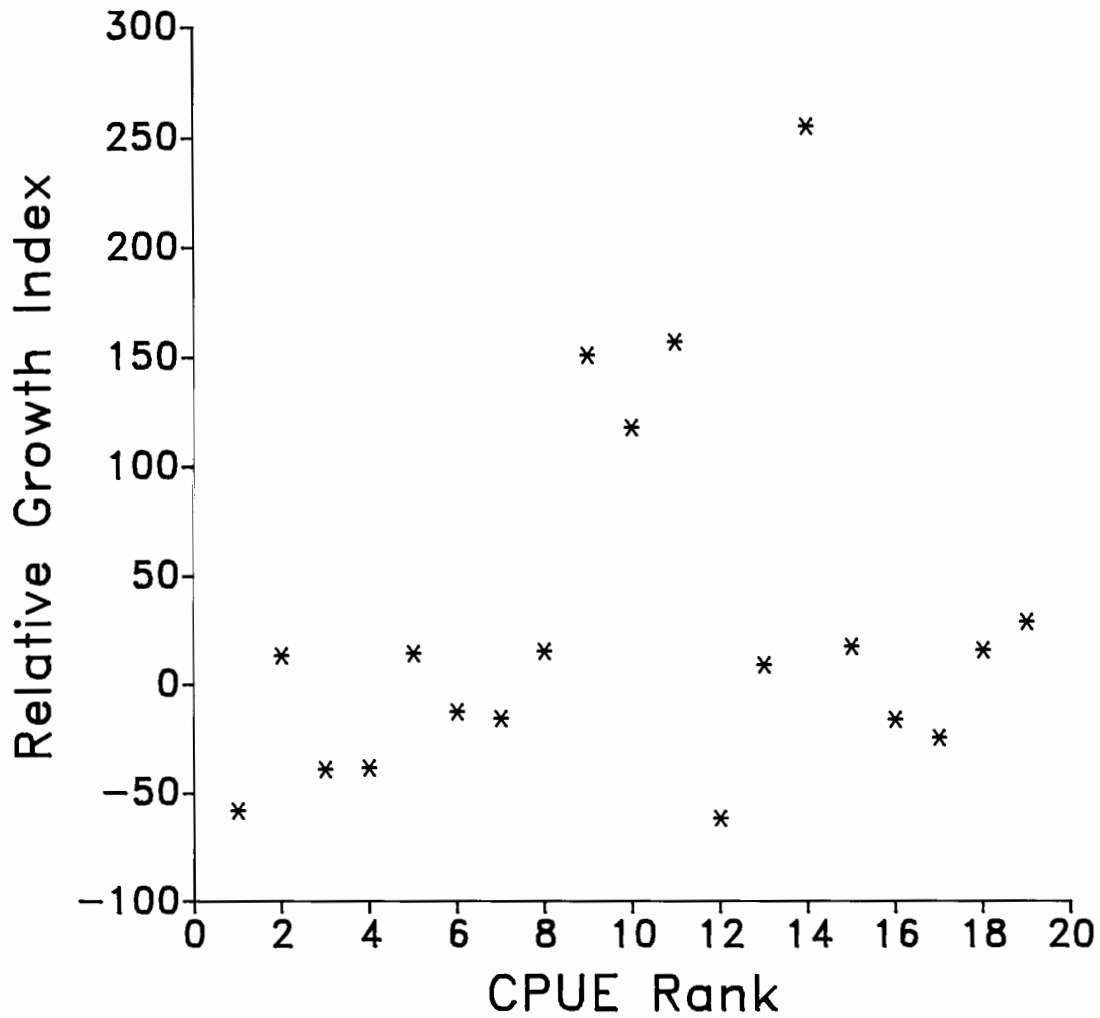
Figure 6. Relationship between relative growth index of Lake St. Clair walleye and rank
transformation of the mean catch per unit effort (CPUE rank) for the 1964–82
year classes. Each point on the graph represents one year class. See text for
method of calculation of the relative growth index; CPUE data are from trap-net
samples.
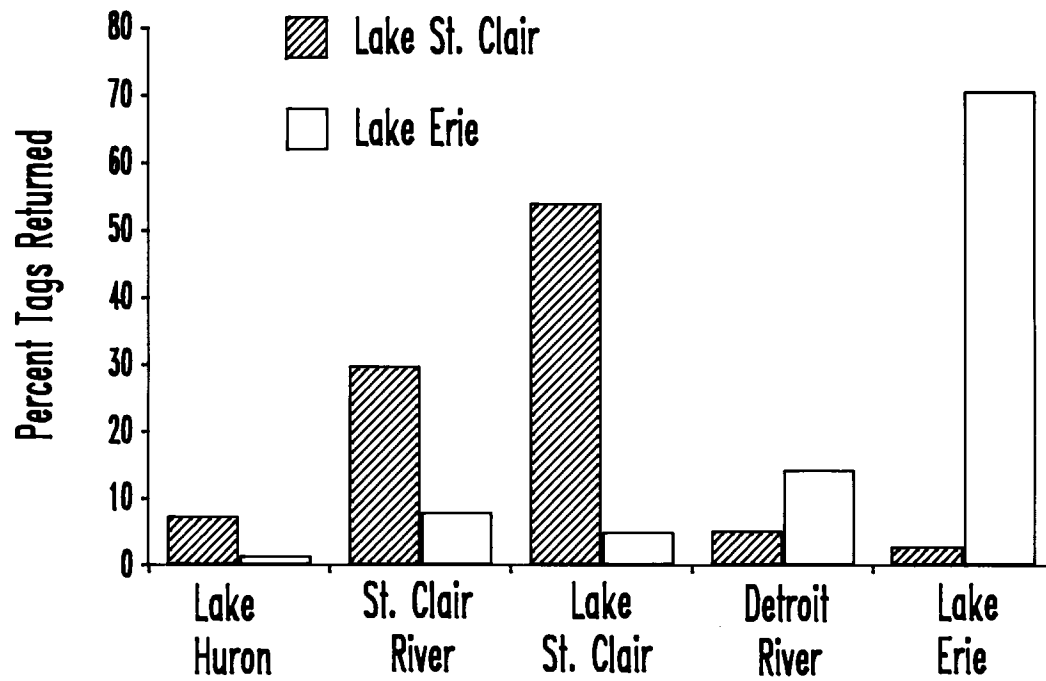
Figure 7. Percent recapture of walleye tagged in Lake St. Clair and Lake Erie reported for five areas.
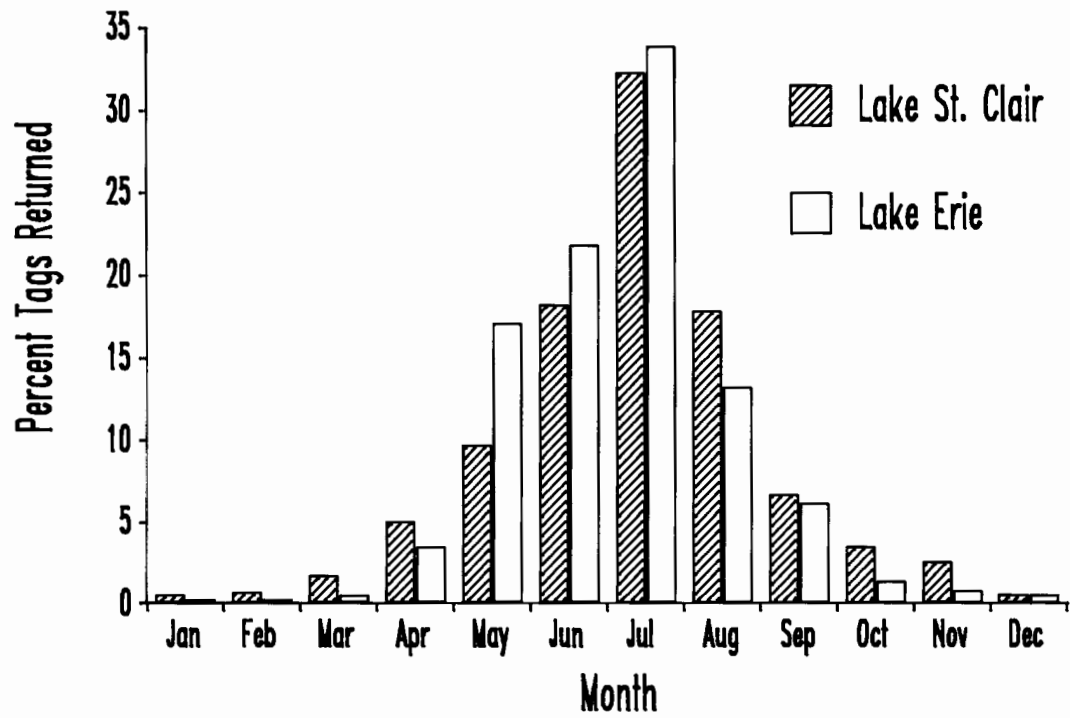
Figure 8. Monthly percent of reported recaptures of walleye tagged in Lake St. Clair and Lake Erie recaptured in Lake St. Clair.
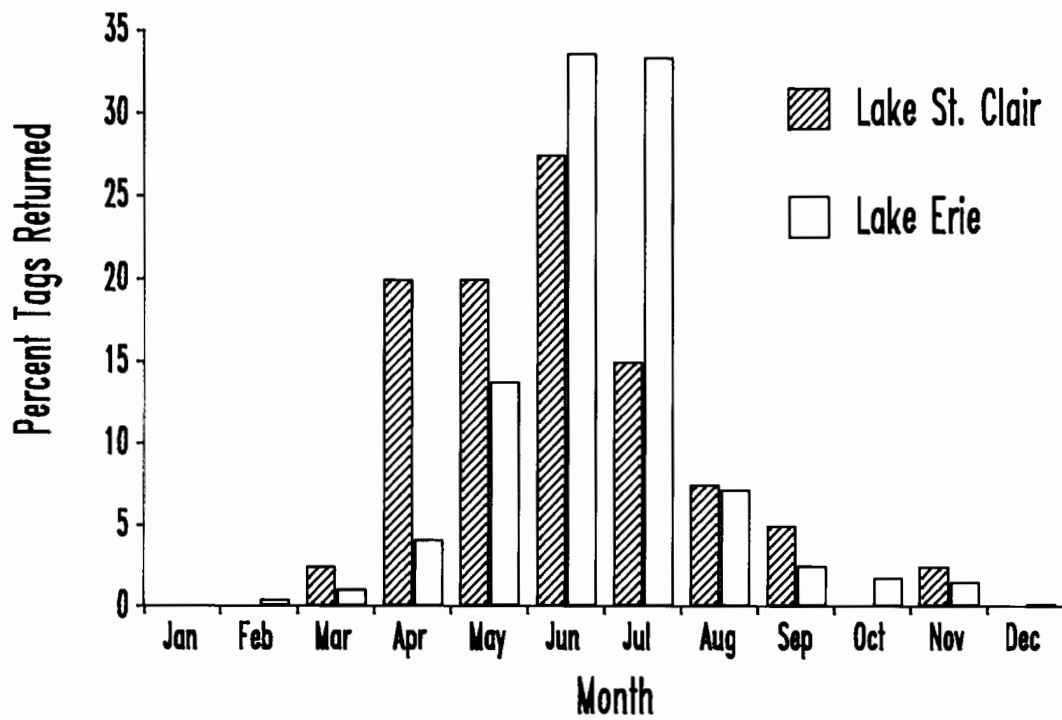
Figure 9. Monthly percent of reported recaptures of walleye tagged in Lake St. Clair and Lake Erie recaptured in Lake Erie.
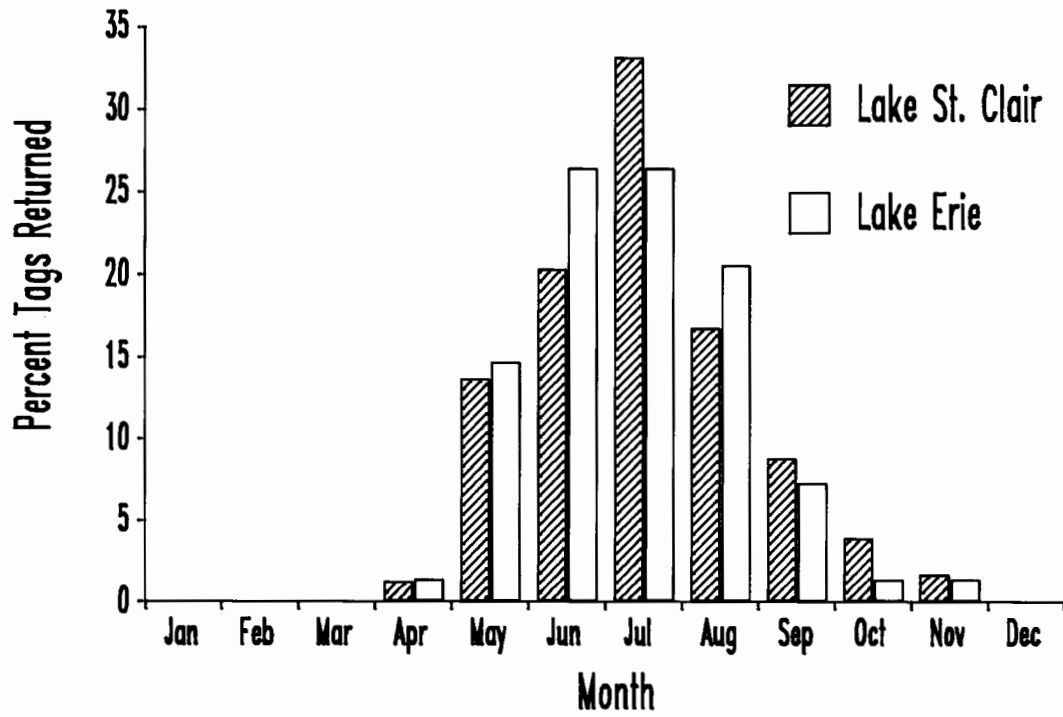
Figure 10. Monthly percent of reported recaptures of walleye tagged in Lake St. Clair and Lake Erie recaptured in the north half of the St. Clair River.
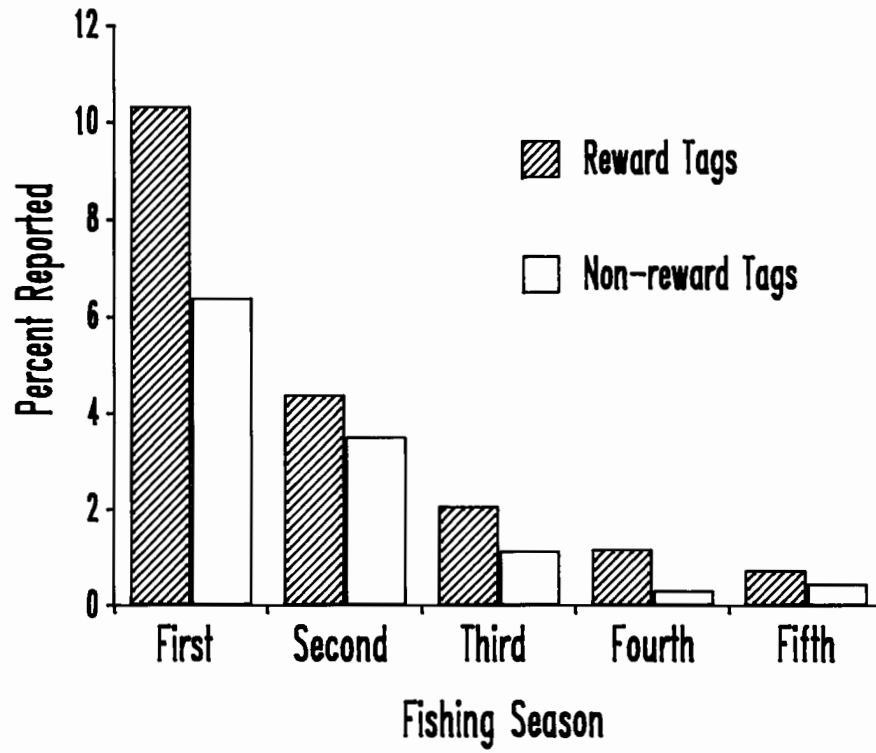
Figure 11. Distribution of angler recaptures of Lake St. Clair walleye with reward and non-reward tags during five subsequent fishing seasons.
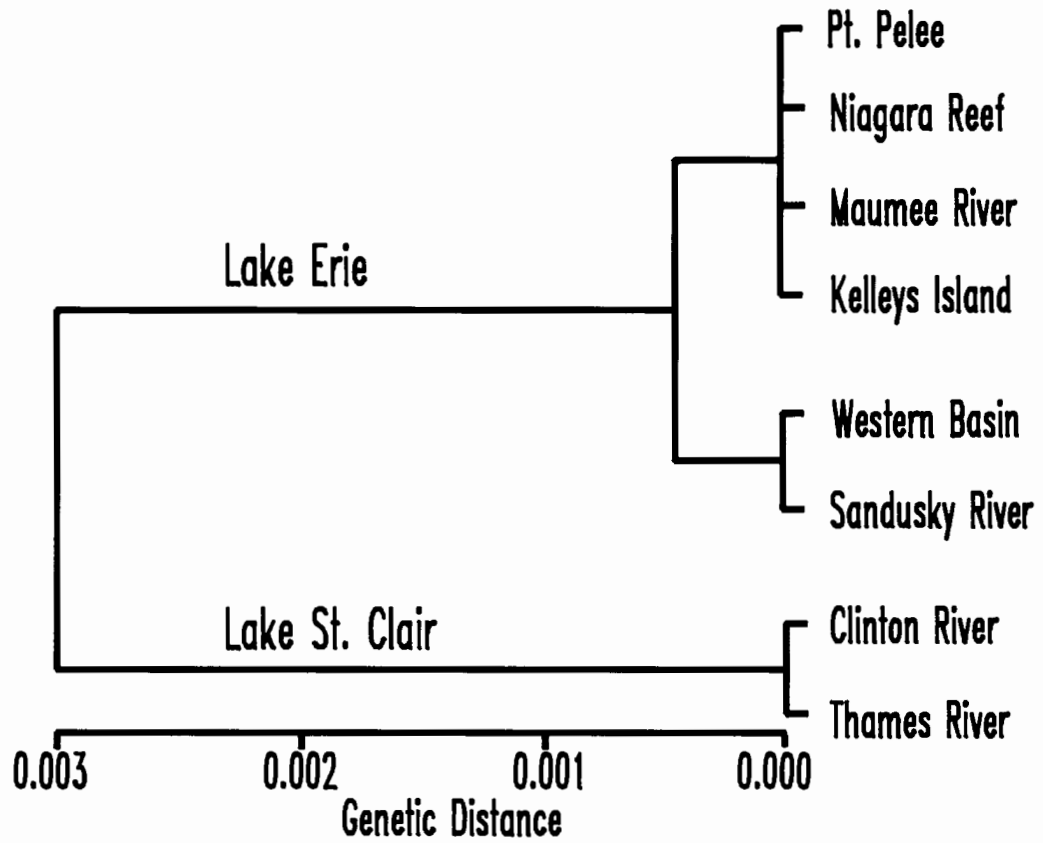
Figure 12. Dendrogram based on unweighted pair-group cluster analysis of Nei's (1978) unbiased minimum genetic distance. Significant separation based on genetic distance occurs at the level separating Lake St. Clair and Lake Erie populations.
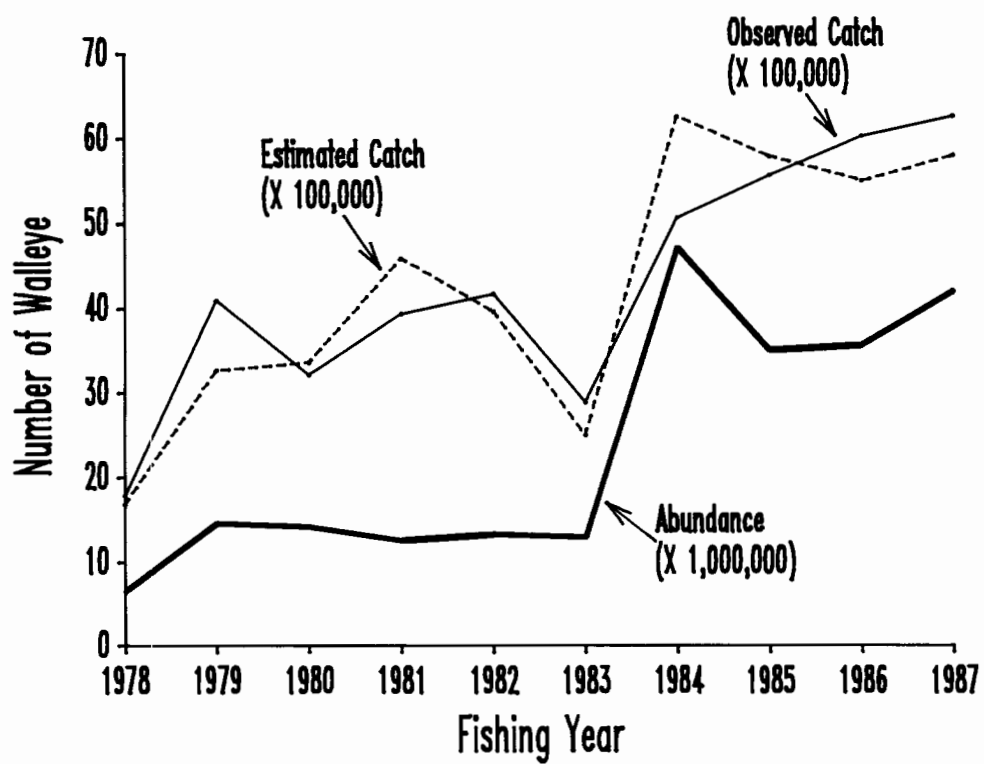
Figure 13. Estimates of walleye abundance and catch from the CAGEAN analysis and observed walleye catch in the western basin of Lake Erie.
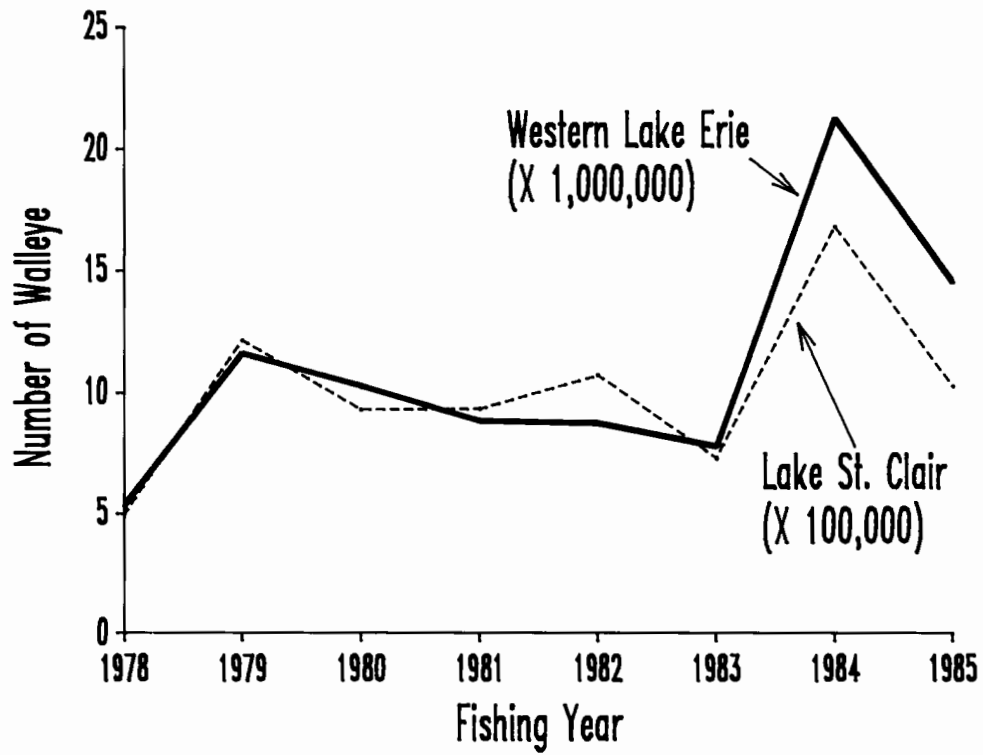
Figure 14. Estimates of walleye abundance in Lake St. Clair and Lake Erie from CAGEAN analyses of comparable data sets.
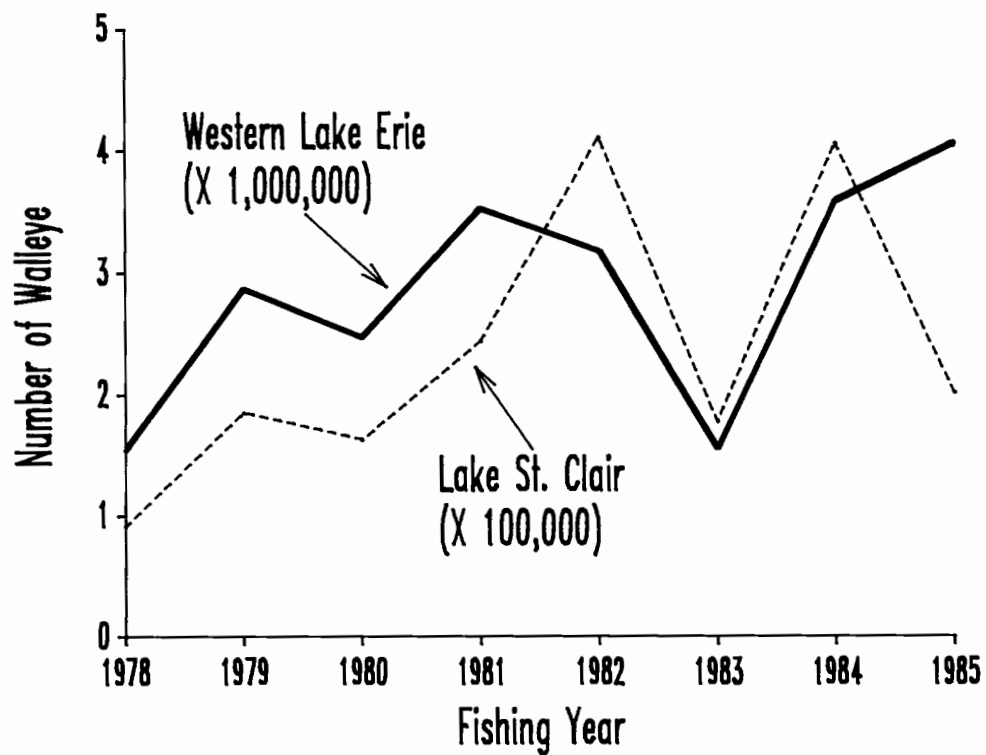
Figure 15. Estimates of walleye harvest in Lake St. Clair and Lake Erie from CAGEAN analyses of comparable data sets.
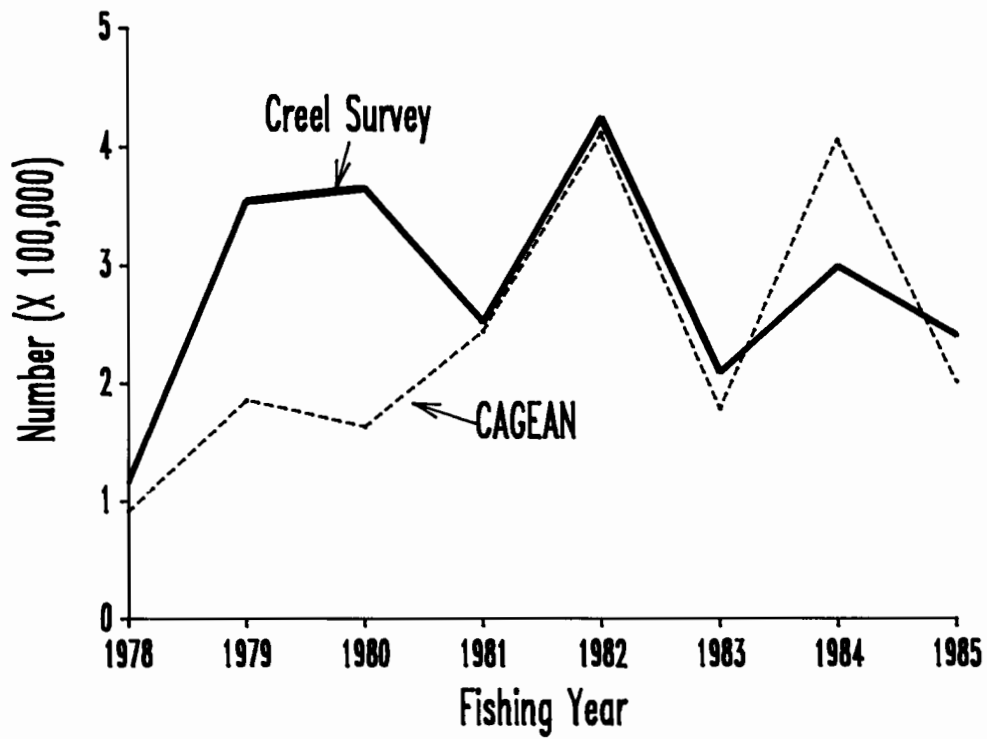
Figure 16. Estimate of walleye harvest from the CAGEAN model compared with observed harvest from the creel surveys for Lake St. Clair.
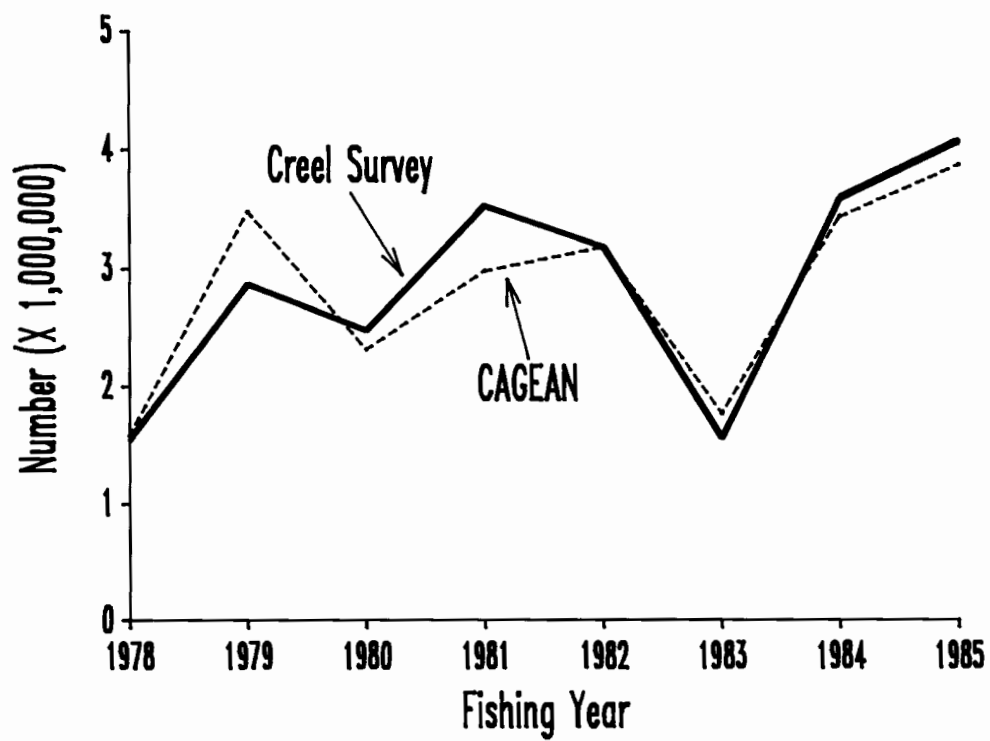
Figure 17. Estimate of walleye harvest from the CAGEAN model compared with observed harvest from the creel surveys for western Lake Erie.

Table 1. Estimated mean catch per unit effort (CPUE) for the 1977–82 year classes of Lake Erie walleye taken in gill nets and trap nets. Only ages 1–5 are represented in these means.

Year class	Gill net	Trap net
1977	32.9	7.0
1978	11.6	1.6
1979	13.8	1.5
1980	17.9	4.0
1981	13.8	3.0
1982	57.9	18.0

Table 2. Mean lengths (mm) and one standard deviation (in parentheses) for 2 to 10 year-old walleye for Lake St. Clair and Lake Erie. The t-statistic for comparison of age-specific means is presented; asterisks denote significance at $P \leq 0.05$.

Location and test	Age								
	2	3	4	5	6	7	8	9	10
Lake St. Clair	339.9 (23.71)	385.3 (30.93)	430.7 (37.38)	480.3 (40.69)	512.6 (45.36)	546.4 (39.26)	577.7 (45.46)	617.4 (47.85)	625.5 (51.02)
Lake Erie	337.4 (22.86)	398.1 (29.43)	451.1 (35.79)	490.2 (40.62)	527.4 (44.68)	553.0 (47.23)	596.4 (60.16)	631.0 (48.98)	608.5 (109.02)
t-statistic	−3.58*	16.52*	16.07*	5.17*	4.41*	1.58	2.85*	1.24	−0.68

Table 3. Mean total length-at-age (mm) of walleye year classes from Lake Erie trap nets and relative growth measures for year classes. See text for definition of relative growth.

Year class	Age									Relative growth
	1	2	3	4	5	6	7	8	9	
1971	—	—	—	—	—	—	—	670	—	—
1972	—	—	—	—	—	551	665	692	—	189.35
1973	—	—	—	—	502	572	547	642	593	9.73
1974	—	—	—	460	521	521	553	599	695	47.63
1975	—	—	417	462	477	517	546	614	649	−30.78
1976	—	370	447	443	473	519	553	621	655	27.86
1977	248	350	397	446	472	517	544	609	590	−115.51
1978	—	331	405	453	492	517	535	579	620	−120.67
1979	225	343	413	475	507	539	551	582	—	−20.65
1980	228	339	404	463	498	544	571	—	—	15.18
1981	219	340	405	457	507	530	—	—	—	−11.80
1982	256	325	387	446	490	—	—	—	—	−32.72
1983	—	328	399	458	—	—	—	—	—	−21.43
1984	212	339	413	—	—	—	—	—	—	−22.50
1985	255	351	—	—	—	—	—	—	—	28.74
1986	247	—	—	—	—	—	—	—	—	—
Mean	236	342	409	456	494	533	563	623	634	—

Table 4. Mean total length-at-age (mm) of walleye year classes from Lake St. Clair trap nets and relative growth measures for year classes. See text for definition of relative growth.

Year class	Age											Relative growth
	2	3	4	5	6	7	8	9	10	11	12	
1962	—	—	—	—	—	—	—	—	655	669	—	—
1963	—	—	—	—	—	—	—	604	627	612	703	—
1964	—	—	—	—	—	—	564	601	597	717	—	−20.3
1965	—	—	—	—	—	551	580	592	619	775	—	68.7
1966	—	—	—	—	507	533	551	591	668	682	—	−33.4
1967	—	—	—	497	517	541	550	615	—	669	—	−25.1
1968	—	—	465	511	514	557	600	639	627	694	—	108.0
1969	—	423	461	489	539	580	615	664	659	—	—	206.3
1970	355	385	436	494	530	547	573	630	652	647	636	−35.5
1971	355	399	430	496	525	557	574	611	612	637	691	−33.6
1972	336	372	463	485	514	541	580	609	626	635	671	−87.3
1973	351	427	439	466	519	553	578	575	631	—	—	−31.8
1974	361	402	434	495	544	528	558	595	618	—	—	−34.3
1975	359	409	465	512	516	545	604	679	—	—	—	150.7
1976	361	434	468	449	505	543	581	581	—	—	—	−16.6
1977	345	380	415	467	501	538	621	—	—	—	—	−58.1
1978	339	400	441	456	505	540	—	—	—	—	—	−61.8
1979	348	393	431	479	531	—	—	—	—	—	—	−16.0
1980	342	379	445	500	—	—	—	—	—	—	—	−13.0
1981	343	403	455	—	—	—	—	—	—	—	—	8.7
1982	326	381	—	—	—	—	—	—	—	—	—	−39.3
Mean	348	399	446	486	519	547	581	613	633	674	675	—

Table 5. Percent of Lake St. Clair (N = 1,333) and Lake Erie (N=1,159) walleye tag returns from five geographic areas.

Tag recovery area	Tag station	
	Lake St. Clair	Lake Erie
Lake Huron	7.50	1.55
St. Clair River	29.93	8.11
Lake St. Clair	54.16	5.18
Detroit River	5.40	14.41
Lake Erie	3.00	70.75

Table 6. Comparison of median Julian day of tagging and tag recovery day for Lake Erie and Lake St. Clair walleye.

Tagged in:	Median tag day recovered in:		Median recapture day in:	
	Lake St. Clair	Lake Erie	Lake St. Clair	Lake Erie
Lake St. Clair	152 (June 1)	151 (May 31)	196 (July 15)	155 (June 4)
Lake Erie	115 (April 25)	116 (April 26)	188 (July 7)	180 (June 29)

Table 7. Mean annual survival rate, recovery rate, and adult life span (years) from walleye tag analyses using the BROWNIE model. These estimates are annual means derived from a tagging experiment began in 1975 in Lake St. Clair and 1978 in Lake Erie and include tag recoveries through 1987. SE is standard error of the mean.

Tag site	Mean survival rate	Mean recovery rate	Mean adult lifespan
Lake St. Clair	53.28	5.32	1.59
SE	1.75	0.24	0.08
95% confidence interval	(49.85–56.71)	(4.86–5.79)	(1.44–1.76)
Lake Erie	60.93	3.21	2.02
SE	1.96	0.13	0.13
95% confidence interval	(57.10–64.77)	(2.95–3.47)	(1.78–2.30)

Table 8. Reporting rate (ratio of reward-tag to standard-tag return rate) for tagging years 1981–83 for Lake St. Clair walleye. N is number of walleye released with reward tags ($2.00–$8.00) and n is number of walleye released with standard tags. The year of tagging is indicated by i, the year following by $i+1$, etc.

Year	N	n	i	$i+1$	$i+2$	$i+3$	$i+4$	$i+5$
1981	317	650	2.237	1.212	1.709	2.051	4.101	2.051
1982	198	259	1.744	1.047	0.727	6.540	0.436	—
1983	394	1,134	1.531	1.367	2.878	2.878	1.151	—

Table 9. Range of non-reporting rates and average non-reporting rates from fish tagging and bird banding studies. Non-reporting rates and their means were taken from cited references or were estimated from data in cited references.

Species	Area	Year	Non-reporting rate (percent)		Reward	Reference
			Range	Mean		
FISH						
Rainbow trout	Lake Lanier, GA	1980–81	—	61	$5.00	Weaver & England 1986
Various estuarine species[1]	Texas Bay systems	1976–78	64–83	71	$1.00 to $25.00	Green et al. 1983
Largemouth bass	Centerhill Reservoir, TN	—	—	46	—	Coomer 1976 (cited in Green et al. 1983)
Largemouth bass	Merle Collins Reservoir, CA	1966–69	15–54	34	$1.00 and $5.00	Rawstron 1972
Largemouth bass White catfish Bluegill	Folsom Lake, CA	1962–68	5–52 22–66 —	38 39 69	$5.00 $5.00 $5.00	Rawstron 1971
Rainbow trout	Lake Tahoe, CA	—	36.–39[2] 51–53[3]	—	$1.00 and $5.00	Rawstron, unpubl. (in Rawstron 1971)
Striped bass	Sacramento-San Joaquin River system, CA	1958–61	31–47	38	$5.00	Chadwick 1968
Cod	Barents Sea (U.K. Fleet)	1959–61	56–67	59	—[4]	Margetts 1963
Cod	West Greenland & North Atlantic	1953–59	69–83	77	—[5]	Horsted 1963
Yellowfin & skipjack tuna	Eastern Pacific	1955–59	10–50	—	—[4]	Schaeffer et al. 1963
Rainbow trout	Kern River, CA	1956–57	—	38	$5.00	Butler 1962
Channel catfish	Sacramento Valley rivers, CA	1955	30–40[6]	40[6]	$200.00 Lottery	McCammon & LaFaunce 1961
Rainbow trout	CA	—	40–60	—	—[7]	Butler, unpubl., cited in McCammon & LaFaunce 1961
Channel catfish	Colorado River, CA	1953–54	—	15	Lottery[8]	McCammon 1956
Brook trout Brown trout Rainbow trout	Millers River, MA	1953 1953 1953	9–25 9–25 9–25	17 25 17	—[9] —[9] —[9]	Mullan 1959
Brook trout Brown trout Rainbow trout	Squannacook River, MA	1953 1953 1953	— — —	60 60 60	—[5] —[9] —[9]	Mullan 1959

Table 9. Continued:

Species	Area	Year	Non-reporting rate (percent)		Reward	Reference
			Range	Mean		
Largemouth bass	Lakes, ponds, and	1950–53	—	25	$1.00[10]	Stroud and Bitzer 1955
Smallmouth bass	reservoirs, MA		—	25	$1.00[10]	
Brown bullhead			—	25	$1.00[10]	
White perch			—	25	$1.00[10]	
Yellow perch			—	25	$1.00[10]	
Chain pickerel			—	25	Lottery	

BIRDS

Species	Area	Year	Range	Mean	Reward	Reference
American black duck	Canada & U. S: Atlantic & Mississippi flyways	1978–80	0–69	57	$15.00	Conroy & Blandin 1984
Mallard	U. S. & Canada	1972–73	0–94	—	$10.00	Henny & Burnham 1976
Mourning dove	U. S.	1970–72	35–69	58	Book	Reeves 1979
Mourning dove	U. S.	1965–66	59–64	60	Book	Tomlinson 1968
Waterfowl (10 species)	U. S.	1954–58	50–57	54	—[11]	Geis & Atwood 1961
Mallard	U. S.	1954–57	32–55	50	—[11]	Geis & Atwood 1961
Mallard	IL	1948–51	0–65	50	$2.00	Bellrose 1955
Mallard	Canada & U. S: Mississippi flyway	1950–51	38–62	56 ·	$2.00	Bellrose 1955

[1] Spotted seatrout, red drum, other seatrout, flounder, Atlantic croaker, black drum, and sheepshead.

[2] First year.

[3] Second year.

[4] Placed tagged fish in catch of commercial vessels.

[5] Assumed one segment of fishery reported all tags.

[6] Used estimates from the literature.

[7] Estimated non-reporting rates from known harvest rate.

[8] Used two types of tags; estimated non-reporting rate by assuming all recoveries of one type of tag were reported.

[9] Estimated non-reporting rates from partial creel census.

[10]Gift certificate.

[11]Estimated non-reporting rate from follow-up survey questionnaire.

Table 10. Allelic frequencies at polymorphic loci, probability of conformance to Hardy-Weinberg expectations (in parentheses), and P, probability of genetic homogeneity for Lake Erie walleye populations. N is sample size. Single asterisk denotes significance at $P \leq 0.05$.

	Population						
Locus	Pelee	W. Basin	Maumee	Niagara	Kelley	Sandusky	P
ADH-1	(0.209)	(0.396)	(0.781)	(0.435)	(0.763)	(0.401)	0.075
N	49	72	388	281	119	97	
75	0.224	0.160	0.170	0.189	0.172	0.144	
100	0.776	0.833	0.830	0.811	0.828	0.856	
140	0.000	0.007	0.000	0.000	0.000	0.000	
GMP-3	(0.944)	(0.349)	(0.641)	(0.807)	(0.596)	(0.044)*	0.561
N	49	72	393	290	120	98	
75	0.449	0.389	0.438	0.398	0.404	0.388	
100	0.551	0.611	0.562	0.602	0.596	0.612	
IDH-1	(0.376)	(0.739)	(0.095)	(0.097)	(0.107)	(0.211)	0.386
N	49	72	390	288	121	98	
80	0.296	0.403	0.332	0.351	0.298	0.357	
100	0.704	0.597	0.667	0.649	0.702	0.638	
120	0.000	0.000	0.001	0.000	0.000	0.005	
MDH-1	——	——	(0.980)	——	(0.964)	(0.960)	0.225
N	49	72	393	290	121	98	
40	0.000	0.000	0.001	0.000	0.004	0.000	
100	1.000	1.000	0.999	1.000	0.996	0.995	
155	0.000	0.000	0.000	0.000	0.000	0.005	
MDH-2	——	——	(0.960)	——	——	——	0.668
N	49	72	393	290	121	98	
100	1.000	1.000	0.997	1.000	1.000	1.000	
140	0.000	0.000	0.003	0.000	0.000	0.000	
MDH-3	(0.484)	(0.642)	(0.193)	(0.300)	(0.109)	(0.707)	0.503
N	49	72	393	290	120	98	
80	0.000	0.000	0.014	0.021	0.008	0.015	
100	0.714	0.743	0.733	0.734	0.754	0.684	
120	0.286	0.257	0.253	0.245	0.237	0.301	
PGM-1	——	——	——	——	(0.963)	(0.960)	——
N	49	72	393	290	120	98	
70	0.000	0.000	0.000	0.000	0.004	0.005	
100	1.000	1.000	1.000	1.000	0.996	0.995	
PGI-1	——	——	——	——	(0.964)	——	0.188
N	49	72	393	290	121	98	
100	1.000	1.000	1.000	1.000	0.996	1.000	
270	0.000	0.000	0.000	0.000	0.004	0.000	

Table 10. Continued:

| Locus | Population | | | | | | P |
	Pelee	W. Basin	Maumee	Niagara	Kelley	Sandusky	
PGI-2	—	—	(0.939)	—	(0.964)	—	0.552
N	49	72	393	290	121	98	
100	1.000	1.000	0.996	1.000	0.996	1.000	
140	0.000	0.000	0.004	0.000	0.004	0.000	
PGI-3		(0.953)	(0.719)	(0.858)		(0.837)	0.168
N	49	72	393	289	120	98	
90	0.000	0.007	0.018	0.010	0.000	0.020	
100	1.000	0.993	0.982	0.990	1.000	0.980	
Total							0.126

Table 11. Allelic frequencies at four polymorphic loci, probability of conformance to Hardy-Weinberg expectations (in parentheses), and probability of genetic homogeneity for Lake Erie and Lake St. Clair walleye. N is sample size. Single asterisk denotes significance at $P \leq 0.05$; double asterisks denote significance at $P \leq 0.01$.

| | Population | | |
Locus	Lake Erie	Lake St. Clair	P
ADH-1	(0.509)	(0.854)	0.141
N	1,006	633	
75	0.175	0.151	
100	0.825	0.849	
GMP-3	(0.447)	(0.828)	0.000**
N	1,022	645	
75	0.415	0.486	
100	0.585	0.514	
IDH-1	(0.003)**	(0.475)	0.018*
N	1,018	642	
80	0.339	0.296	
100	0.660	0.704	
120	0.001	0.0	
MDH-3	(0.026)*	(0.598)	0.000**
N	1,022	643	
80	0.014	0.017	
100	0.731	0.652	
120	0.255	0.331	
Total			0.000**

55

Table 12. Allelic frequencies at polymorphic loci, probability of conformance to Hardy-Weinberg expectations (in parentheses), and probability of genetic homogeneity for Lake St. Clair walleye. N is sample size. Double asterisks denote significance at $P \leq 0.01$.

| | Population | | |
Locus	Clinton River	Thames River	P
ADH-1	(0.144)	(0.256)	0.700
N	313	320	
75	0.147	0.155	
100	0.853	0.845	
GMP-3	(0.566)	(0.792)	0.975
N	320	325	
75	0.486	0.486	
100	0.514	0.514	
IDH-1	(0.456)	(0.077)	0.751
N	320	322	
80	0.300	0.292	
100	0.700	0.708	
MDH-2	—	(0.956)	0.161
N	321	327	
100	1.000	0.997	
140	0.000	0.003	
MDH-3	(0.996)	(0.461)	0.729
N	318	325	
80	0.019	0.015	
100	0.659	0.645	
120	0.322	0.340	
PGM-1	(0.933)	(0.978)	0.307
N	321	327	
70	0.005	0.002	
100	0.995	0.998	
PGI-2	(0.978)	(0.978)	0.972
N	321	327	
100	0.998	0.998	
140	0.002	0.002	
PGI-3	(0.754)	(0.001)**	0.846
N	320	316	
90	0.017	0.016	
100	0.983	0.984	
Total			0.916

Table 13. Length-at-age (mm) for male and female spawning walleye from the Thames and Maumee rivers. *N* is sample size. *P* is probability of a significant difference in length-at-age for the two groups; NS is nonsignificant.

	Age									
	Males					Females				
Rivers	3	4	5	6	7	3	4	5	6	7
Thames	351	404	461	484	510	367	475	489	516	570
N	33	49	22	17	23	10	11	12	46	32
P	0.01	0.01	NS	NS	NS	0.05	NS	0.01	0.01	0.01
Maumee	390	434	459	491	525	409	490	542	559	611
N	130	75	10	21	7	8	32	7	12	15

Table 14. Somatic weight-at-age (g) for male and female spawning walleye from the Thames and Maumee rivers. N is sample size. P is probability of a significant difference in weight-at-age for the two groups; NS is nonsignificant.

	Age									
	Males					Females				
Rivers	3	4	5	6	7	3	4	5	6	7
Thames	395	554	819	933	1,149	438	927	1,031	1,172	1,554
N	33	49	22	17	23	10	11	12	46	32
P	0.01	0.01	NS	0.01	NS	NS	0.05	0.01	0.01	0.01
Maumee	526	749	913	1,139	1,354	609	1,099	1,524	1,716	2,134
N	130	75	10	21	7	8	32	7	12	15

Table 15. Estimated angler effort and harvest of walleye from Lake St. Clair

Year	Ontario fishery		Michigan fishery	
	Angler hours	Walleye harvest (number)	Angler hours	Walleye harvest (number)
1977	82,260	11,700	—	—
1978	546,558	47,073	—	—
1979	541,909	157,602	—	—
1980	580,441	133,767	—	—
1981	457,512	91,423	—	—
1982	740,684	164,021	—	—
1983	459,022	85,959	1,524,065	131,529
1984	486,245	119,136	1,447,117	132,221
1985	270,339	82,125	—	—
Mean	462,774	99,201	1,485,591	131,875

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Report approved by W. C. Latta

Appendix 1. List of fishes caught during spring trap-net surveys in Lake St. Clair and Lake Erie 1975–87.

Species	Scientific name	Lake St. Clair	Lake Erie
Lake sturgeon	*Acipenser fulvescens*	Present	Absent
Longnose gar	*Lepisosteus osseus*	Present	Present
Bowfin	*Amia calva*	Present	Present
Alewife	*Alosa pseudoharengus*	Present	Present
Gizzard shad	*Dorosoma cepedianum*	Present	Present
Mooneye	*Hiodon tergisus*	Present	Absent
Northern pike	*Esox lucius*	Present	Present
Muskellunge	*Esox masquinongy*	Present	Present
Black bullhead	*Ictalurus melas*	Present	Present
Brown bullhead	*Ictalurus nebulosus*	Present	Present
Channel catfish	*Ictalurus punctatus*	Present	Present
Stonecat	*Noturus flavus*	Absent	Present
American eel	*Anguilla rostrata*	Present	Absent
Burbot	*Lota lota*	Absent	Present
White perch	*Morone americana*	Present	Present
White bass	*Morone chrysops*	Present	Present
Freshwater drum	*Aplodinotus grunniens*	Present	Present
Lake whitefish	*Coregonus clupeaformis*	Absent	Present
Lake trout	*Salvelinus namaycush*	Present	Absent
Coho salmon	*Oncorhynchus kisutch*	Absent	Present
Splake	*Salvelinus fontinalis* x *S. namaycush*	Present	Absent
Goldfish	*Carassius auratus*	Present	Present
Common carp	*Cyprinus carpio*	Present	Present
Quillback	*Carpiodes cyprinus*	Present	Present
White sucker	*Catostomus commersoni*	Present	Present
Hogsucker	*Hypentelium nigricans*	Present	Present
Bigmouth buffalo	*Ictiobus cyprinellus*	Present	Present
Spotted sucker	*Minytrema melanops*	Present	Present
Silver redhorse	*Moxostoma anisurum*	Present	Present
Golden redhorse	*Moxostoma erythrurum*	Present	Present
Northern redhorse	*Moxostoma macrolepidotum*	Present	Present
Unid. redhorse	*Moxostoma* spp.	Present	Present
River redhorse	*Moxostoma carinatum*	Present	Absent
Smallmouth buffalo	*Ictiobus bubalus*	Present	Absent
Silver chub	*Hybopsis storeiana*	Absent	Present
Golden shiner	*Notemigonus crysoleucas*	Absent	Present
Rock bass	*Ambloplites rupestris*	Present	Present
Green sunfish	*Lepomis cyanellus*	Absent	Present
Pumpkinseed	*Lepomis gibbosus*	Present	Present
Bluegill	*Lepomis macrochirus*	Present	Present
Smallmouth bass	*Micropterus dolomieui*	Present	Present
Largemouth bass	*Micropterus salmoides*	Present	Present
White crappie	*Pomoxis annularis*	Present	Present
Black crappie	*Pomoxis nigromaculatus*	Present	Present
Yellow perch	*Perca flavescens*	Present	Present
Sauger	*Stizostedion canadense*	Absent	Present
Walleye	*Stizostedion vitreum*	Present	Present

Appendix 2. Mean number of fish caught per trap-net lift in Lake St. Clair. Catch per effort is number caught in 24 hours.

Species	Year											Mean
	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	
Smallmouth bass	6.7	3.6	12.6	21.2	16.7	39.9	36.2	11.2	14.9	26.2	29.1	19.85
Yellow perch	6.8	0.4	2.6	5.1	7.3	4.2	0.9	1.4	5.3	21.7	15.4	6.46
Rock bass	52.5	11.8	34.5	27.8	52.8	50.1	32.4	50.0	62.5	48.8	38.5	41.97
White bass	0.7	0.1	0.9	1.1	3.9	4.3	1.6	7.7	2.8	1.4	0.7	2.29
White perch	0.0	0.0	0.0	0.0	0.0	0.0	0.0	<0.1	<0.1	<0.1	<0.1	0.01
Pumpkinseed	3.7	8.8	11.7	4.9	5.5	25.8	12.0	29.1	10.9	27.1	51.2	17.34
Bluegill	0.4	0.5	0.3	0.3	0.1	0.2	0.2	0.1	0.0	0.2	0.8	0.27
Black crappie	0.6	1.5	0.4	1.0	0.6	4.2	12.0	1.6	1.5	5.6	6.8	3.25
Channel catfish	17.1	10.5	15.2	12.7	29.6	14.9	4.9	8.0	11.9	17.3	6.1	13.47
Brown bullhead	1.8	0.7	0.6	1.2	1.1	0.7	0.5	0.3	0.2	0.2	0.1	0.68
Muskellunge	0.7	0.0	0.1	0.4	0.3	0.0	0.1	0.1	0.3	0.1	0.1	0.21
White sucker	1.0	0.4	0.6	1.0	0.7	0.7	0.4	1.1	0.5	0.5	0.3	0.66
Redhorse	2.5	0.9	1.0	1.9	1.7	1.9	1.5	2.0	1.3	0.0	0.0	1.34
Freshwater drum	2.2	2.7	1.5	7.6	2.7	2.4	3.3	3.0	1.4	2.6	4.6	3.09
Common carp	5.5	9.9	4.6	6.1	2.7	3.2	2.6	5.0	1.9	2.3	4.8	4.42
Goldfish	0.8	0.3	0.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.14
Gizzard shad	0.1	0.2	1.7	0.1	0.1	0.4	0.0	0.4	0.1	0.2	0.2	0.33
Longnose gar	0.0	0.0	0.1	0.1	0.2	0.1	0.0	0.0	0.0	0.0	0.2	0.07
Bowfin	0.1	0.7	0.6	0.5	0.3	0.7	0.4	0.8	0.1	0.2	0.1	0.40
Mooneye	0.1	0.0	0.0	0.0	<0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.01
Quillback	0.2	0.2	0.3	0.3	0.6	1.0	0.4	1.0	0.6	0.6	0.6	0.51
Stonecat	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00
Total	103.5	53.4	89.6	93.4	127.0	154.8	109.4	122.6	116.3	155.0	159.5	116.77

Appendix 3. Mean number of fish caught per trap-net lift in Lake Erie. Catch per effort is number caught in 24 hours.

Species	Year										Mean
	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	
Smallmouth bass	0.1	0.0	0.0	0.1	0.2	0.1	0.1	0.1	0.1	0.0	0.08
Yellow perch	377.0	320.0	669.0	512.0	146.0	257.0	129.0	156.0	40.2	174.0	278.02
Rock bass	1.2	0.8	1.9	0.9	1.5	1.3	1.0	1.5	0.7	1.5	1.23
White bass	1.5	1.5	3.7	1.4	10.5	4.9	2.5	2.8	7.6	0.4	3.68
White perch	0.0	0.1	0.3	0.5	24.6	35.0	10.9	38.9	30.3	43.5	18.40
Pumpkinseed	0.1	0.0	0.0	0.1	0.1	0.1	0.0	0.1	0.0	0.1	0.06
Bluegill	0.0	0.0	<0.1	0.0	0.0	<0.1	<0.1	<0.1	0.0	<0.1	0.01
Black crappie	0.2	0.0	0.2	0.0	0.1	0.0	0.1	0.1	0.2	0.2	0.11
Channel catfish	3.5	9.7	5.4	5.8	4.9	10.6	4.6	5.5	5.4	2.7	5.79
Brown bullhead	0.2	1.1	1.6	1.9	1.7	4.2	2.5	1.5	4.1	0.9	1.97
Muskellunge	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	<0.1	0.0	<0.01
White sucker	7.8	8.3	7.9	12.2	8.7	6.7	10.2	33.0	10.2	7.0	11.20
Redhorse	2.4	1.2	0.6	1.0	0.8	1.5	1.7	0.3	0.0	0.0	0.96
Freshwater drum	37.4	66.8	14.0	42.9	13.4	23.5	25.1	30.6	25.3	9.1	28.81
Common carp	5.1	26.1	4.7	8.2	6.9	14.9	3.5	2.0	1.9	0.6	7.39
Goldfish	4.8	2.4	0.3	0.4	0.4	2.5	0.6	0.2	0.1	0.0	1.17
Gizzard shad	4.4	4.7	2.3	3.9	17.8	28.4	18.1	17.4	2.7	2.3	10.19
Longnose gar	0.1	0.0	0.0	<0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.02
Bowfin	0.0	0.0	0.0	<0.1	0.0	0.0	0.0	0.0	<0.1	0.0	<0.01
Mooneye	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00
Quillback	4.0	18.6	1.8	2.0	2.4	5.6	2.0	1.9	1.7	1.8	4.18
Stonecat	<0.1	<0.1	0.0	0.1	0.0	0.0	0.1	<0.1	<0.1	<0.1	0.03
Total	449.7	461.4	713.6	593.3	240.1	396.3	212.0	291.9	90.4	70.2	416.04

Appendix 4. Mean number of walleye caught per trap-net day in Lake St. Clair, 1972–85

Age	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	Mean
								Year							
2	2.76	0.20	0.51	0.02	1.26	0.72	0.22	4.84	0.08	3.21	0.97	1.48	3.44	0.04	1.41
3	0.57	3.92	0.44	1.06	0.22	2.72	1.87	0.14	11.32	1.28	1.36	4.16	0.81	8.33	2.73
4	1.11	0.46	2.64	0.52	1.07	0.15	1.67	0.80	0.44	9.46	0.46	0.96	1.58	0.41	1.55
5	0.35	0.46	0.32	1.43	0.60	1.10	0.40	1.02	0.83	0.34	2.40	0.49	0.52	0.77	0.79
6	0.54	0.19	0.42	0.31	1.53	0.49	3.49	0.59	0.53	0.25	0.08	1.11	0.27	0.28	0.72
7	1.46	0.21	0.30	0.31	0.17	1.70	1.60	0.44	0.44	0.23	0.06	0.06	0.52	0.20	0.55
8	0.51	0.61	0.25	0.18	0.19	0.11	1.60	1.16	0.33	0.18	0.15	0.06	0.02	0.15	0.39
9	0.16	0.12	0.86	0.08	0.09	0.06	0.22	0.18	0.19	0.13	0.08	0.04	0.00	0.02	0.16
10	0.00	0.05	0.08	0.41	0.02	0.00	0.22	0.01	0.03	0.07	0.09	0.05	0.02	0.01	0.08
11	0.10	0.05	0.04	0.04	0.02	0.06	0.12	0.06	0.00	0.03	0.02	0.02	0.00	0.00	0.04
12	0.06	0.01	0.12	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.00	0.02
13	0.00	0.01	0.02	0.00	0.00	0.00	0.05	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.01
14	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	<0.01
Sum	7.61	6.32	5.99	4.36	5.15	7.12	11.48	9.26	14.21	15.19	5.69	8.44	7.19	10.23	8.45
Net days	73	111	143	216	105	129	79	141	110	61	84	184	190	194	130

Appendix 5. Mean number of walleye caught per trap-net day in Lake Erie, 1978–87.

Age	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	Mean
1	0.18	0.00	0.04	0.10	0.03	0.16	0.00	0.02	0.30	0.16	0.10
2	0.38	26.03	3.46	4.65	11.99	7.14	14.29	0.83	10.02	7.12	8.59
3	6.29	0.58	3.69	2.46	1.84	4.06	3.17	38.02	2.22	5.39	6.77
4	3.40	4.42	0.20	2.78	1.47	0.67	2.20	2.55	27.78	1.25	4.67
5	0.25	0.81	0.45	0.16	2.10	0.47	0.41	1.60	2.29	9.91	1.84
6	0.32	0.12	0.14	0.44	0.29	0.73	0.23	0.68	0.83	0.77	0.45
7	0.00	0.12	0.02	0.12	0.27	0.08	0.51	0.25	0.20	0.52	0.21
8	0.00	0.12	0.02	0.04	0.12	0.14	0.05	0.31	0.41	0.19	0.14
9	0.00	0.00	0.00	0.00	0.01	0.02	0.05	0.15	0.11	0.15	0.05
10	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.04	0.02	0.01	0.01
11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00
12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00
Total	10.82	32.19	8.03	10.77	18.13	13.49	20.91	44.45	44.22	25.48	22.85
Net days	130	87	97	71	84	106	85	85	70	73	89

Appendix 6. Mean number of walleye caught per gill-net gang in Lake Erie, 1978–87

	Year										
Age	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	Mean
1	91.00	19.00	44.00	43.00	33.50	29.00	4.50	69.75	98.00	96.75	52.85
2	7.00	37.00	25.00	13.50	21.50	21.25	91.75	12.00	34.25	42.50	30.58
3	25.75	5.25	22.67	6.00	5.00	14.50	7.75	95.75	4.00	20.50	20.72
4	8.25	10.50	2.83	9.00	5.50	4.25	5.00	3.75	44.25	5.00	9.83
5	0.50	3.50	3.50	1.00	5.00	2.50	2.25	5.25	2.75	28.50	5.48
6	0.75	0.25	0.33	2.00	1.50	2.50	1.75	2.00	2.25	2.25	1.56
7	0.00	0.00	0.17	1.50	0.50	0.25	3.00	0.50	0.50	0.50	0.69
8	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.50	1.25	0.50	0.24
9	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.50	0.25	0.00	0.13
Total	133.25	75.50	98.67	76.00	72.50	74.25	116.50	190.00	187.50	196.50	122.07

Appendix 7. Average annual harvest by walleye anglers in the Lake Erie-Lake St. Clair system, tag recovery ratios, stock composition estimates (from tag recovery ratios), and approximate composition of the harvest by numbers.

Area	Average annual harvest	Tag recovery ratio[1]	Percent Lake Erie[2]	Lake Erie walleye	Lake St. Clair walleye
Lake Erie	7 million	740/776	95	7 million	trace
Lake St. Clair	132,000	60/782	8	10,560	121,440
Northern St. Clair River	120,000	—	23	27,600	92,400
Detroit River	164,000	167/239	70	114,800	49,200
Total				7 million	263,000

[1]The ratio of the number of walleye harvested in a particular area that were tagged in Lake Erie to the total number of tags recovered in that area.

[2]Derived from the tag recovery ratio, except that the northern St. Clair River estimate is from the genetic analysis (see text).

Appendix 8. Number of walleye with reward tags and the number reported by anglers in subsequent years from Lake St. Clair.

Recovery year	Reward tag value				Reward	Non-reward
	$2.00	$4.00	$6.00	$8.00		
1981 Tags						
1981	5	6	9	4	24	22
1982	4	2	3	4	13	22
1983	1	3	0	1	5	6
1984	0	0	0	3	3	3
1985	1	2	0	1	4	2
1986	0	1	0	0	1	1
1987	0	0	0	0	0	0
Number tagged	79	77	80	81	317	650
Total number recovered	11	14	12	13	50	56
Percent recovery	13.92	18.18	15.00	16.05	15.77	8.62
1982 Tags						
1982	3	3	9	5	20	15
1983	1	3	2	2	8	10
1984	1	2	1	1	5	9
1985	1	4	0	0	5	1
1986	1	0	0	0	1	3
1987	0	0	0	0	0	0
Number tagged	50	48	51	49	198	259
Total number recovered	7	12	12	8	39	38
Percent recovery	14.00	25.00	23.53	16.33	19.70	14.67
1983 Tags						
1983	12	12	9	17	50	94
1984	3	3	8	5	19	40
1985	1	3	2	3	9	9
1986	0	1	1	1	3	3
1987	1	0	0	1	2	5
Number tagged	95	100	100	99	394	1,134
Total number recovered	17	19	20	27	83	151
Percent recovery	17.89	19.00	20.00	27.27	21.07	13.32

Appendix 9. Population statistics for western Lake Erie walleye from the CAGEAN model.

Fishing year	Instantaneous fishing mortality rate	Annual survival rate	Commercial exploitation rate
1978	0.3325	0.5871	0.0316
1979	0.2829	0.6170	0.0406
1980	0.3027	0.6049	0.0678
1981	0.5144	0.4895	0.0818
1982	0.3973	0.5503	0.0705
1983	0.2398	0.6442	0.0920
1984	0.1580	0.6991	0.0532
1985	0.2008	0.6698	0.0632
1986	0.1862	0.6797	0.0510
1987	0.1648	0.6943	0.0373

Fishing year	Angler exploitation rate	Numerical abundance	Numerical catch
1978	0.2263	6,508,554	1,678,292
1979	0.1840	14,545,434	3,266,564
1980	0.1702	14,115,936	3,359,890
1981	0.2861	12,464,676	4,586,210
1982	0.2290	13,212,614	3,956,338
1983	0.1022	12,839,993	2,492,817
1984	0.0796	47,090,436	6,255,436
1985	0.1022	34,934,950	5,779,240
1986	0.1035	35,556,303	5,493,318
1987	0.1008	41,950,221	5,794,971