Factors influencing the Year-Class Strength of Reef Spawned Walleye in Western Lake Erie

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By

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ABSTRACT

FACTORS INFLUENCING THE YEAR-CLASS STRENGTH OF REEF SPAWNED
WALLEYE IN WESTERN LAKE ERIE

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Variation in egg and larval survival have been suspected to be principal sources of

walleye *Stizostedion vitreum* recruitment variability in Lake Erie. I examined walleye egg

deposition and survival and larval vital rates in western Lake Erie in 1994 and 1995.

Densities of eggs and larvae were higher in 1994 than 1995. Growth of larval walleye was

greater in 1994. Larval densities were greater at western sites in 1994 and greater at

eastern and south-eastern sites in 1995. Slow water warming rates and frequent intense

winds contributed to the low density and survival of eggs on reefs in 1995 by prolonging

incubation periods and increasing the vulnerability of eggs to mortality factors. Optimal

year-class strength could result with precisely timed events providing high egg densities,

fast water warming rates and few wind storms in spring providing good egg survival and

high larval densities.

Dedicated to Ma, Dad, EOR,
and Dennis Hugick

ACKNOWLEDGMENTS

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THESIS INTRODUCTION

Walleye (*Stizostedion vitreum*) have supported important sport and commercial

fisheries in Lake Erie for over 150 years (Regier et al. 1969). Commercial landings of

walleye increased steadily through the early part of the 20th century exceeding 6.8 million

kg in the mid 1950's (Figure 1). Catches declined dramatically in the late 1950's when the

population diminished due to exploitation, pollution, and degraded spawning habitat. The

discovery of high levels of mercury in the tissue of walleye prompted closure of the fishery

in 1970 allowing the population to rehabilitate. The fishable stock increased from about

83,000 walleye in 1970 to over 14 million in 1976 (Hatch et al. 1987).

The Lake Erie walleye population is now managed under a quota system allocating

portions of the stock to the Ontario sport and commercial fisheries and sport anglers in

Michigan, New York, Ohio, and Pennsylvania (Koonce et al. 1983). The harvestable

amount of the stock is determined using output from a catch-at-age model relying on

sequential projections of recruitment and reports of withdrawals from the stock (Deriso et

al. 1988).

Lake Erie walleye populations exhibit wide fluctuations in recruitment (Hatch et al.

1987). The abundance of age-2 fish varied as much as 60-fold since 1979 (Figure 2).
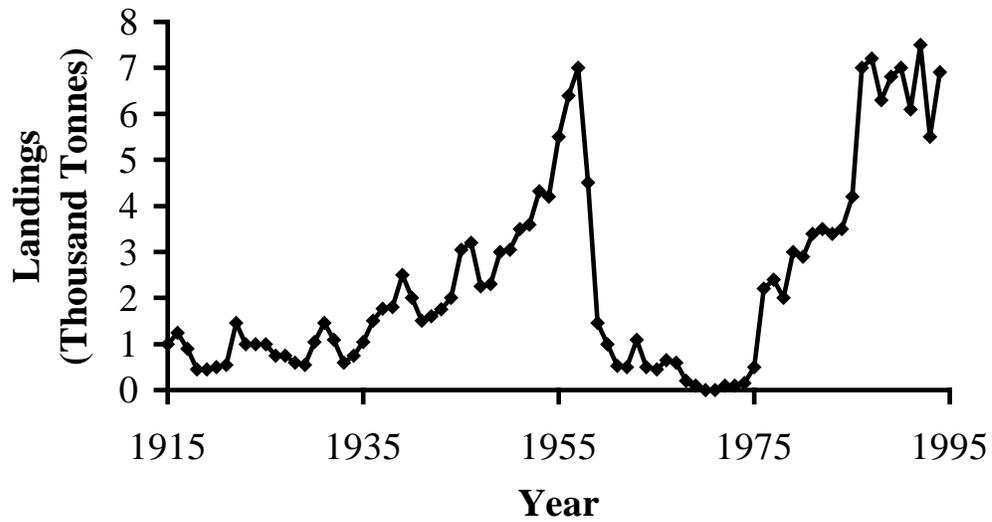
Figure 1. Landings of walleye from United States and Ontario waters of Lake Erie, 1915-1994. Data from Regier et al. 1969; Hatch et al. 1987; Walleye Task Group Report 1995.
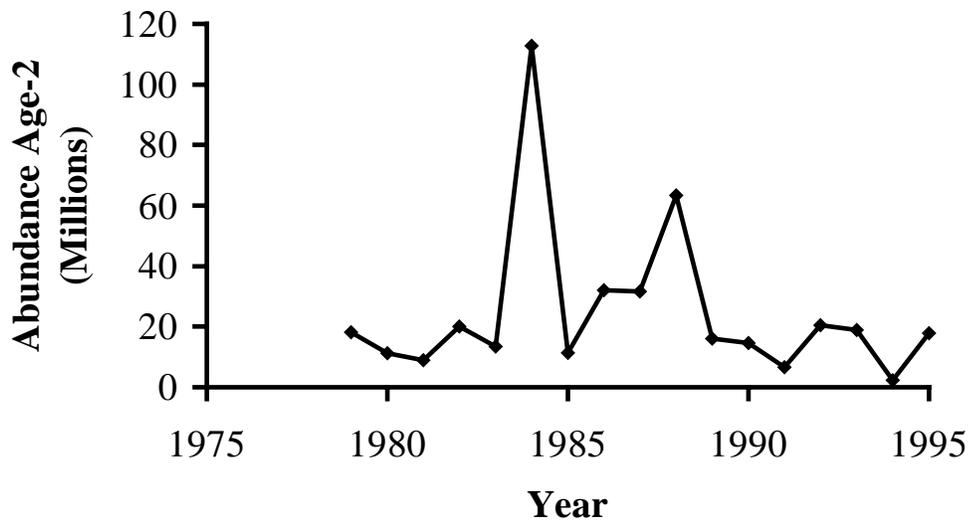
Figure 2. Abundance of age-2 walleye in Lake Erie as determined by CAGEAN model estimates, 1978-1995. Data from 1995 Lake Erie Walleye Task Group Report 1995.

Although causes of Lake Erie walleye recruitment variation are speculative, interannual variation in egg and larval survival is considered the principal source of recruitment variability in many walleye populations (Carlander and Payne 1977; Koonce et al. 1977; Ney 1978; Forney 1980). Density-independent and density-dependent factors that affect egg survival, and growth and survival of individual larval walleye may be the driving force behind year class strength formation in western Lake Erie walleye populations.

Interannual variation in egg survival can contribute to recruitment variation in Lake Erie walleye populations. Many naturally spawning walleye populations experience high levels of mortality during the egg stage (Priegel 1970; Forney 1976, 1980). Substantial egg mortality is thought to be caused by dislodging from severe wind and wave action and temperature reversals during spawning and incubation periods (Johnson 1961; Allbaugh and Manz 1964; Hurley 1972; Busch et al. 1975; Koonce et al. 1977; Forney 1980; Serns 1982). Predation by fishes and invertebrates may also contribute to egg mortality (Carlander et al. 1960; Wolfert et al. 1975). Optimal egg survival occurs when water temperatures increase at a rate of 1 C/day (Smith and Koenst 1975). Incubation periods are lengthened when water warms slowly thereby increasing vulnerability to predation, disease, and dislodging by wind generated currents (Hartman 1969).

Small changes in growth or mortality rates of larval fishes can cause major changes in recruitment (Houde 1987; Madenjian and Carpenter 1991; Madenjian et al. 1991; Jensen 1992; Pepin 1993). Houde (1987) conjects that coarse controls (i.e. nutrition, climatological factors) in the larval stage may have greater impacts on recruitment potential than finer controls (i.e. cannibalism, parasitism) in subsequent stages.

Body size often dictates the survival probability of larval fishes (Miller et al. 1988). Swimming and foraging ability, size of food particles ingested, and susceptibility to starvation and predation are all functions of body size (Houde 1969; Mathias and Li 1982; Serns 1982). Jensen (1992) determined that the earlier in the growing season age-0 walleye achieve a large size the more likely they are to survive and relates faster growth to prey community characteristics. The ability of larval walleye to compensate for small size by increased growth may improve their chance of survival if survival is size selective (Jensen 1992). Additionally, high levels of initial mortality may generate compensatory responses in growth rates of survivors resulting in increased survival to age-1 (Mills and Forney 1988).

Diet directly influences growth and survival of larval walleye (Houde 1967; Forney 1980; Mathias and Li 1982). Experiments have revealed that a critical period for larval mortality due to nutrition deficiency may occur when postlarvae switch from endogenous to exogenous feeding. Larval walleye growth, survival, and amount of exogenous food consumed is a function of fish density and positively related to water temperature and the abundance of adequate sized prey (Li and Mathias 1982; Fox 1989; Moodie et al. 1989).

Noble (1972) discovered that larval walleye in Oneida Lake, New York became concentrated in protected bays as a result of wind generated currents. Foraging success of larval walleye in bays is determined by variations in prey densities common to large lakes (Watson 1976; Patalas and Salki 1992). High prey densities can enhance growth rate and increase larval survival (Houde 1987) whereas low prey densities can result in delayed growth rate and increased mortality (Crowder et al. 1987).

Variability in year class strength of many fish species in large aquatic ecosystems is primarily caused by variation in growth and survival during the early life stages. Relatively small changes in growth and survival rates of these early life stages can translate into large annual fluctuations in subsequent year-class strength (Houde 1987). My hypotheses is that a combination of abiotic and biotic factors occurring during the incubation and pelagic larval stages is important in controlling the year-class strength of walleye in western Lake Erie. The goal of this project was to measure important parameters during the early life history stages to allow for the identification of causal mechanisms controlling year-class formation of walleye. My specific objectives were to:

1.   Estimate walleye egg abundance and survival at selected depths and substrate types on mid-lake spawning reefs.

2.   Estimate larval walleye abundance, distribution, and growth in areas adjacent to mid-lake spawning reefs.

3.   Quantify diet of larval walleye and diet's influence on larval growth rate.

4.   Monitor forage community composition and abundance.

5.   Quantify abiotic factors (temperature, wind events, substrate morphology) during walleye egg incubation and larval development period and relate to walleye survival, growth, and recruitment success.

Study Area

The study area encompasses the area of western Lake Erie located between latitudes N 41° 30' to N 41° 43' and longitudes W 82° 50' to W 83° 14'.

The mid-lake reef complex is located between latitudes N 41° 37' to 41° 40' and longitudes W 82° 57' to 83° 06' (Figure 3). Detailed descriptions of egg and larval sample locations are given in each chapter. Latitude and longitude coordinates for egg and larval sampling sites are listed in Appendix 1.

Physical and chemical characteristics of western Lake Erie are well documented (Herderndorf and Braidech 1972; Boyce et al. 1987). The western basin has a mean depth of 7.4 m and a total surface area of about 3,700 km^2. Mean water residence time is about 2.4 months (Burns 1985). Generally, the western basin is isothermal throughout the year due to mixing of its shallow waters and seldom becomes anoxic. Bottom substrates consist primarily of sand and clay, although dolomite limestone forms several major reef complexes including Toussaint and Niagara reefs (Herdendorf and Braidech 1970).

Walleye are the dominant predator in the western basin supported by a prey base of gizzard shad (*Dorosoma cepedianum*), alewife (*Alosa pseudoharengus*), shiners (*Notropis atherinoides* and *N. husonius*), white perch (*Morone americana*), white bass (*Morone chrysops*), and yellow perch (*Perca flavescens*). Other common fish species include carp (*Cyprinus carpio*), freshwater drum (*Aplodinotus grunniens*), rainbow smelt (*Osmerus mordax*), channel catfish (*Ictalurus punctatus*), and suckers (Catostomidae) (Knight and Vondracek 1993).
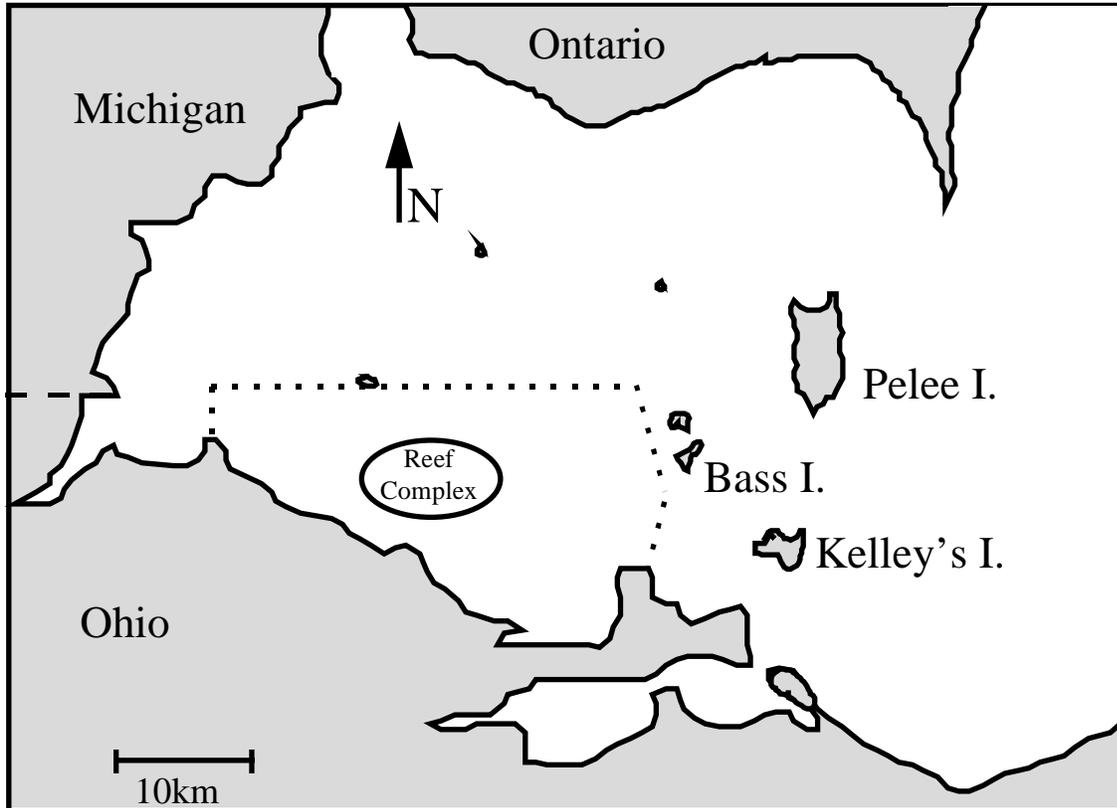
Figure 3. Map of western Lake Erie study area. The dashed line delineates the extent of larval sampling and the ellipse encompasses the mid-lake reef complex.

Chapter 1

WALLEYE EGG DEPOSITION AND SURVIVAL ON REEFS
IN WESTERN LAKE ERIE

Abstract

Variation in egg survival has been suspected to be a principal source of walleye *Stizostedion vitreum* recruitment variability in Lake Erie. I sampled walleye eggs and larvae in western Lake Erie in 1994-95. Densities of eggs and larvae were higher in 1994 than 1995. Mean egg density peaked at over 8,000 per 2-min tow in 1994 and only 2,700 per 2-min tow in 1995. Egg survival for depths and reefs pooled averaged 37% in 1994 and 13% in 1995. I found white perch *Morone americana* to consume large numbers of walleye eggs on reefs in 1995. Mean density of larvae from the date of first hatch through the end of May was 14 times higher in 1994 than 1995. Relatively slow water warming rates and frequent intense winds contributed to the low density and survival of eggs on reefs in 1995 by prolonging incubation periods and increasing the vulnerability of eggs to predation and severe wind events.

Introduction

Lake Erie walleye *Stizostedion vitreum* populations exhibit wide fluctuations in recruitment (Hatch et al. 1987). Interannual variation in egg deposition and survival are considered major sources of recruitment variability for many walleye populations (Carlander and Payne 1977; Koonce et al. 1977; Ney 1978; Forney 1980) as many naturally spawning walleye populations experience high levels of mortality during the egg stage (Priegel 1970; Forney 1976, 1980). Observed egg survival rates range from 0.00003 in Spirit Lake, Iowa (Jennings 1969) to 0.357 in Lake Winnibigoshish, Minnesota (Johnson 1961). Substantial egg mortality is thought to be caused by dislodging from severe wind and wave action during spawning and incubation periods (Johnson 1961; Busch et al. 1975; Koonce et al. 1977; Forney 1980; Serns 1982). Walleye egg survival has also been directly related to fluctuations in water temperature during incubation periods (Johnson 1961; Allbaugh and Manz 1964; Hurley 1972; Serns 1982), with optimal egg survival occurring when water temperatures increase from 5° C at a rate of 1° C/day (Smith and Koenst 1975). Incubation periods are lengthened when water warms more slowly, thereby increasing vulnerability to severe wind events and predation. Faster warming rates shorten incubation time and reduce the time eggs are vulnerable to detrimental factors (Carlander et al. 1960; Hartman 1969; Wolfert et al. 1975).

Research investigating walleye egg deposition on western Lake Erie reefs conducted from 1960 - 70 revealed that walleye spawning usually peaks during the third

week of April when water temperatures range from 5.4 to 8.3° C (Baker and Manz 1971).

Walleye spawning and egg density were higher at depths < 5 m where hard substrates

persist which walleye actively spawned over. No relationship was observed between egg

deposition, viability, and year class strength, but a direct relationship between walleye

year-class strength and water temperatures was observed (Busch et al. 1975) with the

strength of the incoming year-class being inversely proportional to incubation time (Baker

and Manz 1971; Busch et al. 1975).

In this chapter I investigate walleye egg deposition and survival across a range of

depths on Toussaint and Niagara reefs in western Lake Erie in 1994 and 1995. I examine

the hypothesis that environmental factors influence walleye egg survival and that year

class strength is strongly related to egg abundance and survival.

Study Area Description

Toussaint and Niagara reefs are the largest reefs among a large bedrock reef

complex located in the western basin of Lake Erie (Figure 4). This complex of reefs

encompasses over 70 km^2 of surface area and extends to within 1.5 m of the surface. The

surfaces of the reefs have numerous crevices and cavities as well as a varied substrate

composition ranging from silt to boulders and exposed bedrock. The relative shallowness

of the reefs allows their surface to be scoured by ice movements as well as wind-

generated wave and current action. The lake bottom surrounding the reefs has low relief

at depths from 7 to 10 m and is covered with silt and mud (Hartley 1961; Herdendorf and

Braidech 1970; Bolsenga and Herdendorf 1993).
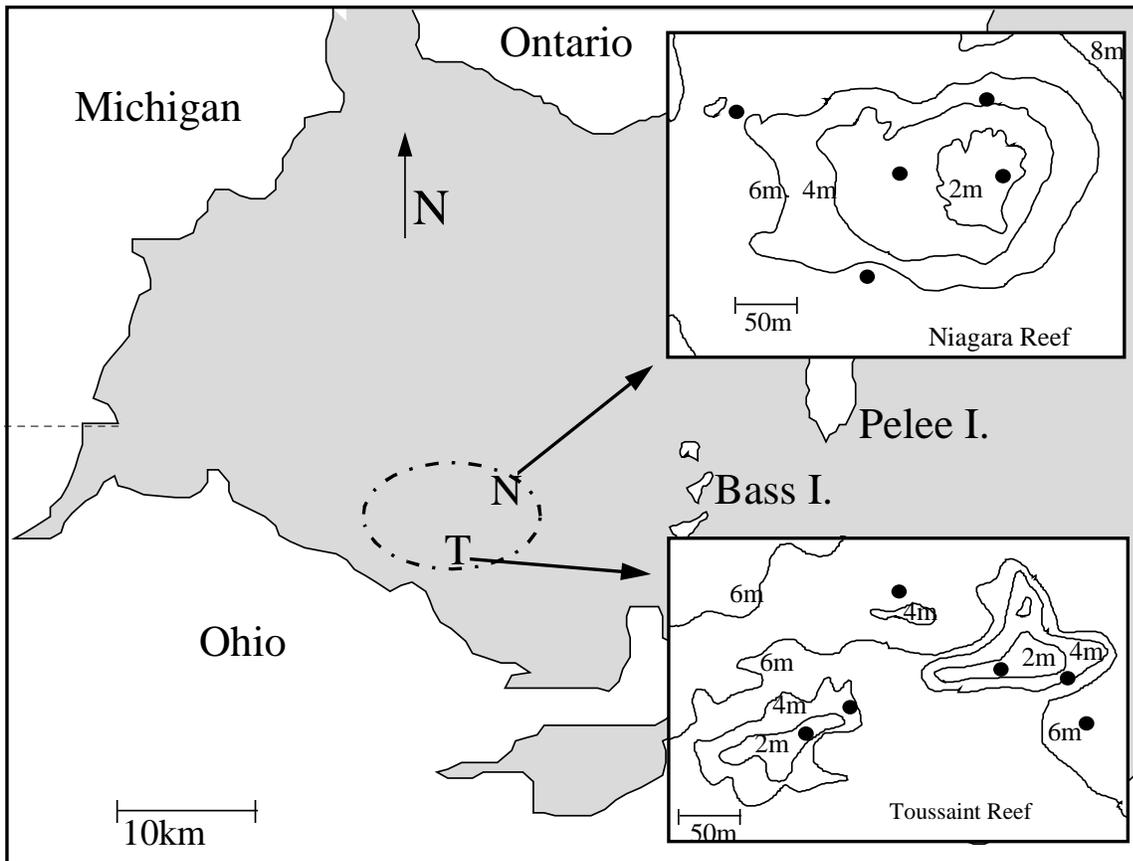
Figure 4. Map identifying egg sampling reefs; N = Niagara reef; T = Toussaint reef. Inlays are bathymetric representations of Niagara and Toussaint reef; filled circles represent egg sampling sites.

Methods

Egg Collection

I sampled walleye eggs during 1994 and 1995 on Toussaint and Niagara reefs

beginning in late March and continuing through to mid-May when spawning ceased and

catches of walleye eggs were negligible. I used a 39-kg iron sled (0.25 m wide) attached

to a diaphragm pump at the surface by a flexible hose 5 cm in diameter for egg

collections (Stauffer 1981). At each site, the sled was towed for 2 min at 0.5 m/s,

typically sampling 15 m^2 in area. Egg sampling was stratified by depth to examine egg

deposition patterns; depths of < 3 m, 3-5 m, and 5-7 m were sampled (Figure 4). These

depth strata encompass the range of depths where walleye eggs were collected in a

previous study (Baker and Manz 1971). Three samples were taken at each sampling site

on each sampling day. I located sample sites by global positioning system coordinates

and marked them with an anchored buoy.

Eggs and benthic debris (Dreissenid mussels and shells, sand, benthic organisms)

were deposited from the pump apparatus into a 0.5 m^3 basket lined with 0.5 mm square

mesh netting. The net liner containing the sample was then removed and placed in a

labeled plastic bag. Samples were refrigerated at 5° C until they could be sorted at the

laboratory 2.5 to 24 hours later. I found no indication that delays in processing of up to

24 hours influenced viability or survival estimates.

At the laboratory, samples were rinsed through a galvanized steel wire screen (6

mm bar mesh) to separate large debris from finer particles and eggs. The small

particulate matter was then examined for walleye eggs which were counted entirely or subsampled. A single subsample was taken when there appeared to be more than 1,000 eggs in the total sample. Subsamples were typically 10% of the mass of the drained fine particulate matter. Identification of eggs was based on egg diameter (mm), egg color, and subsequent hatching of eggs. I found 3 sizes of eggs on the reefs during this study; 3 mm, 2 mm, and 1.5 mm. Several eggs of each size category were placed in aquaria with aerated lake water and incubated at 15° C. Hatched larvae were identified according to Auer (1982). Collected eggs were examined with 10X magnification for viability and measured (nearest 0.1 mm) before being preserved in Stockards solution (Galat 1972). All eggs that were ruptured or showed signs of opaqueness or fungal growth were classified as dead eggs. All clear or eyed eggs were classified as viable eggs.

Walleye eggs were classified by developmental stage (Nelson 1968; McElman and Balon 1979) using a phase-contrast microscope with variable magnification. Stage 1 eggs are pre-organogenesis stage (28 thermal units (TU); a thermal unit is each degree C above a daily base temperature of 0° C; Allbaugh and Manz 1964) and stage 3 eggs are late embryonic stage with developed eyes, pectoral fin buds, and caudal mesenchyme rays as well as chromatophores along the ventral line and yolk sac (>97 TU). Stage 2 eggs show intermediate development. Hatching normally occurs when at least 115 TU's have accumulated (Nelson 1968; Hurley 1972; McElman and Balon 1979). Egg survival ($\underline{s}$) was estimated as

$$\underline{s} \ = \ (\text{\# stage 3 on day } \underline{x} \ ) / (\text{\# stage 1 on day 0})$$

Day $\underline{x}$ was a function of the temperature dependent development rate. I pooled egg

survival data from all depths on each reef because wind and wave action displaced eggs

from shallow sites to deep sites over the study period.

Egg Production

  I estimated total walleye egg production on each reef by summing the numbers of

stage 1 eggs collected from each depth stratum on Toussaint and Niagara reefs

individually over the course of the incubation period. Egg numbers were then

extrapolated using the amount of area each depth stratum contributes to each reef

(Bolsenga and Herdendorf 1993) to estimate the number of eggs deposited on each reef as

well as on the entire reef complex. I estimated the total number of stage 1 eggs deposited

by linear extrapolation between sampling dates and adjusting these numbers based on

temperature dependent development rates (Allbaugh and Manz 1964). I calculated the

mean number of stage 1 eggs using the Toussaint and Niagara reef data and then applied

these means to estimate egg production on other reefs in the complex. Because the egg

pump applies suction only 50% of the time due to the action of the diaphragm pump, I

doubled my estimates of egg production to account for the reduced effort of the gear.

  I estimated total potential fecundity for the entire Lake Erie walleye population

using age-specific fecundities reported by Muth and Ickes (1993) and stock size estimates

derived from the CAGEAN model (Lake Erie Walleye Task Group 1995). I assumed a

1:1 sex ratio and estimated the numbers of age-7, 8, 9, 10, and 11 fish by expanding the

CAGEAN model estimates beyond the reported value given for age-7+ fish (Appendix 2).

Physical, Limnological, and Climatological Parameters

Water temperatures (^{o}C) on the reef complex were recorded with continuous monitoring thermographs (Ryan Instruments, Inc.). Bottom dissolved oxygen was measured on the bottom at each sampling site using a calibrated YSI Model 50B dissolved oxygen meter. Secchi disk readings (nearest 0.1 m) were taken at each egg sampling site as an index of water clarity. Wind direction, intensity, and duration at South Bass Island, Ohio were recorded daily from the National Oceanographic and Atmospheric Administration weather observation broadcasts. Additional wind speed and direction data recorded at South Bass Island were obtained from the National Climatological Data Center in Asheville, North Carolina. I used criteria described by Busch et al. (1975) to determine the significance of wind events. Busch et al. examined a time series of water temperature and wind direction and intensity data from western Lake Erie and concluded that winds from N to NE exceeding 14.5 km/h, from the S to SW exceeding 17.5 km/h, and from the W to NW exceeding 20.5 km/h mixed western basin waters enough to reduce water temperatures by 0.5^o C/day and be detrimental to incubating walleye eggs.

Substrate composition on the reefs was examined by SCUBA diving at each egg sampling site. Divers measured substrate composition at three to five points at each egg sampling site in 1994 and 1995. Substrate particle sizes are based on the modified Wentworth scale (Cummins 1962).

Egg Predator Diet Examination

Variable mesh gillnets were fished overnight on Toussaint reef during the peak

spawning period in 1994 and 1995 to collect potential walleye egg predators. Two 40 m

gillnets were fished simultaneously in 1994 and 3 were fished in 1995. The nets

consisted of a single 8 m x 2 m panel of each of the following stretch mesh sizes: 2.2 cm,

4.4 cm, 5.5 cm, 6.6 cm, and 8.8 cm. Gillnets were fished on the bottom in 2.3 m to 4.2 m

of water on Toussaint reef. Upon capture, potential egg predators were measured to the

nearest 1 mm and stomachs were removed and preserved in 10% formalin. I counted all

eggs in stomachs anterior to pyloric caecum and in the anterior portion of the gut prior to

the first flexure for greater redhorse sucker *Moxostoma valenciennesi*. Identification of

eggs in fish stomachs was based on egg size. I matched egg sizes observed in stomachs

with concurrent catches from egg pump samples. I also examined the gut contents of

fishes captured incidentally in egg pump samples in 1995. These fish were preserved

whole in 10% formalin and dissected later.

Larval Abundance

I used a 2.0 m^2 framed ichthyoplankton net fitted with 583 mm mesh netting to

sample pelagic larval fishes. A flow meter was positioned in the center of the mouth of

the net to record the volume of water sampled. The net was towed in the upper 2.0 m of

the water column at approximately 1.0 m/sec. for 5 min. I sampled from 15 to 40 sites

(Figure 5) per sample day and typically filtered 600 m^3 of water during each tow. Larval

fishes were preserved in 95% ethanol and identified following Auer (1982). Catches of

larval fish were Log_e (x+1) transformed to produce normalized data with homogeneous variance (O'Gorman 1984). I used mean larval density for the period from the first hatch through 31 May as an index of larval abundance to compare between years.

Index of Year-Class Strength

I use the catch of age-0 walleye in the Ohio Division of Wildlife's assessment bottom trawls in August (Ohio Division of Wildlife 1996) as an index of relative year-class strength.

Statistical Analysis

I calculated weighted averages of the numbers of walleye eggs collected per 2 min tow on each reef using the proportion of the reef surface area shallower than 7.0 m that each depth strata contributes to the total area as weighting factors. Surface area proportions were estimated from bathymetric maps of the reefs (Herdendorf and Braidech 1970). I used analysis of variance to test for differences in egg viability between depth strata and reefs. I used analysis of variance in the form of a general linear model (SAS 1985) to detect differences in the numbers of eggs collected per 2 min tow between depth strata and reefs. In all analyses I used an α - level of 0.05.
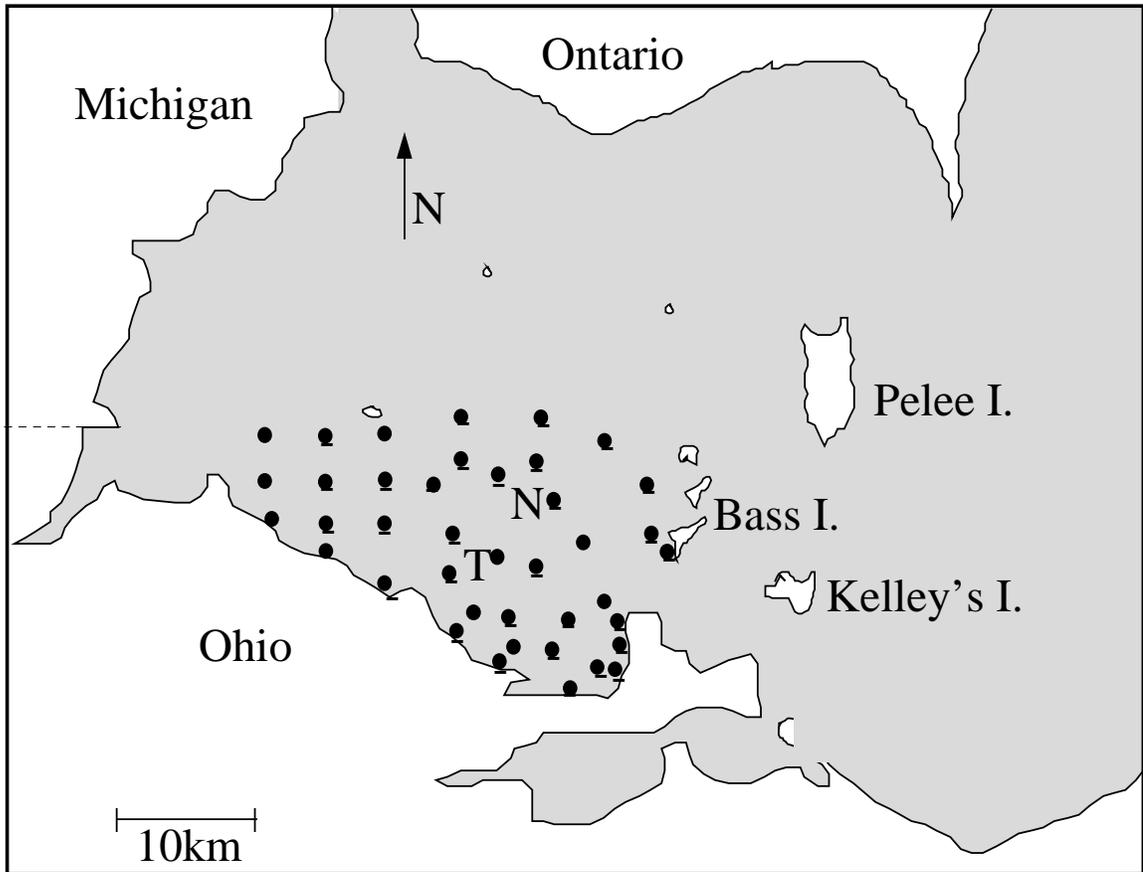
Figure 5. Map of western Lake Erie identifying larval sampling sites (filled circles).

Results

Reef Substrates

Substrate composition varied at each depth stratum on both reefs. In general, the

upper portions of the reefs (< 3 m) were composed of primarily large and small cobble (>

10 cm) and coarse gravel with little or no sand and silt. Sites with depths 3-5 m had

highly variable substrates ranging from 40% exposed bedrock to 50% silt. Silt depths at

the 3-5 m sites ranged from 0 to 20 cm. Gravels, cobbles, and boulders composed from 5

to 50% of the substrate at these sites.   Sites 5 - 7 m deep were observed to have from 50 -

75% silt ranging from 2 to 40 cm deep with a conglomeration of gravels and small

cobbles underneath.

Walleye Egg Deposition

Reefs were first sampled on 31 March 1994 but no walleye eggs were collected.

Walleye eggs first appeared in samples from all depths at both reefs on 8 April 1994

when the water temperature was $4.2\,^{o}$ C. In 1994 only walleye eggs were collected until

18 May when yellow perch *Perca flavescens* and *Morone* spp. eggs also appeared in the

samples. Equipment failure prevented any egg sampling between 28 April and 17 May

1994. In 1995, walleye eggs first appeared in samples on 31 March when the water was

$4.8\,^{o}$ C. No samples were taken prior to this date in 1995.   In 1995, lake whitefish

Coregonus clupeaformis eggs were collected in the earliest samples and yellow perch,

Morone spp. and sucker (Catostomidae) eggs were collected in late April and May. Lake

whitefish eggs were the only large eggs (> 3.0 mm) identified. Walleye and sucker eggs accounted for all the intermediate sized eggs (approximately 2.0 mm), but were easily distinguished because sucker eggs have a much darker pigmentation than walleye eggs which are clear to yellow. The smallest eggs (< 1.5 mm) were those of yellow perch and *Morone* spp.

Walleye egg density peaked on 20 April 1994 on Toussaint reef, and on 10 April 1994 on Niagara reef when an average of over 11,300 and 5,500 eggs were collected per 2 min tow respectively (Figure 6). Viable eggs persisted in samples at all sites through 18 May 1994 when less than 100 walleye eggs were collected per 2 min tow.

Egg densities were roughly 50% lower on Toussaint and Niagara reefs in 1995. Densities peaked on Toussaint reef on 24 April 1995 and on 21 April 1995 on Niagara reef when only 3,300 and 1,900 eggs were collected per 2 min tow respectively (Figure 7). Viable walleye eggs were collected through 17 May 1995 when less than 50 walleye eggs were collected per 2 min tow.
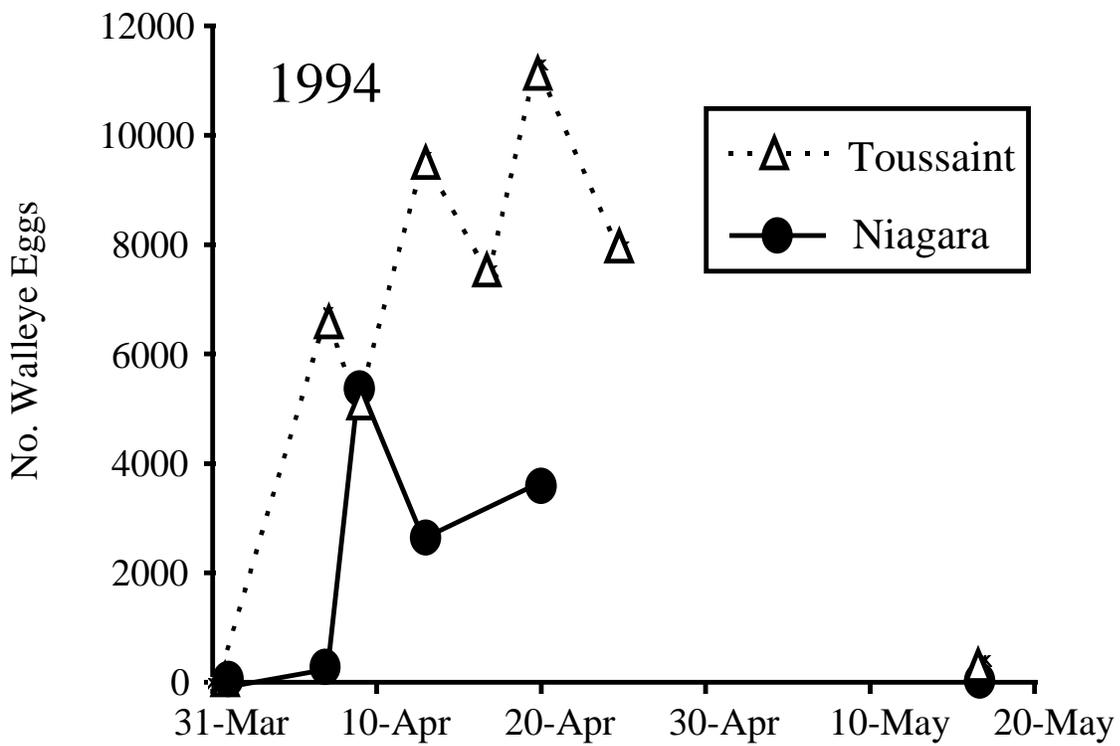
Figure 6. Weighted mean numbers of walleye eggs collected per 2 - min tow on Toussaint and Niagara reefs, 1994. No eggs were collected in samples taken on 31 March 1994; no egg samples were taken between 28 April and 17 May 1994.

In 1994, egg density was generally higher at sites < 5 m deep than at sites 5 - 7 m

on both reefs (p < 0.05) (Figure 8) but in 1995, significantly more eggs were collected

from sites < 5 m deep only on Toussaint reef (p<0.05).   No significant difference in egg

densities between depths was observed on Niagara reef in 1995 (p = 0.17), however,

more eggs were collected from sites < 5 m deep on Niagara reef until 2 May when the

deeper sites were observed to contain more eggs (Figure 9). Significantly more eggs were

collected per unit effort from Toussaint reef than Niagara reef in both 1994 and 1995

(mean = 3,907 and 1,734 per tow respectively for 1994 and 1,874 and 880 per tow

respectively for 1995; p < 0.05).

Walleye Egg Viability and Survival

Egg viability estimates were generally higher in 1994 than 1995 (Figure 10) with

the exception of three sample dates in mid-April 1995. Egg viability ranged from 41 to

74% between depths and reefs over the 1994 sampling period (mean = 56%) and did not

differ significantly between depths or reefs (ANOVA; p = 0.51). In 1995, walleye egg

viability ranged from 6 to 76% across the sampling period and did not differ significantly

between depths or reefs (ANOVA; p = 0.29). Viability estimates generally increased in

early April 1995 reaching 70% by mid-April and declined to less than 40% in late April

and May.
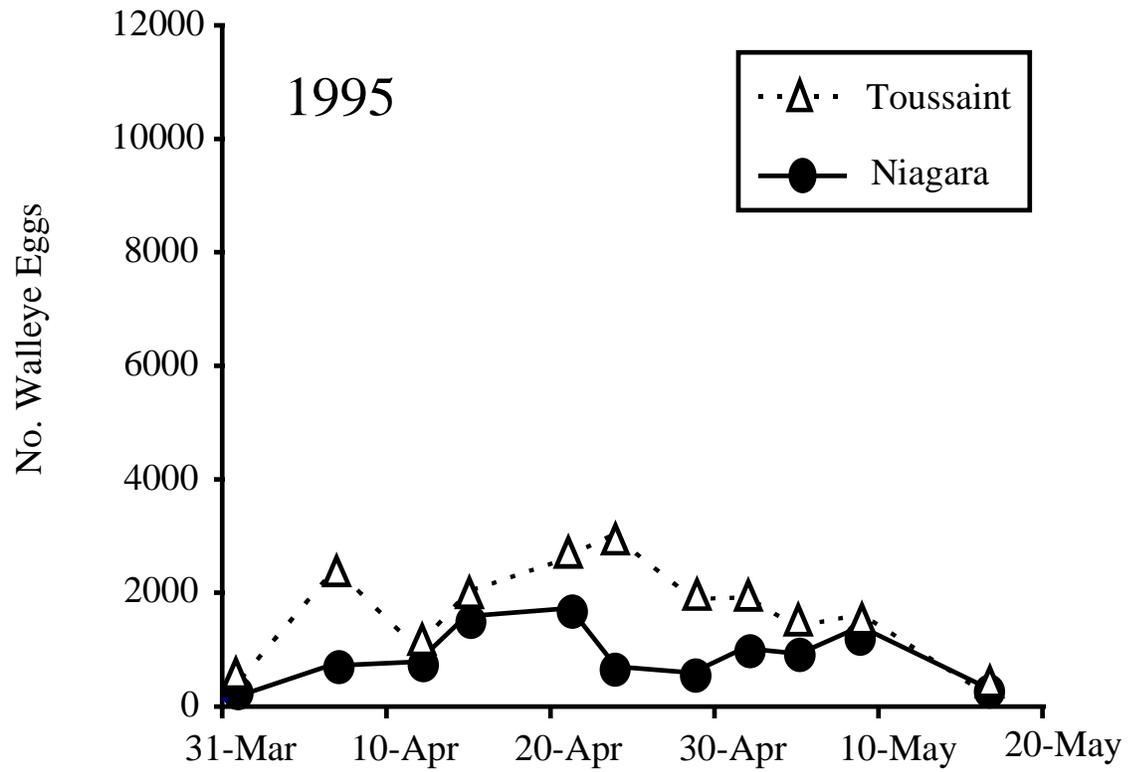
Figure 7. Weighted mean numbers of walleye eggs collected per 2 - min tow on Toussaint and Niagara reefs, 1995.
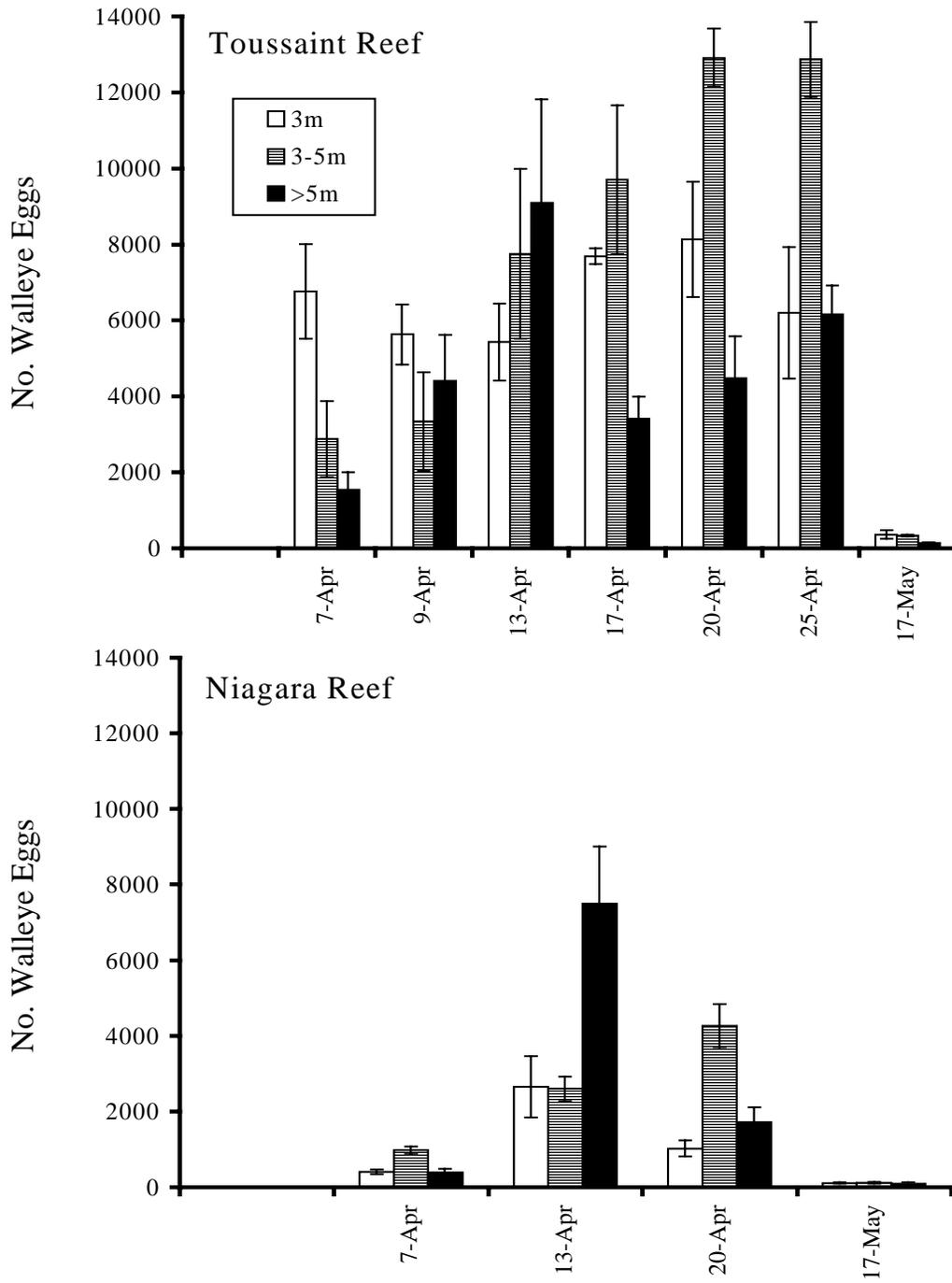
Figure 8. Mean numbers of walleye eggs (± 1 S.E.) collected per 2 - min tow from different depth strata on Toussaint and Niagara reefs, 1994.
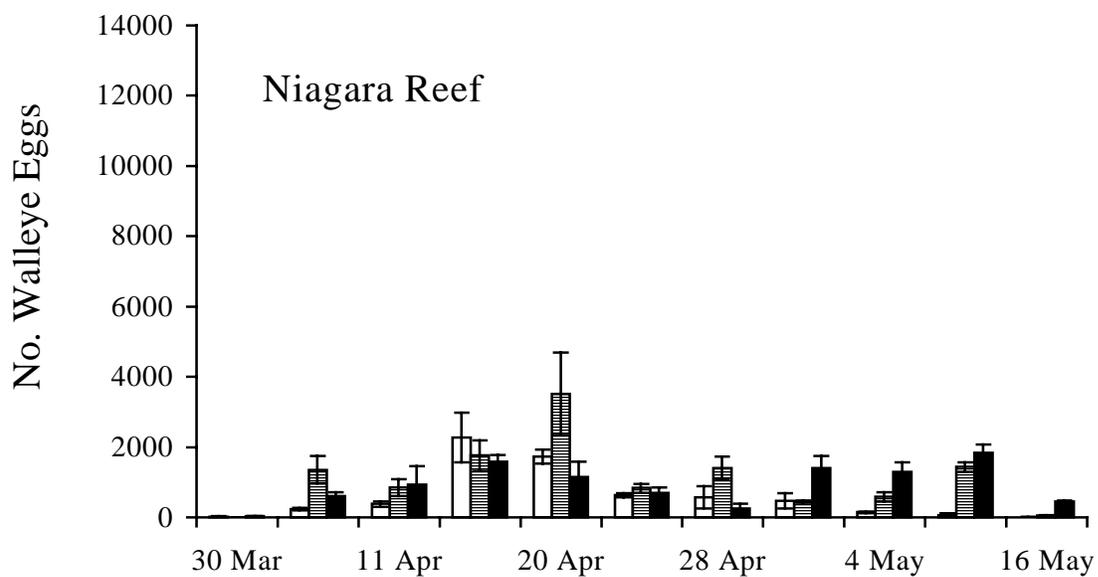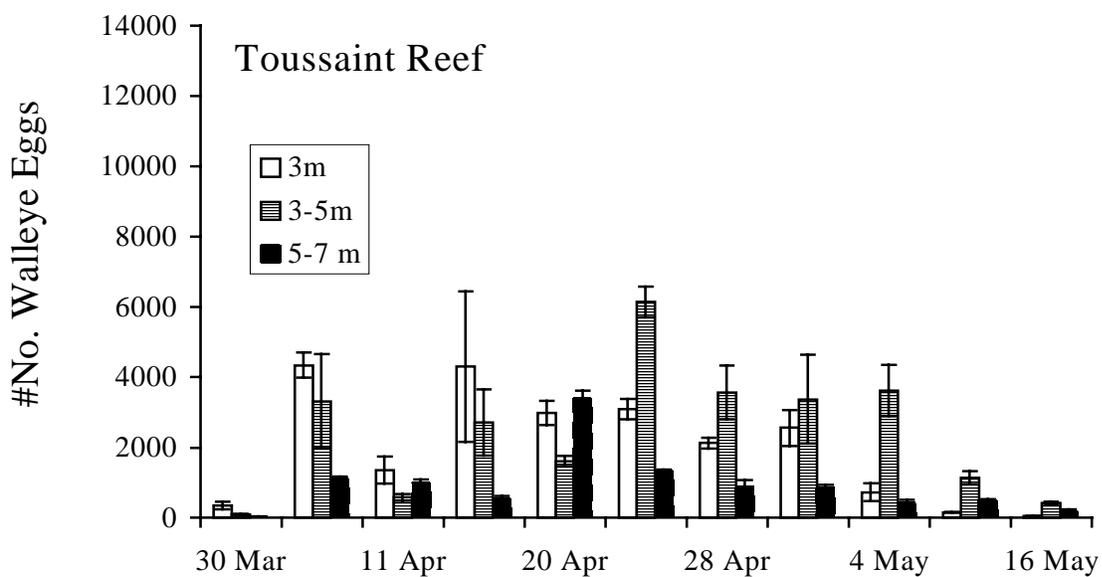
Figure 9. Mean numbers of walleye eggs (± 1 S.E.) collected per 2 - min tow from different depth strata on Toussaint and Niagara reefs, 1995.

Estimates of walleye egg survival were higher in 1994 than 1995. My samples allowed for a single estimate of egg survival from 10 April to 21 April 1994 (102 TU's). Egg survival for pooled depths was calculated at 43% for Toussaint reef and 30% for Niagara reef and did not differ significantly between reefs (p=0.48). I calculated 2 separate survival estimates for each reef in 1995. Walleye egg survival to stage 3 for the period 7 April through 29 April 1995 (99 TU's) was estimated at 14 % for Toussaint reef and 7 % for Niagara reef. Survival for the period 15 April through 9 May (113 TU's) was estimated at 16 % and 15 % for Toussaint and Niagara reefs respectively.

Egg Production

Egg production on the entire reef complex was estimated at approximately 47.4 million stage-1 eggs in 1994 and 33.0 million stage-1 eggs in 1995. Toussaint reef was observed to produce 36% of the 1994 total and 26% of the 1995 total, the highest of any of the reefs in the complex (Table 1) and also had higher egg densities than Niagara reef in both years of the study (Figures 6 and 7). These estimates are conservative as they do not account for the efficiency of the egg collecting pump and assume homogenous egg deposition rates across the reef complex for all substrate types. I estimated the total potential fecundity (number of eggs) of the stock to be 2.7 trillion in 1994 and 2.2 trillion in 1995. The potential total fecundity decreased despite an increase in the abundance of the stock (Appendix 2). Changes in the age structure of the stock between the two years account for the decease in fecundity. My estimates of egg deposition on the reef complex
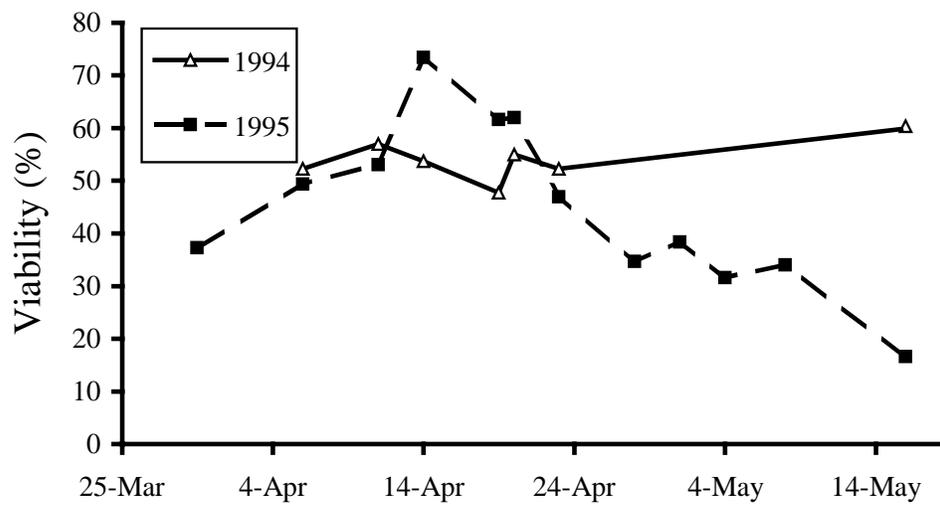
Figure 10. Walleye egg viability estimates for pooled samples from Toussaint and Niagara reefs, 1994 and 1995.

account for less than 0.003 % of the total potential fecundity of the walleye stock in both years.

Table 1. Approximate area < 7m depth and estimated egg production with 95% confidence limits in parentheses for reefs in western Lake Erie, 1994 and 1995. Reef area estimates from Bolsenga and Herdendorf (1993). * indicates reefs that were sampled, all other egg production values are extrapolated.

		Egg Production (millions)	
Reef	Area (m2)	1994	1995
Cone	670	1.95 (1.50-2.40)	1.43 (1.15-1.71)
Crib	850	2.47 (1.90-3.04)	1.81 (1.46-2.16)
Locust	930	2.71 (2.09-3.33)	1.98 (1.59-2.37)
Little Pickerel	720	2.09 (1.61-2.57)	1.53 (1.23-1.83)
Niagara*	2490	2.52 (1.94-3.10)	3.65 (2.94-4.36)
Round	880	2.56 (1.91-3.15)	1.87 (1.51-2.23)
Toussaint*	1229	8.33 (6.41-10.25)	4.27 (3.44-5.10)
Total	7769	22.63 (17.15-28.11)	16.54 (13.31-19.77)

Egg Predator Diet Examination

No fish other than spawning walleye were collected in gillnets fished overnight on

20 and 26 April 1994. In 1995, a total of 49 fish were captured in 3 nights of gillnetting

from 12 April through 3 May and an additional 7 fish were collected with the egg pump

(Table 2). Few fish were captured in gill nets set on 12 April (n = 4) but the catch

increased on subsequent nights, especially of white perch, the most common species

collected.

Table 2. Average numbers of walleye eggs observed in fish stomachs collected from
Toussaint and Niagara reefs, 1995.

Species	# Fish	Mean TL (mm)	# Empty Stomachs	Average # Walleye Eggs	Frequency of Occurrence (%)
Grtr. Redhorse	1	225	1	0	0
Johnny Darter	1	44	0	2	100
Logperch	3	68	1	10	66
Rock Bass	1	195	1	0	0
Sculpin	1	76	0	21	100
Trout Perch	13	107	6	4	38
White Perch	35	225	6	349	86
Yellow Perch	1	81	0	5	100

The stomachs of trout perch *Percopsis omiscomaycus*, yellow perch, log perch *Percina caprodes*, johnny darter *Etheostoma nigrum*, white perch, and an unidentified sculpin (Cottidae) contained walleye eggs. The stomachs of a single rock bass *Ambloplites rupestris* and greater redhorse sucker did not contain walleye eggs. Walleye eggs appeared in 86% of white perch stomachs and each white perch stomach contained an average of 349 walleye eggs (Table 2).

Age-0 Walleye Abundance and Index of Year-Class Strength

I collected the first walleye fry on 29 April 1994 and 3 May 1995. In 1994, the catch peaked on 2 May when I captured 1328 fry in 33 tows for an average density of 95.2 fry / 1,000 m^3 (Figure 11). Equipment failure prevented any larval sampling between 2 May and 18 May 1994. In 1995, the peak catch occurred on 20 May when a total of 87 walleye fry were captured in 40 samples for an average density of 3.5 fish / 1,000 m^3. Mean density of walleye fry for the period from first hatch through the end of May was 14 times higher in 1994 than 1995 (28.4 and 2.0 fry / 1,000 m^3 respectively). The catch of age-0 walleye in assessment bottom trawl surveys in August also demonstrated that the 1994 year-class was stronger than 1995; Ohio Division of Wildlife (1996) reported a catch rate of 18.2 age-0 walleye per hour of trawling in August 1994 and only 1.9 fish per hour in 1995.

Physical, Limnologic, and Climatological Parameters

Water temperatures warmed steadily in April and May 1994. Water temperatures were slightly warmer in late March and early April 1995 but warming was slower than in 1994 (Figure 12). I calculated the average rate of warming per day from 1 April through 15 May which historically encompassed the walleye spawning and incubation periods in western Lake Erie. The average rate of warming per day for this 45-day period was 0.19 $^{\circ}$ C/day in 1994 and 0.18 $^{\circ}$ C/day in 1995. In contrast, the average rate of warming per day from the date eggs were first observed on the reefs to the date fry were first observed in samples was more rapid at 0.22 $^{\circ}$ C/day in 1994 and lower in 1995 at 0.16 $^{\circ}$ C/day.

Major wind events were more frequent in 1995 than 1994 (Table 3). Twenty one days were observed to have winds qualifying as detrimental to incubating walleye eggs in 1995 whereas only 14 days were identified in 1994. Winds were primarily from the W-NW in 1994 whereas E-NE winds predominated in 1995.

Secchi disk readings were generally greater on Toussaint Reef in 1994 than 1995 ranging from 0.3 m to 2.3 m in 1994 and 0.2 to 1.3 m in 1995. On Niagara reef, secchi disk readings ranged from 0.5 m to 1.2 m in 1994 and 0.3 to 1.9 m in 1995. Low secchi readings in 1995 were a result of the continued mixing of the water due to the persistent winds.

Bottom dissolved oxygen levels ranged from 3.8 mg/l to 6.2 mg/l on Toussaint Reef and remained above 5.0 mg/l at all sites on Niagara Reef over the 1994 walleye egg incubation period. In 1995, bottom dissolved oxygen levels were greater than 6.0 mg/l at

all sites on both reefs through 15 April. I observed a decline in bottom dissolved oxygen

levels at sites > 3 m after 15 April when dissolved oxygen levels declined to a low of 1.3

mg/l at one site 5 - 7 m deep on Niagara reef on 17 May.

Table 3. Number of wind events that caused significant mixing of western Lake Erie waters in 1994 and 1995. Wind direction and intensity criteria based on Busch et al. (1975).

Wind Direction and Intensity	1994	1995
N - NE ≥ 14.5 km/h	4	12
S - SW ≥ 17.5 km/h	0	6
W - NW ≥ 20.5 km/h	10	3
Total	14	21
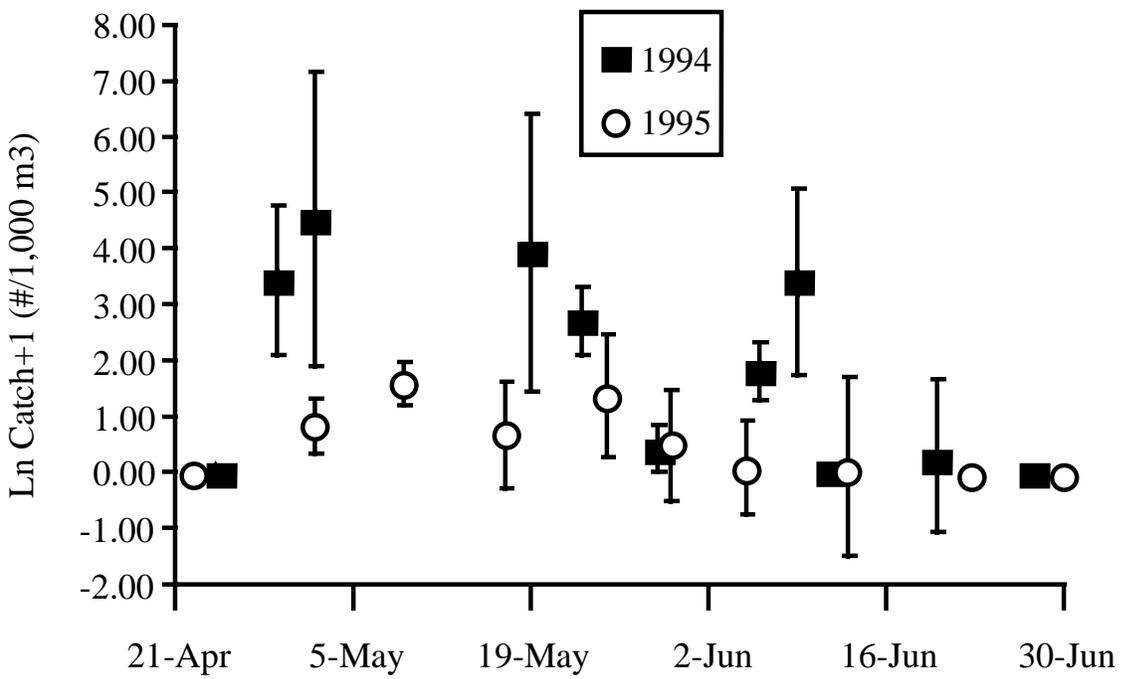
Figure 11. Densities of larval walleye (± 1 s.e.) collected at sites on and adjacent to reef complex in western Lake Erie, 1994-95.
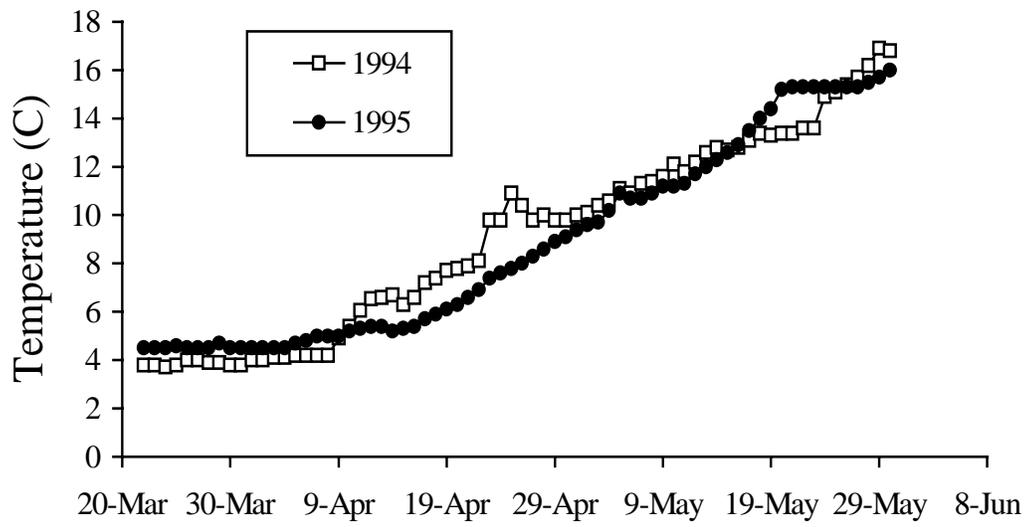
Figure 12. Mean daily water temperatures recorded at Niagara Reef for spring of 1994 and 1995.

Discussion

A combination of frequent intense winds, lower water warming rate, and egg predation appears to have been largely responsible for the reduced egg densities and lower survival rates observed in 1995.   Intense wind events cause mixing of lake waters which retards water warming and creates currents that dislodge walleye eggs from shallow reef substrates and deposit them in areas unsuitable for incubation (Eschmeyer 1950; Johnson 1961; Busch et al. 1975). I observed more intense wind events in 1995, especially winds from the E - NE which have long fetches, contributing to the slow water warming rate and displacing walleye eggs from reef habitats.

Many displaced eggs are likely deposited in deeper waters where silt substrates and reduced bottom dissolved oxygen levels can suffocate the embryos. I observed lower secchi readings in 1995 due to the continued mixing of lake waters caused by the more frequent intense winds. Precipitation of suspended particles from the water column contributes to low bottom dissolved oxygen readings (Zapotsky and Herdendorf 1980) and can cover deposited walleye eggs. I observed bottom dissolved oxygen levels as low as 1.3 mg/l at a site 5-7 m deep on Niagara reef in 1995 and presume that oxygen levels were also low at deeper sites surrounding the reefs. McMahon et al. (1984) maintain that dissolved oxygen levels above 6.0 mg/l are necessary for optimal walleye embryo development and survival. Therefore, it is likely that the majority of walleye eggs displaced to deep, silt habitats experience high mortality.

The warming rate of western Lake Erie waters was greater in 1994 than 1995, especially during the period from the first observation of eggs on the reefs to the time fry were first observed. Other studies have concluded that spawning and incubation temperatures are strongly related to hatching success (Busch et al. 1975). Rapid warming reduces incubation time and consequently reduces vulnerability to low oxygen, siltation, disease, predation, and storm generated turbulence and currents that can occur on the reefs.

Prolonged walleye egg incubation periods increase the potential for predation on walleye eggs. Wolfert et al. (1975) observed that yellow perch were the most consistent predators of walleye eggs on Kelley's Island Shoal in a study conducted in 1969-71. These authors concluded that the loss of walleye eggs to fish predation appeared to be important only when the rate of water warming slowed or stopped and the walleye and yellow perch reproductive periods overlapped. Our study shows the same temperature effect on incubation periods, but with white perch as the most abundant fish on the reef and the most important walleye egg predator.

Because I caught no potential egg predators in our gillnets in 1994, I feel that the reproductive periods of walleye and potential egg predators probably did not overlap to any point that could have significantly impacted the incubating walleye eggs. I did observe clearer water on Toussaint reef in 1994 than in 1995 which may have contributed to low gillnet catches in 1994. Hanson and Rudstam (1995) conclude that increased water clarity can lead to reduced catches and consequently diminish the effectiveness of sampling programs. Additionally, the faster water warming rate allowed many of the

walleye eggs to hatch before substantial numbers of white perch occupied the reef. Our gillnet catches in 1995 show a gradual increase in the number of white perch inhabiting Toussaint reef and that there was a significant temporal overlap with the incubating walleye eggs in late April and May. Examination of gut contents indicate that white perch were the most important consumers of walleye eggs, though it is difficult to assess the impact that their predation may have on the reproductive success of walleye. I concur with Wolfert et al. (1975) that an overlap in reproductive periods when waters warm slowly gives potential predators more opportunity to consume the incubating walleye eggs as seen in 1995. The longer the walleye eggs incubate, the more opportunity there is for predation and the greater the potential for deleterious effects on walleye reproductive success.

Changes in the abundance of adult fish in Lake Erie do not appear to explain the differences in egg densities between 1994 and 1995 on Toussaint and Niagara reefs. The Lake Erie walleye population (age 2 and older) was estimated at 40.2 million fish in 1994 and was projected to increase by 6% to 42.8 million fish in 1995 (Lake Erie Walleye Task Group 1995). However, the age-structure of the population did change (Lake Erie Walleye Task Group 1995) and accounts for a decrease in total potential fecundity of 17.7% from 1994 to 1995. Shuter and Koonce (1977) deduced that stock size explains only a small part of the variation in recruitment of the western Lake Erie walleye population.

My estimates of egg production on the reefs account for only about 0.003% of the total potential fecundity of the Lake Erie population. My estimates are very likely biased

by several factors. First, I have no estimates of efficiency of the egg pump device on the

different substrates present on the reef. I would expect the gear to operate more

efficiently on smooth substrates (bedrock areas) than on more complex substrates like

gravel and boulder areas. This method still provides a reliable index of egg abundance

useful for year to year and site to site comparisons. Secondly, I assumed that the mean

egg density observed on Toussaint and Niagara reefs represents the entire reef complex. I

immediately know that egg deposition is not homogenous across the reefs by looking at

the disparity between Toussaint and Niagara reefs. This may be a good question to

address in future studies of walleye spawning in western Lake Erie. Lastly, I have no

estimates of the number and age structure of the spawners that reproduce on the reefs.

Energy surplus and allocation in female walleye may partially explain the lack of

consecutive strong year classes experienced in Lake Erie. Walleye growth rate was

higher in 1993 than in 1994, likely due to a preponderance of gizzard shad in 1993 (Ohio

Division of Wildlife 1996), the preferred prey of walleye in western Lake Erie (Knight et

al. 1984). The abundant gizzard shad provided the energy surplus needed to produce

gametes and allowed the majority of females to spawn in 1994 possibly accounting for

the higher egg densities observed in 1994. Henderson and Nepszy (1994) propose that

good year-classes of walleye are only possible if most spawning females accumulate a

surplus of energy the previous growing season and can direct this energy towards gamete

production. Replenishment of energy depleted by reproduction may not be accomplished

by all females thus limiting the number of fish capable of spawning the next year.

Additionally, some females may resorb their eggs in order to satisfy their own metabolic

needs if conditions are bad (i.e. harsh winter, cold spring, lack of prey) (Henderson and Nepszy 1994). Presently, fisheries managers and ecologists do not know how many females actually spawn on reefs in any given year nor do the managers and ecologists fully understand the mechanisms that determine which females will spawn.

Additionally, females can allocate more or less energy to gametes depending on conditions encountered during the growing season (Roff 1983). Gamete size and energy content can vary from year to year influencing the survival probability of different sized eggs (Moodie et al. 1989; Brown and Taylor 1992). Larger eggs generally contain more energy and produce larger larvae upon hatching providing a stronger survival probability than small eggs (Miller et al. 1988; Moodie et al. 1989). Brown and Taylor (1992) discovered that lake whitefish eggs with higher caloric content produced larger larvae and that the endogenous growth of larvae was highly dependent on egg lipid content. Moodie et al. (1989) found that large walleye eggs contained more energy than small eggs and the subsequent larvae from the large eggs hatched at a larger size, began exogenous feeding sooner, and had greater survival than fry from small eggs.

Chapter 2

DISTRIBUTION, DIET, GROWTH, AND SURVIVAL OF
AGE-0 WALLEYE IN WESTERN LAKE ERIE.

Abstract

Walleye year-class strength in Lake Erie exhibits high interannual variability. Interannual variability in growth and survival rates of walleye larvae and juveniles is suspected to cause much of this variability. I examined the spatial distribution, diet, growth, and survival of pelagic larval and early demersal juvenile walleye in western Lake Erie in 1994 and 1995. Pelagic walleye larvae were approximately 14 times more abundant in 1994 than 1995 ($28.4/1,000 \text{ m}^3$ in 1994). Growth of larval walleye was significantly greater in 1994 than 1995 with a mean length at the end of June of 46.2 mm and 25.6 mm TL, respectively. Instantaneous mortality rates of pelagic walleye were estimated at 0.078/day in 1994 and 0.053/day in 1995 and did not differ significantly. Total mortality rates for pelagic larvae were approximately 75% in 1994 and 73% in 1995. Dispersal and distribution patterns of walleye larvae in both years were similar. Calanoid copepods and large cladocerans dominated pelagic larval diets in both years. Fish became the dominant prey in diets in early June of 1994 and late June 1995. Age-0 walleye were exclusively piscivorous by the end of June in both years. The relative strength of the 1994 year-class was 14 times greater than the 1995 cohort during the larval stage yet only 9 times stronger

by the end of August as indexed in bottom trawls indicating increased juvenile mortality during the 1994 summer or an influx of fish from other regions of Lake Erie in 1995.

Introduction

Year class strength of many walleye populations is set by late fall (Kempinger and Churchill 1972); however, the timing and controlling mechanisms of year class establishment have not been satisfactorily identified for walleye populations in Lake Erie (Lake Erie Walleye Task Group 1995). The greatest potential for year-class regulation in many fish populations exists during the larval stage (Houde 1987). Variation in individual larval growth and survival rates in response to density-independent and density-dependent factors potentially influence recruitment success in many fish populations (Crecco and Savoy 1985; Houde 1987; Rice et al. 1987; Jensen 1992). Jensen (1992) identified the relationship between mortality and size as the most effective form of compensatory process for larval walleye. Increases in larval size that result in a decrease in mortality may substantially increase recruitment (Houde 1987; Jensen 1992; Pepin 1993). Examination of the characteristics and variability of distribution, diet, and growth rate of the survivors will elucidate factors influencing larval survival.

Walleye larvae are limnetic and consequently are subject to passive transport by water currents (Houde and Forney 1970). Spatial distribution may influence survival of these larvae, as suggested for many marine species (Powles and Stender 1976; Thayer et al. 1983). Noble (1972) discovered that larval walleye in Oneida Lake, New York became

concentrated in protected bays as a result of wind generated currents. Foraging success of larval walleye in bays is determined by variations in prey densities common to large lakes (Watson 1976; Patalas and Salki 1992). High prey densities can enhance growth and increase larval survival (Houde 1987) whereas low prey densities can result in reduced growth rate and increased mortality (Crowder et al. 1987).

Body size often dictates the survival probability of larval fishes (Miller et al. 1988). Swimming and foraging ability, size of food particles ingested, and susceptibility to starvation and predation are all functions of body size (Houde 1969; Mathias and Li 1982; Serns 1982). Jensen (1992) determined that the earlier in the growing season age-0 walleye achieve a large size the more likely they are to survive and relates faster growth to prey community characteristics. The ability of larval walleye to compensate for small size by increased growth may improve their chance of survival if survival is size selective (Jensen 1992). Additionally, high levels of mortality may generate compensatory responses in growth rates of survivors resulting in increased survival (Mills and Forney 1988).

Diet directly influences growth and survival of larval walleye (Houde 1967; Forney 1980; Mathias and Li 1982). Experiments have revealed that a critical period for larval mortality due to nutrition deficiency may occur when postlarvae switch from endogenous to exogenous feeding. Larval walleye growth, survival, and amount of exogenous food consumed is a function of fish density and positively related to water temperature and the abundance of adequate sized prey (Li and Mathias 1982; Fox 1989; Moodie et al. 1989).

Cannibalism among larval walleye is considered a major cause of mortality in walleye culture, occurring in fish as small as 9.0 mm (Cuff 1980; Li and Mathias 1982).

The heaviest losses to cannibalism of cultured walleye larvae occurred at the onset of

exogenous feeding and is considered a function of larval density and prey density (Li and

Mathias 1982). Cannibalism in natural walleye populations is thought to have the greatest

impact when members of older age-classes eat younger fish as a compensatory response to

reduced prey densities or excessive walleye density (Chevalier 1973). The significance of

cohort cannibalism in natural larval walleye populations is unknown, but thought to be

minimal (Loadman et al. 1986).

In this chapter I will describe mechanisms governing the growth and survival of

larval walleye in western Lake Erie in 1994 and 1995. Because individual size often

dictates the survival probability of larval fishes (Miller et al. 1988), I have selected an

approach to investigate walleye early life history dynamics that focuses on size-dependent

mechanisms. In this chapter I document the dispersal and distribution of pelagic walleye

larvae and investigate the diet, growth, and survival of the 1994 and 1995 cohorts.

Methods

Larval Distribution and Abundance

I used a 2.0 m^2 framed ichthyoplankton net fitted with 583 mm mesh netting to

sample pelagic larval fishes. A flow meter was positioned in the center of the mouth of

the net to record the volume of water sampled. The net was towed in the upper 2.0 m of

the water column at approximately 1.0 m/sec. for 5 min. I sampled from 15 to 40 sites
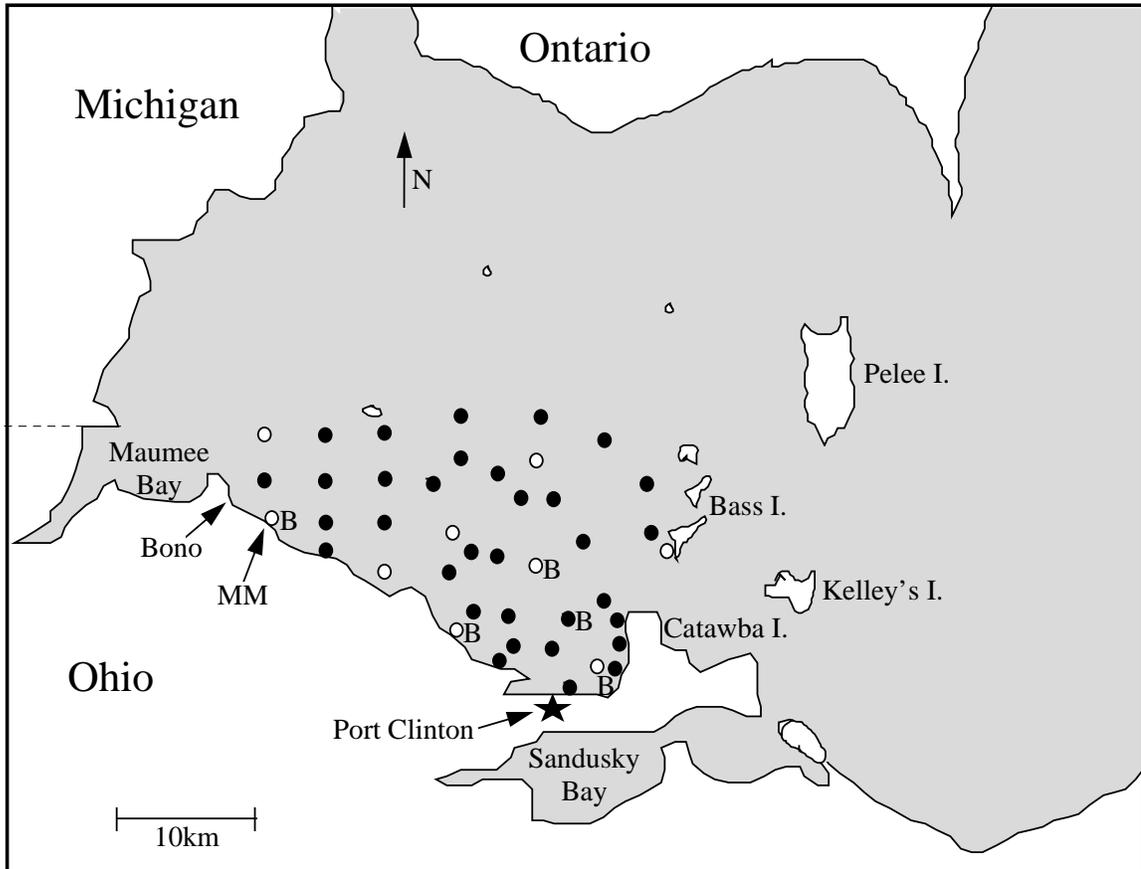
Figure 13. Map of western Lake Erie identifying sampling sites; all circles represent larval sampling sites; white filled circles represent zooplankton sampling sites; B indicates bottom trawl stations.

(Figure 13) per sample day and typically filtered 600 m^3 of water during each tow. Larval

fishes were anesthetized with tricaine methanesulfonate to prevent egestion of stomach

contents and preserved in 95% ethanol. Identifications of larval fish follow Auer (1982).

I calculated the density of larvae at each sample site for each date. Numbers of larvae

caught during each trawl were adjusted to number of larvae per 1,000 m^3 of water

filtered. I used mean larval density for the period from the first hatch through 31 May as

an index of larval abundance to compare between years.

I estimated the total number of walleye larvae in both years using estimates of the

volume of water in three distinct depth zones in my sample area. I used area and volume

values reported by Heniken (1977) and adjusted these values to account for differences in

study area size and lake water level (Appendix 6). Lake water level information was

obtained from the National Climatological Data Center in Asheville, North Carolina. I

calculated an average walleye larvae concentration for each depth zone on the date of

peak larval abundance and multiplied this value by the volume estimate of the depth zone

to provide an abundance estimate. I used peak larval abundance because the majority of

these fish should have emerged from the reefs and the river larvae will not have infiltrated

the population to a great extent at this time.

I used a semi-balloon bottom trawl (3.4 m headrope; 4.3 m footrope; 12.7 mm cod

end; 6 mm stretch mesh cod liner) to collect demersal fishes at 5 sites adjacent to the reef

complex (Figure 13). I towed the trawl for 10 min at about 1.5 m/sec at each site

beginning the first week of June in 1994 and in mid-May in 1995. Bottom trawl samples

were taken weekly through June and once monthly in July, August, September, and

October in both years. Trawls typically sampled 3,900 m^2 area. I selected bottom trawl

sites based on substrate and morphologic compatibility with the gear and catches of age-0

walleye. Bottom trawl samples were only used to investigate growth and diet of age-0

walleye.

Age-0 Walleye Growth

Fish total length (TL) was measured to the nearest millimeter and wet weight to

the nearest 0.001 g. I measured dry weight (0.0001 g) by drying larvae at 60°C until no

further weight loss was observed. I calculated length-dry weight regressions (Ricker

1975) for walleye and other larval fishes in both years (Appendix 3). I calculated specific

growth rate (SGR) (Ricker 1975) for pelagic walleye larvae.

Age-0 Walleye Survival

I estimated instantaneous mortality rates (Z) for larval walleye using the decline in

catch per unit effort as used by Noble (1972) and Henderson et al. (1984). Catches from

neuston samples were converted to number of larvae/1,000 m^3 of water. I then

transformed these catch data to $\log_e (x +1)$ to produce normalized data with homogeneous

variance (O'Gorman 1984) and plotted these against time. Mortality was estimated as the

slope of the descending limb of each catch curve (Ricker 1975).

Index of Year-Class Strength

        I used the catch of age-0 walleye in the Ohio Division of Wildlife's assessment bottom trawls in August (Ohio Division of Wildlife 1996) as an index of relative year-class strength.

Age-0 Walleye Diets

        Stomach contents of individual fish were removed by dissection under a dissecting microscope. For larvae < 15mm TL when the digestive tract was undifferentiated, prey items were identified and counted throughout the digestive tract. For larvae > 15 mm TL, I counted all prey anterior to the pyloric caecum. All prey in the stomach were identified according to the categories defined in Appendix 4, counted, and measured using 20 X magnification projected onto a computer-interfaced digitizing pad. I applied length-dry weight regressions (R. Haas, MI DNR Mt. Clemens Fisheries Station, unpublished data; Cornell University Biological Field Station, unpublished data) to prey lengths to estimate the dry mass of prey items. When organisms were unmeasurable due to breakage or digestion, I used average values for the same prey item from fish examined from the same date.

        Walleye diets were characterized by frequency of occurrence and percent composition by biomass. I estimated dry weight biomass of fish remains in walleye stomachs using species-specific length-dry weight regressions derived from prey species captured concurrently with age-0 walleye (Appendix 3). Prey electivity was estimated using the Manly-Chesson index α_i calculated as:

$$\alpha_i = (r_i / n_i) / \sum_{i=1}^{m} r_i / n_i$$

where m is the number of prey sizes or species, r_i is the proportion of prey i ingested, and n_i is the proportion of prey i in the environment (Chesson 1983; Lechowicz 1982) .

For m prey species in a sample, an alpha value $> 1/m$ indicates positive selection of

species i. Electivity values were calculated using samples collected at sites 32, 33, and 34 because these sites produced consistent catches of walleye and are located near the mouth of the Toussaint River in close proximity to each other . I used prey proportions estimated from zooplankton and ichthyoplankton samples taken concurrent with walleye samples to calculate electivity values for pelagic fish. For demersal age-0 walleye collected in bottom trawls, I used prey fish proportions estimated from concurrent catches in the bottom trawls.

Zooplankton Sampling

Zooplankton abundance and composition were determined from weekly vertical hauls with a 0.5-m diameter plankton net equipped with 153-mm mesh netting at two to seven sites in western Lake Erie (Figure 13). Samples were immediately preserved in sugar-formalin (Haney and Hall 1973). One to 3 1-mL subsamples were withdrawn with a Hensen-Stemple pipette from a known volume of sample. Additional subsamples were counted until at least 150 individual zooplankters had been enumerated. All cladocerans were identified to species while copepods were identified as Cyclopoida, Calanoida, or nauplii (Pennak 1978; Balcer et al. 1984). Cladocera and copepods were measured for total length using 20 X projection onto a digitizing pad interfaced with a microcomputer. Numbers of organisms were transformed into biomass using taxon-specific length-dry weight regressions (Cornell University Biological Field Station, unpubl. data). I calculated average biomass and average numbers per liter for the pooled zooplankton samples.

Statistical Analysis

I used a single factor analysis of variance (ANOVA) to assess the significance of

the differences in zooplankton size between 1994 and 1995. I used analysis of covariance

(ANCOVA) with a general linear model (SAS 1985) to assess differences in growth rates

for the log-transformed lengths and dry-weights of walleye larvae between 1994 and

1995. I also used analysis of covariance to assess the difference in survival rate as

estimated by the slopes of the descending limbs of the catch curves. I used a Log_e (x+1)

transformation for the ANCOVA tests to produce normalized data with homogeneous

variance (O'Gorman 1984). I used the sample correlation coefficient to assess

relationship between SGR and water temperature, zooplankton biomass, ichthyoplankton

biomass, ichthyoplankton density, walleye gut contents biomass, and walleye density.

Results

Age-0 Walleye Distribution and Abundance

Walleye larvae first appeared in neuston samples towed over the reef complex on

29 April 1994 (Figure 14 and 15). Walleye larvae were present over the reefs only during

hatching and dispersed to inshore sites southwest and southeast of the reefs in both years.

In 1994, walleye larvae became concentrated at inshore sites southeast and southwest of

the reef complex (Figures 15-18). The most consistent catches in 1994 came from

inshore sites near Metzger Marsh and the mouths of the Toussaint and Portage rivers. In

areas where age-0 walleye were abundant, the catch was highest in water 2.7 - 6 m deep. Few walleye larvae were collected from sites north of the reef complex (Figures 15-18).

Catches of larval walleye were much lower in 1995 than 1994 (Figure 14). The most consistent catches of pelagic walleye larvae in 1995 were from sites southwest of the reef complex (Figures 19-21) although some walleye larvae were collected from inshore sites near the mouths of the Toussaint and Portage rivers, similar to 1994. In 1995 we also observed a lack of pelagic walleye larvae at sites north of the reef complex (Figures 19-21).

In 1994, the catch of pelagic walleye larvae peaked on 2 May when I captured 1328 fry in 33 tows for an average density of 95.2 fry / 1,000 m^3 (Figure 14). Equipment failure prevented any larval sampling between 2 May and 18 May 1994. In 1995, the peak catch occurred on 11 May when a total of 85 walleye fry were captured in 40 samples for an average density of 3.9 fish / 1,000 m^3. Mean density of walleye fry for the sample period was 14 times higher in 1994 than 1995 (28.4 and 2.0 fry / 1,000 m^3 respectively). On the date of peak abundance, the larval population in my study area was estimated at 70,277,000 fish ($\pm$ 19 %) in 1994 and 2,616,000 fish ($\pm$ 15%) in 1995.
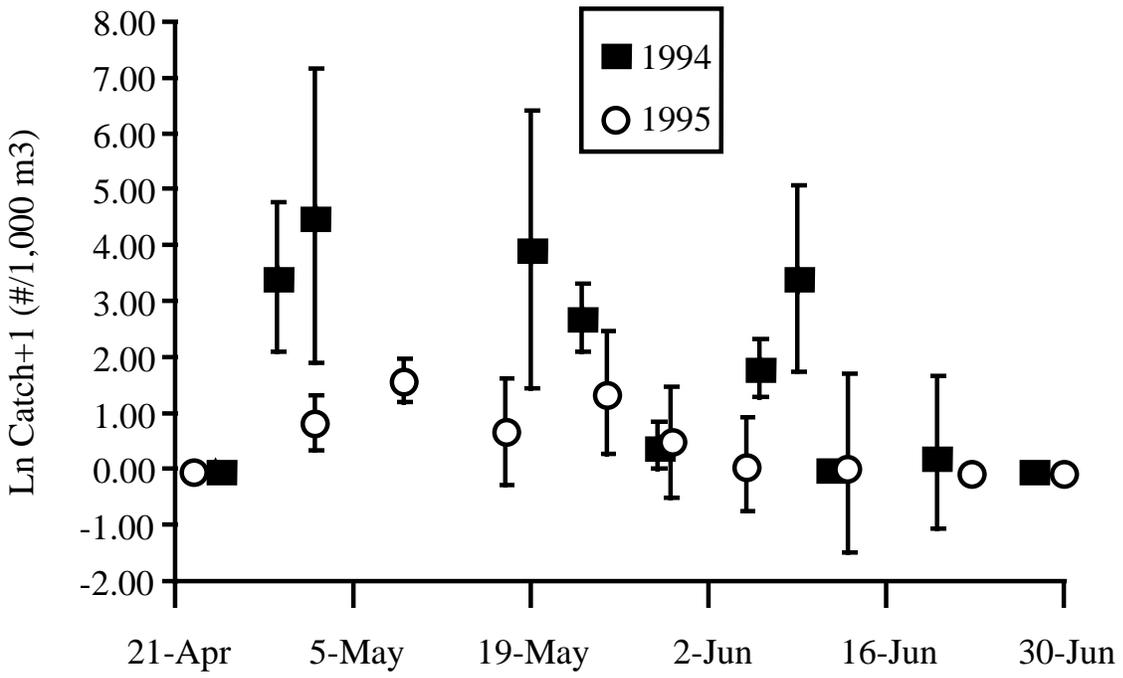
Figure 14. Decline in pelagic walleye abundance based on catches in neuston samplers taken at 15 to 40 sites in western Lake Erie in the spring of 1994 and 1995. Values are mean density (#/1,000 m^3) ± s.e. using Ln (catch +1) transformed data.

Figure 15. Distribution and density (#/1,000 m^3) of pelagic walleye larvae in western Lake Erie based on catches in neuston samples 29 April (top) and 2 May (bottom) 1994. Circles identify reef sites where egg sampling occurred.

28 0 0 0 0

9 0 0 0 0 0 0 0 0

2 0 0

436 20

Metzger
Marsh

18 8 0

N

30 0 99 9

0 191 26

579

Toussaint R.

Portage R.

10km

19 May1994

28 3 0 0 0

5 0 0 0 0 22 0 0

0

2 18

Metzger 0 94

Marsh 4 7

9

N

6 17 9 0

144 15 91

3 2

Toussaint R.

Portage R.

10km

23 May1994

Figure 16. Distribution and density (#/1,000 m^3) of pelagic walleye larvae in western
Lake Erie based on catches in neuston samples 18 May (top) and 23 May (bottom) 1994.
Circles identify reef sites where egg sampling occurred.
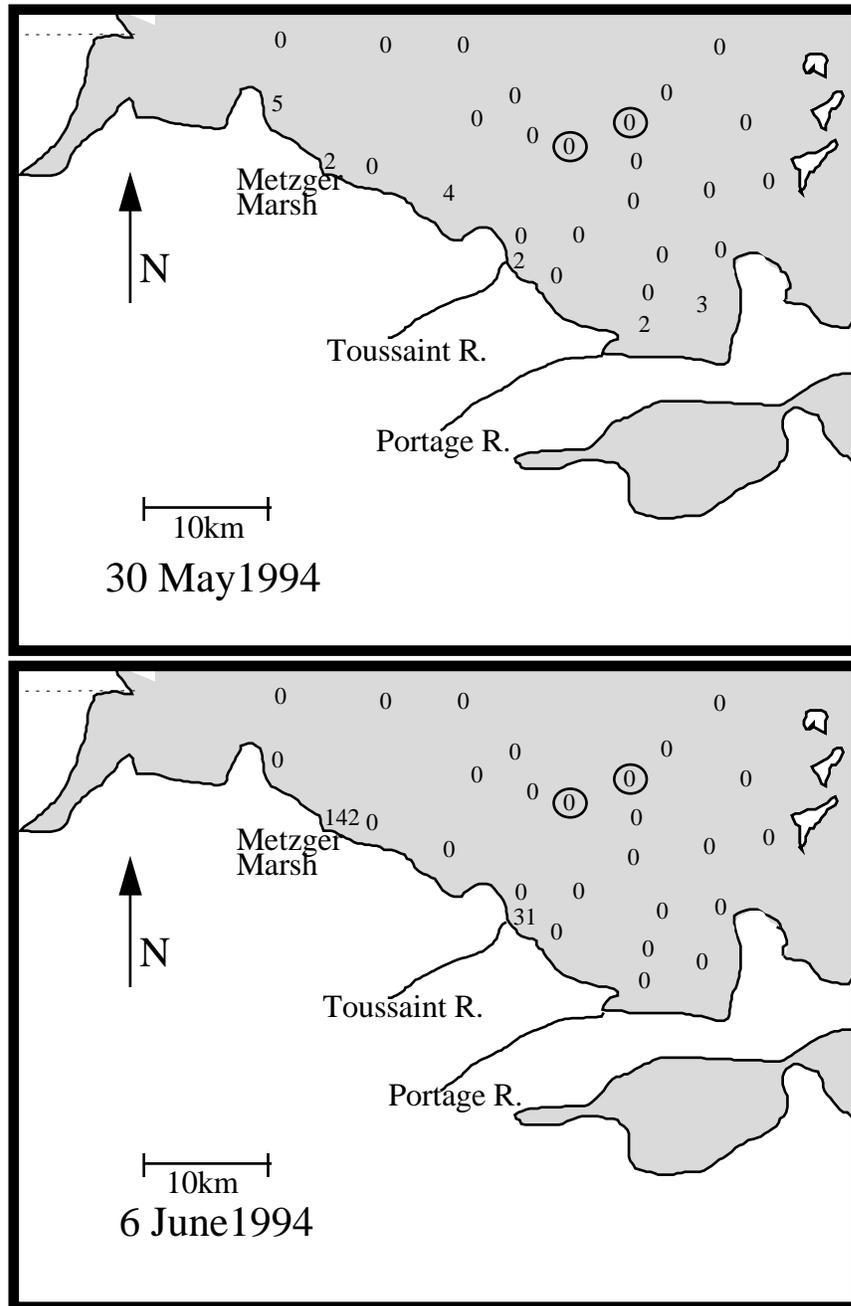
Figure 17. Distribution and density (#/1,000 m^3) of pelagic walleye larvae in western Lake Erie based on catches in neuston samples 30 May (top) and 6 June (bottom) 1994. Circles identify reef sites where egg sampling occurred.
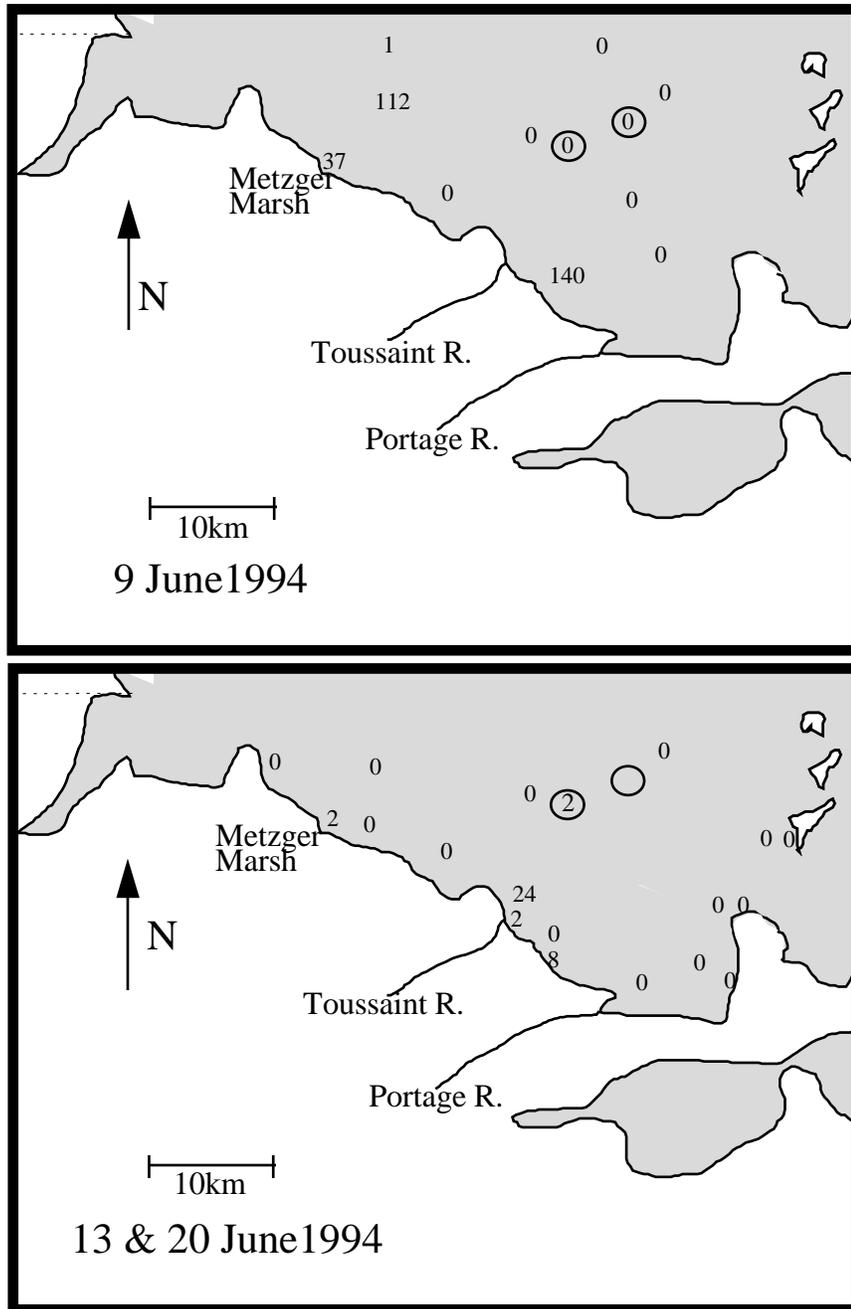
Figure 18. Distribution and density (#/1,000 m^3) of pelagic walleye larvae in western Lake Erie based on catches in neuston samples 9 June (top), 13 and 20 June (bottom) 1994. Circles identify reef sites where egg sampling occurred.

Figure 19. Distribution and density (#/1,000 m^3) of pelagic walleye larvae in western Lake Erie based on catches in neuston samples 3 and 5 May (top), and 11 and 12 May (bottom) 1995. Circles identify reef sites where egg sampling occurred.

Figure 20. Distribution and density (#/1,000 m³) of pelagic walleye larvae in western Lake Erie based on catches in neuston samples 18 May (top) and 26 May (bottom) 1995. Circles identify reef sites where egg sampling occurred.

Figure 21. Distribution and density (#/1,000 m³) of pelagic walleye larvae in western Lake Erie based on catches in neuston samples 30 May (top) and 6 and 13 June (bottom) 1995. Circles identify reef sites where egg sampling occurred.

I collected the first demersal walleye in bottom trawls towed off the mouth of the Toussaint River and near Metzger Marsh on 6 June 1994 and 6 June 1995. No bottom trawl samples were taken prior to 6 June 1994. My catches of age-0 walleye were consistent throughout the summer and fall (through 22 October) of 1994 but only one age-0 walleye was collected in my bottom trawls after 20 June 1995 despite continued monthly sampling through October.

Age-0 Walleye Diets

I examined the diets of 112 pelagic walleye larvae and 520 demersal age-0 walleye in 1994. In 1995 I examined the diets of 55 pelagic walleye larvae and 22 demersal age-0 walleye. Summaries of the percent composition (dry-weight biomass) of the diet items observed in walleye guts in 1994 and 1995 are listed in Tables 4 and 5, respectively. The mean total prey biomass per gut (dry-weight) for pelagic walleye larvae did not exceed 0.08 mg/gut in either year. In both years, calanoid copepods and large cladocerans comprised the bulk of pelagic larval diets, typically accounting for over 60% of dry-weight biomass. Cyclopoid copepods usually ranked third in biomass while fish, small cladocerans, rotifers, and nauplii always accounted for less than 20% (usually less than 10%) of the stomach contents biomass of pelagic walleye larvae in both years. In 1995 I observed the biomass of fish in pelagic larval diets to increase from a mean of 3.8% of gut contents biomass on 3 May to 19.3% on 30 May (Table 5) while the mean biomass of fish in the diets of pelagic larvae in 1994 did not exceed 3.4% of gut contents biomass (Table 4).

Percent frequency of occurrence for prey items observed in age-0 walleye diets in 1994 and 1995 are listed in Tables 6 and 7, respectively. Calanoid copepods were observed in 60% to 80 % of the pelagic larval walleye stomachs examined in both years. Large cladocerans were observed in 17% to 80% of the diets in both years. Cyclopoid copepods typically occurred in less than 30% of the pelagic walleye guts examined while small cladocerans, rotifers, and nauplii were typically observed in less than 20% of the pelagic larval walleye guts examined. Fish were observed less frequently in pelagic larval guts in 1994 occurring in only 6% of the fish examined on both 2 May and 18 May and not at all on 29 May (Table 6). Fish appeared more frequently in pelagic larval diets in 1995 ranging from 12-83% frequency of occurrence (Table 7).

The diets of demersal age-0 walleye typically contained more fish than the pelagic diets, especially in 1994 when fish usually accounted for over 88% of the dry-weight biomass observed in guts (Table 4). Large cladocerans and copepods comprised 68.4% of the dry-weight biomass of demersal age-0 walleye on 6 June and 34.6% of the biomass on 13 June in 1995. Fish accounted for nearly 100% of the diet of demersal age-0 walleye examined from 27 June through 22 October 1994 (Table 4) and on 20 June 1995 (Table 5). Benthic macro-invertebrates typically accounted for less than 5% of observed dry-weight biomass in both years.

The frequency of occurrence for copepods and large cladocerans combined dropped below 30% for demersal age-0 walleye in 1994 but remained high in 1995. In 1995 calanoid copepods were identified in 75% of walleye guts examined on 6 June and 27 % of the guts examined on 13 June while large cladocerans were identified in 75% of

Table 4. Percent composition of age-0 walleye diets collected in pelagic neuston samples and bottom trawls from western Lake Erie in 1994. * indicates walleye collected in bottom trawls; % MT = percent of empty stomachs observed; TL = walleye total length; TPB = total dry-weight biomass of prey items in walleye guts excluding empty stomachs; SC = small cladocerans; Cal = calanoid copepods; Cyc = cyclopoid copepods; LC = large cladocerans; Ben = benthic invertebrates; Spin = spiny-rayed fish prey; Sof = soft-rayed fish prey; UFR = unidentifiable fish remains.

Date	Number Examined	% MT	TL (mm)	TPB (mg)	Rot	SC	Cal	Cyc	LC	Ben	Spin	Sof	UFR
2 May	52	19	9.8	0.04	4.1	9.2	59.7	12.3	11.3	0	0	0	3.4
18 May	50	16	10.2	0.04	4.7	16.3	27.6	17.5	31.5	0	0	0	2.4
29 May	10	30	15.0	0.03	2.8	5.3	40.3	11.7	39.9	0	0	0	0
8 June*	46	15	24.2	1.62	0	0	0.8	1.7	8.9	0	33.2	24.4	31.0
13 June*	48	13	39.2	3.23	0	0	5.8	0.5	5.3	0.2	59.7	10.0	18.5
27 June*	50	12	48.0	3.32	0	0	0	0	0	1.2	36.7	32.0	30.1
26 July*	64	24	97.8	78.6	0	0	0	0	0	0.3	55.7	32.0	12.0
21 Aug*	79	30	135.6	114.2	0	0	0	0	0	0.1	25.3	52.5	22.1
24 Sept*	96	23	168.1	225.1	0	0	0	0	0	0.1	13.3	75.2	11.4
22 Oct*	137	20	174.9	288.3	0	0	0	0	0	0	5.4	83.8	10.8

Table 5. Percent composition of age-0 walleye diets collected in pelagic neuston samples and bottom trawls from western Lake Erie in 1995. * indicates walleye collected in bottom trawls; % MT = percent of empty stomachs observed; TL = walleye total length; TPB = total dry-weight biomass of prey items in walleye guts; SC = small cladocerans; Cal = calanoid copepods; Cyc = cyclopoid copepods; LC = large cladocerans; Ben = benthic invertebrates; Spin = spiny-rayed fish prey; Sof = soft-rayed fish prey; UFR = unidentifiable fish remains.

Date	Number Examined	% MT	TL (mm)	TPB (mg)	Rot	SC	Cal	Cyc	LC	Ben	Spin	Sof	UFR
3 May	5	20	9.2	0.03	10.2	3.6	52.8	14.6	15.0	0	0	0	3.8
11 May	25	24	9.4	0.05	3.5	8.2	65.8	10.3	9.1	0	0	0	3.1
18 May	7	0	10.7	0.05	2.1	3.6	38.3	11.2	39.2	0	0	0	5.6
25 May	12	8	10.7	0.05	1.1	0	25.9	7.5	50.0	0	0	0	15.5
30 May	6	0	14.0	0.08	0	0	29.4	9.2	42.1	0	0	0	19.3
6 June*	8	13	14.8	0.05	0	0	20.3	7.1	41.0	1.3	10.0	10.0	10.3
13 June*	11	27	20.5	1.15	0	0	7.9	5.2	21.5	5.0	16.5	9.4	34.5
20 June*	3	33	31.5	2.50	0	0	0	0	0	0	0	78.0	22.0

Table 6. Frequency of occurrence (%) of prey items observed in age-0 walleye stomachs collected in neuston nets and bottom trawls (*) in western Lake Erie, 1994. Number examined = number of fish stomachs examined; % MT = percent of empty stomachs encountered; TL (mm) = mean total length of fish examined; R-N = rotifers and nauplii; SC = small cladocerans; Cal = calanoid copepods; Cyc = cyclopoid copepods; LC = large cladocerans; Ben = benthic invertebrates.

Date	Number Examined	% MT	TL (mm)	R-N	SC	Cal	Cyc	LC	Ben	Fish
2 May	52	19	9.8	6	4	81	17	17	0	6
18 May	50	16	10.2	8	12	80	22	80	0	6
29 May	10	30	15.0	10	20	60	20	60	0	0
8 Jun	46	15	24.2	0	0	7	4	17	0	58
13 Jun	48	13	39.2	0	0	6	4	8	4	63
27 Jun	50	12	48.0	0	0	0	0	0	4	86
26 Jul	64	24	97.8	0	0	0	0	0	3	76
21 Aug	79	30	135.6	0	0	0	0	0	4	70
24 Sept	96	23	168.1	0	0	0	0	0	3	77
22 Oct	137	20	174.9	0	0	0	0	0	0	80

Table 7. Frequency of occurrence (%) of prey items observed in age-0 walleye stomachs collected in neuston nets and bottom trawls (*) in western Lake Erie, 1995. Number examined = number of fish stomachs examined; % MT = percent of empty stomachs encountered; TL (mm) = mean total length of fish examined; R-N = rotifers and nauplii; SC = small cladocerans; Cal = calanoid copepods; Cyc = cyclopoid copepods; LC = large cladocerans; Ben = benthic invertebrates.

Date	Number Examined	% MT	TL (mm)	R-N	SC	Cal	Cyc	LC	Ben	Fish
3 May	5	20	9.2	20	20	80	20	60	0	20
11 May	25	24	9.4	8	12	72	28	28	0	12
18 May	7	0	10.7	14	14	71	29	71	0	43
25 May	12	8	10.7	8	0	75	42	42	0	42
30 May	6	0	14.0	0	0	50	33	83	0	83
6 Jun	8	13	14.8	0	0	75	25	75	13	75
13 Jun	11	27	20.5	0	0	27	18	55	9	64
20 Jun	3	33	31.5	0	0	0	0	0	0	66

the diets on 6 June and 55% of the diets on 13 June. Fish were observed in 58% to 86% of the demersal age-0 walleye diets examined in June 1994 (Table 6) and 64% to 75% of the guts examined in 1995 (Table 7).

Zooplankton Community

Zooplankton community dynamics for the spring of 1994 and 1995 are illustrated in Figures 22, 23, and 24. Taxonomic descriptions of zooplankton groupings are listed in Appendix 4. Calanoid copepods dominated the zooplankton community in April and early May in both years. Although cyclopoid copepods were numerically most abundant throughout May and June (Figure 24), the dry-weight biomass of both calanoid copepods and large cladocerans was greater (Figure 22). In 1994, the abundance of copepods and large cladocerans increased steadily through the month of May from an average of about 15 individuals per liter to over 50 individuals per liter by June (Figure 24). Zooplankton biomass also increased steadily during this period, averaging about 50 μg/L in April and peaking at over 450 μg/L in late June (Figure 22). Mean size of zooplankton in 1994 varied between 0.9 mm and 1.1 mm through the end of June (Figure 23).

Zooplankton biomass and abundance in May and early June of 1995 were generally less than those observed in 1994. The abundance of copepods and large cladocerans remained below 20 individuals per liter until late May in 1995 when a large increase in the abundance of large cladocerans was observed (Figure 24). Zooplankton
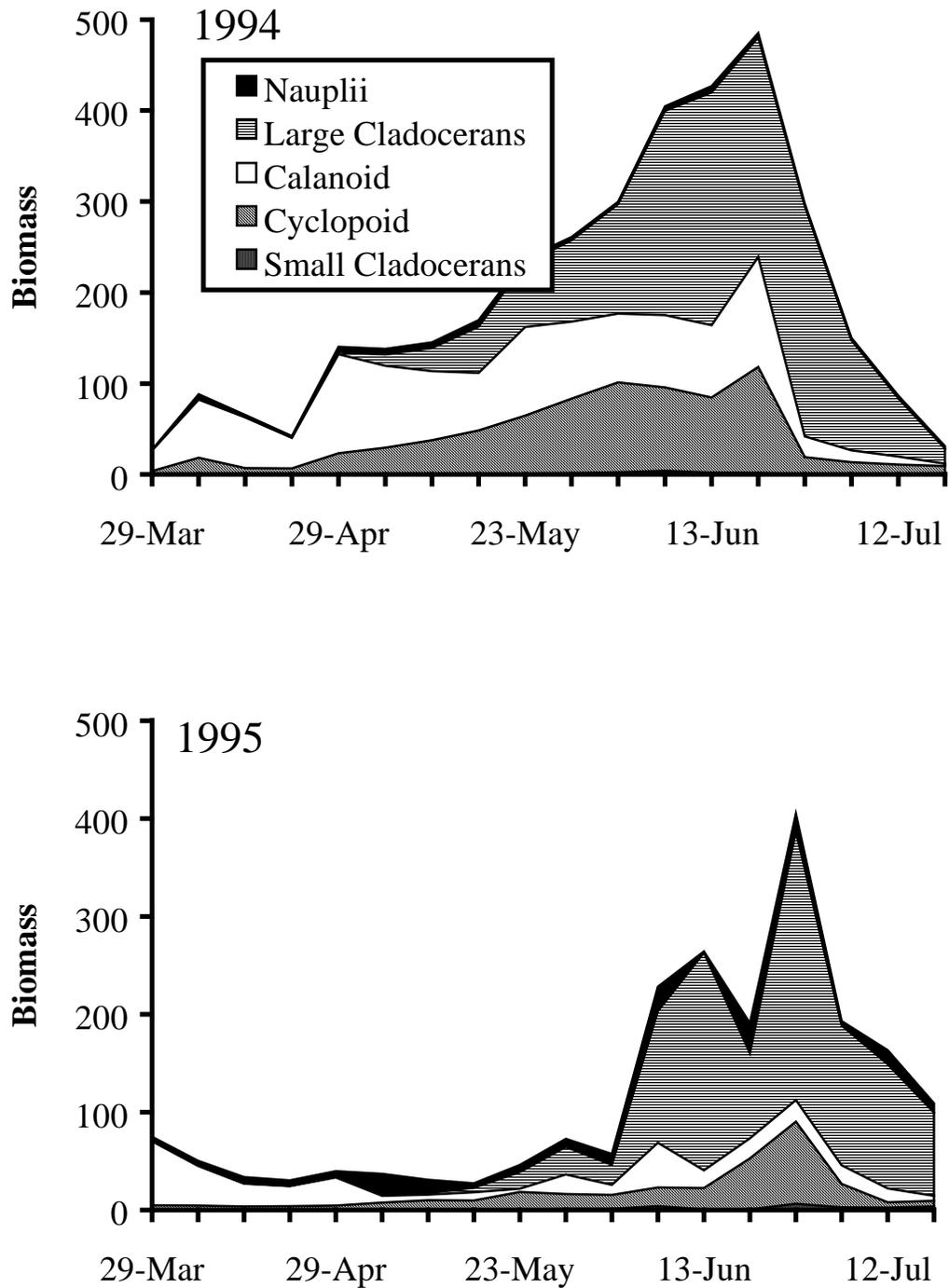
Figure 22. Mean zooplankton dry-weight biomass (µg/l) in western Lake Erie estimated from vertical tows at 3 to 7 sites in spring of 1994 (top) and 1995 (bottom).
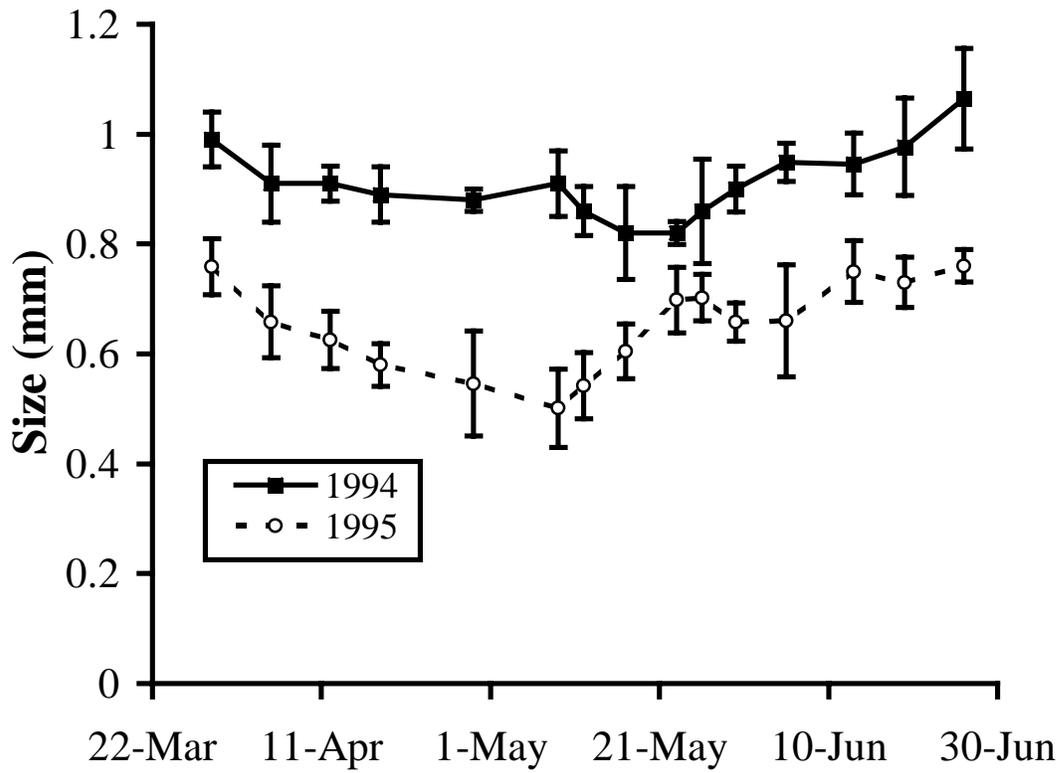
Figure 23. Mean size of crustacean zooplankton in the spring in western Lake Erie, 1994 and 1995.
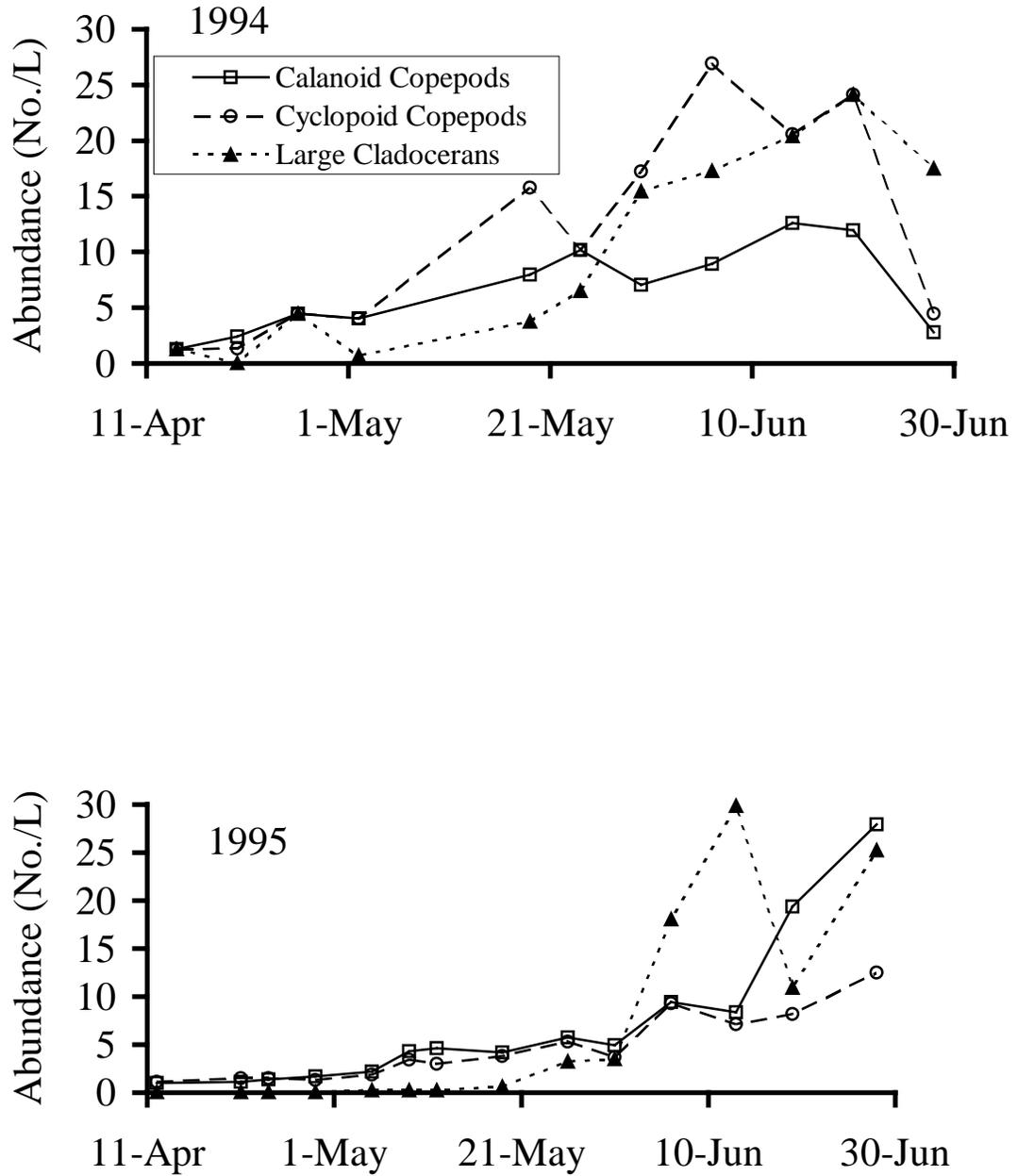
Figure 24. Abundance of cyclopoid and calanoid copepods and large cladoceran zooplankton in western Lake Erie in spring of 1994 (top) and 1995 (bottom).

biomass averaged about 50 µg/L until late May when the biomass increased dramatically

to nearly 300 µg/L in early June (Figure 22) coinciding with the increase in abundance of

large cladocerans (Figure 24). Mean size of zooplankton in 1995 varied between 0.5 and

0.9 mm through the end of June and was significantly less than in 1994 (ANOVA; $p <$

0.001) when the mean size varied between 0.9 and 1.1 mm (Figure 23).

Ichthyoplankton Prey Community

Ichthyoplankton community abundance for 1994 and 1995 are illustrated in Figure

25 and the dynamics of ichthyoplankton biomass are shown in Figure 26. In 1994, the

average abundance of ichthyoplankton increased from about 25 fish/1,000 m^3 in early

May 1994 to over 4,400 fish/1,000 m^3 by late June. The abundance of both soft- and

spiny-rayed ichthyoplankton species varied throughout the spring (Figure 25). Dry-

weight biomass of ichthyoplankton increased from about 0.04 g/1,000 m^3 in late April

1994 and early May to over 120 g/1,000 m^3 in late June 1994 (Figure 26).

Ichthyoplankton densities were consistently over 120 fish/1,000 m^3 and biomass above

0.045 g/1,000 m^3 during May and early June 1994, the period when age-0 walleye began

feeding on them.

Ichthyoplankton densities were generally much lower in 1995 than 1994. The

average abundance of ichthyoplankton in 1995 increased from about 20 fish/1,000 m^3 in

late April and early May to over 140 fish/1,000 m^3 at the end of June (Figure 25). Dry-

weight biomass of ichthyoplankton in 1995 increased from about 0.04 g/1,000 m^3 in early

May to over 2.2 g/1,000 m^3 in late June. Ichthyoplankton densities averaged less
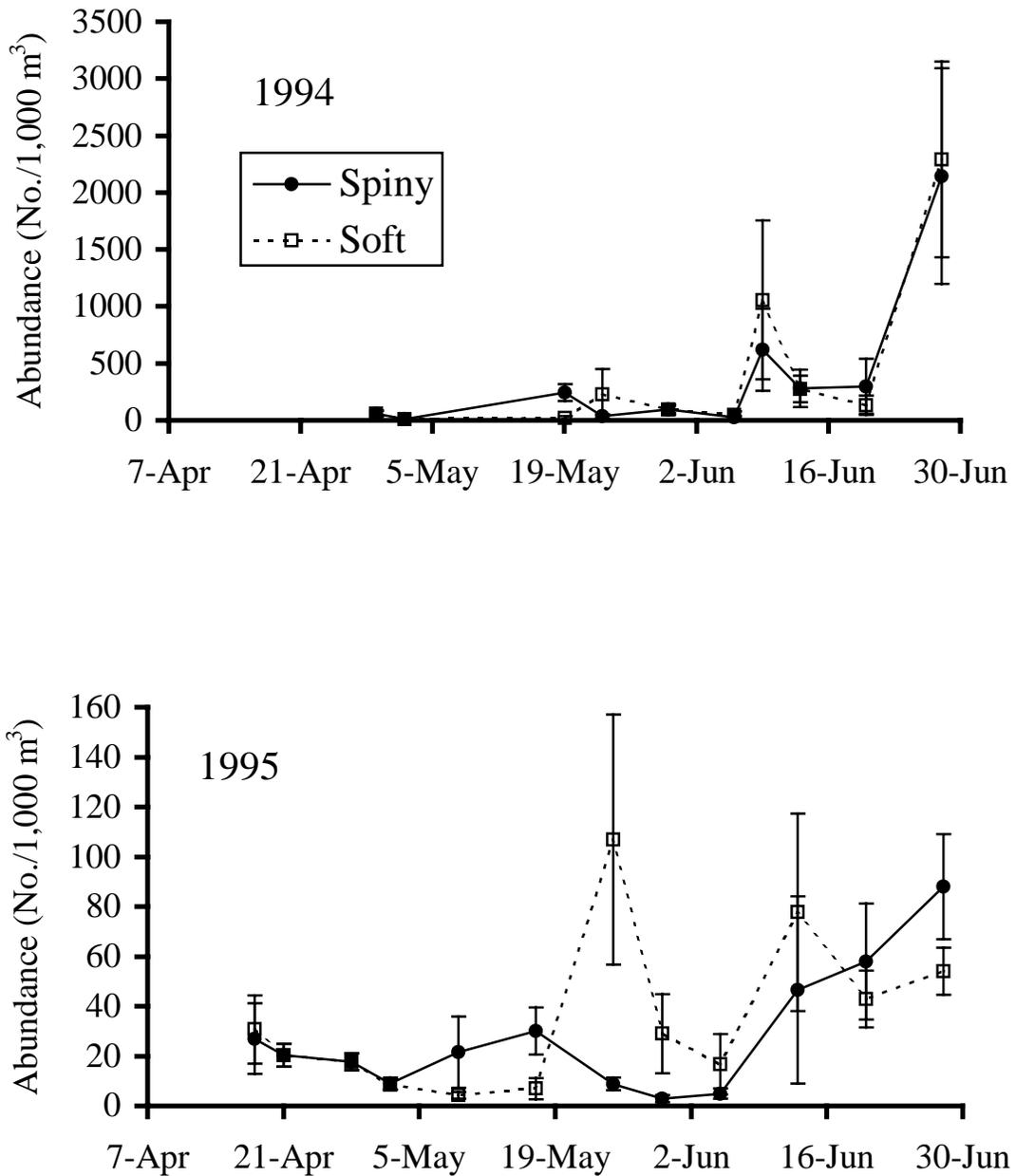
Figure 25. Density of spiny and soft-rayed ichthyoplankton (excluding walleye) in western Lake Erie estimated from weekly catches in neuston nets in the spring of 1994 (top) and 1995 (bottom). Ordinate scale varies.
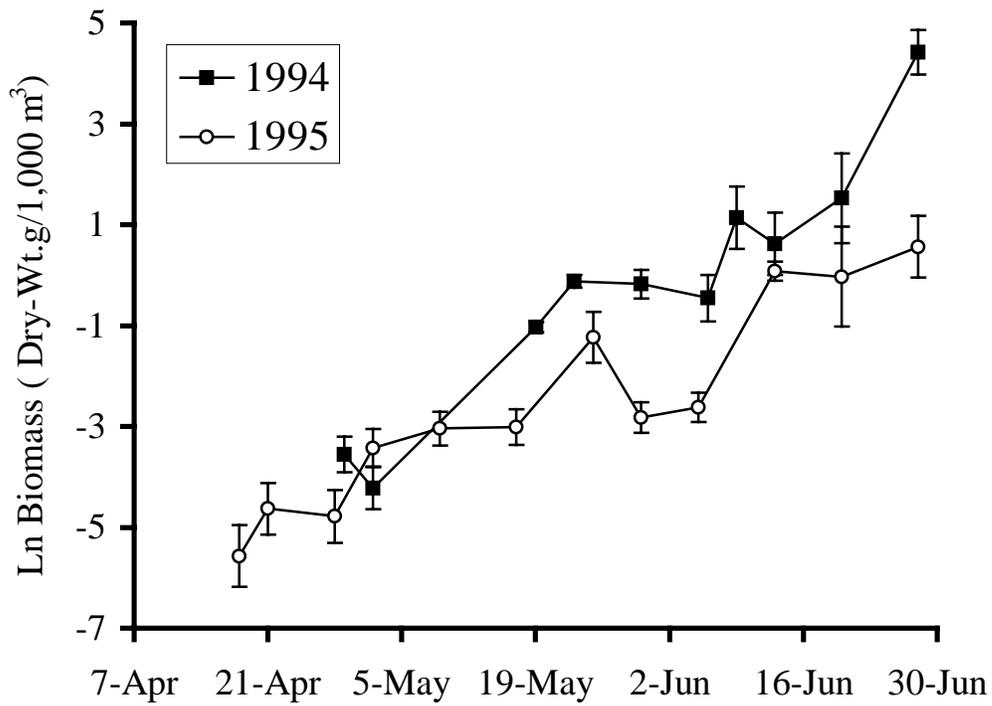
Figure 26. Dry-weight biomass (Ln g/1,000 m^3) of ichthyoplankton in western Lake Erie in the spring of 1994 and 1995.
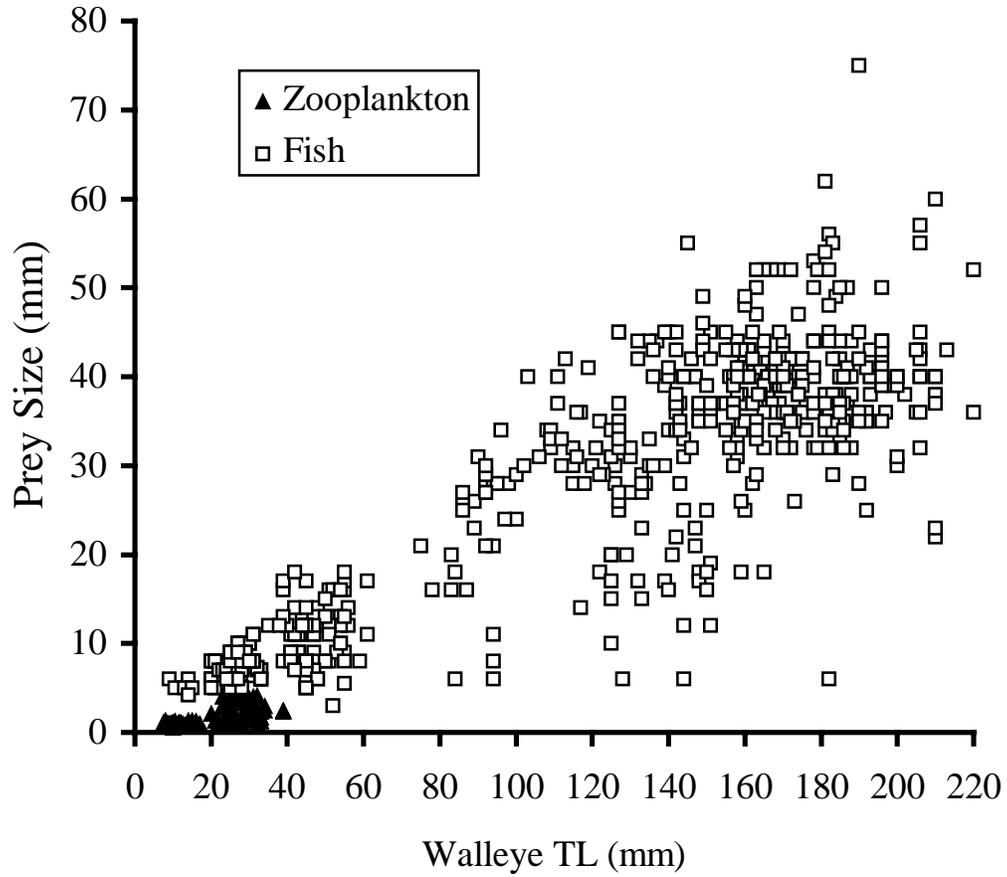
Figure 27. Relationship between walleye size and size of prey observed in gut for 1994 and 1995 diets pooled. Zooplankton sizes are total lengths while fish prey sizes are standard length.

than 80 fish/1,000 m^3 and biomass less than 0.06 g/1,000 m^3 during May 1995 exceeding 100 fish/ 1,000 m^3 and 0.25 g/1,000 m^3 in early June.

Age-0 Walleye Prey Selectivity

Pelagic age-0 walleye ranging in size from 9 - 17 mm TL consumed a narrow range of prey sizes compared to walleye larger than 17 mm in both years. The mean size of prey items observed in guts at this size range was approximately 1 mm. Prey sizes observed in diets of fish > 17 mm TL ranged from 1 to 12 mm for walleye 17 - 30 while larger walleye diets contained fish prey items as large as 18 mm SL (Figure 27).

I calculated electivity values (Chesson's α) for all prey categories except benthic invertebrates. I grouped all fish prey into one functional group. Electivity values for each prey category are detailed in Figures 28 and 29. Calanoid copepods occurred in age-0 walleye diets in greater proportions than in the zooplankton community until late June in both years. However, the α-values were usually not much greater than 0.167, the value of neutral selection (1/n) indicating that the walleye were eating calanoid copepods in about the same proportions that the prey occurred in the environment (Figure 28).

Electivity index values suggest strong positive selection for large cladocerans in both years, especially during May and early June when α-values often exceeded 0.5 (Figure 28) indicating that large cladocerans occurred in walleye diets in greater proportions than in the zooplankton community. Electivity values for large cladocerans declined in mid June of both years and was estimated at 0.0 on the last sampling date in June when no large cladocerans were observed in diets (Table 4 and 5).
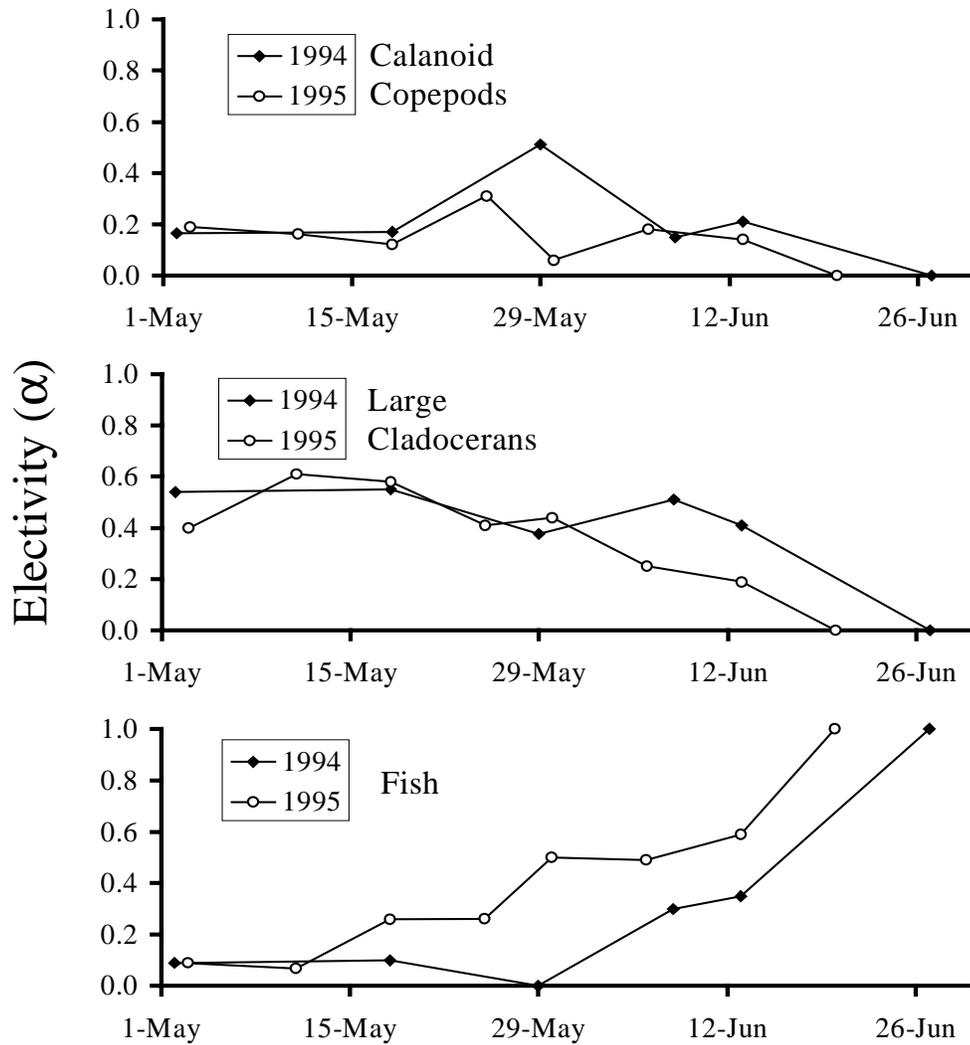
Figure 28. Electivity values (Chesson's α) for calanoid copepods (top), large cladoceran (middle), and fish (bottom) prey items estimated for age-0 walleye diets in 1994 and 1995.

Age-0 walleye increased their consumption of fish prey throughout May 1994 and June 1995 (Table 4 and 5) and this increase is reflected in the increasing α-values for this prey type (Figure 28). Electivity values for fish in 1994 remained below 0.167 (1/n) throughout May and increased above neutral selection in early June when the walleye were demersal. This suggests that age-0 walleye did not eat fish in greater proportions than they were available in the pelagic environment but did select for fish during the demersal stage in 1994. In 1995, α-values for fish were initially below 0.167 during the first two weeks of May but increased steadily through the remainder of May reaching 0.5 by early June and 1.0 by the last sample date on 27 June (Figure 28) when fish were observed to be the only prey item in diets (Table 5). Electivity values for nauplii and rotifers, small cladocerans, and cyclopoid copepods rarely exceeded 0.167 indicating that these prey items occurred in walleye diets in equal or lower proportions than in the zooplankton community (Figure 29).

Age-0 Walleye Growth

Growth rate of age-0 walleye from hatch through the end of June was significantly greater in 1994 than 1995. The regression of the log transformed total lengths over day-of-year (DOY) in 1994 was Ln TL = 0.0353 (DOY)-2.5012 and for 1995 the regression equation was Ln TL = 0.0245 (DOY) - 1.1825. The slopes of these regression lines are significantly different indicating that walleye grew faster in 1994 than 1995 (ANCOVA p<0.01). Newly hatched sac-fry walleye averaged between 6.0 and 7.2
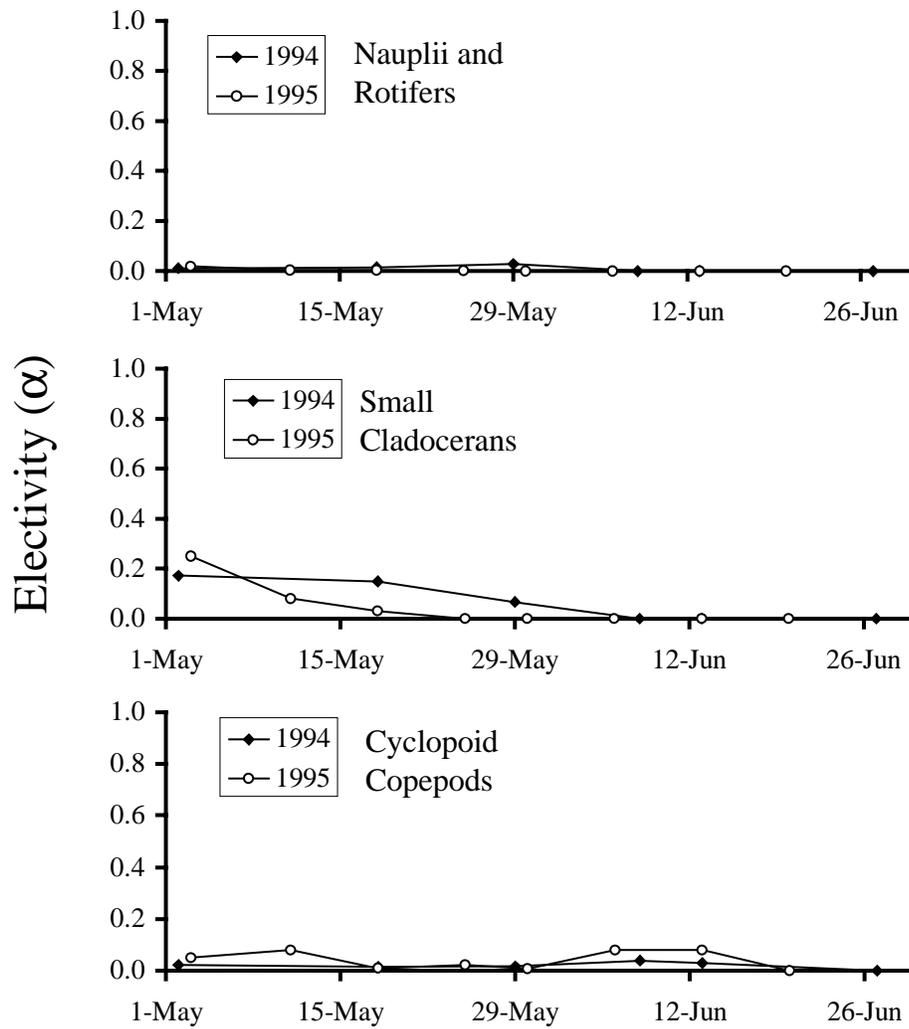
Figure 29. Electivity values (Chesson's α) for nauplii and rotifers (top), small cladocerans (middle), and cyclopoid copepods (bottom) prey items estimated for age-0 walleye diets in 1994 and 1995.
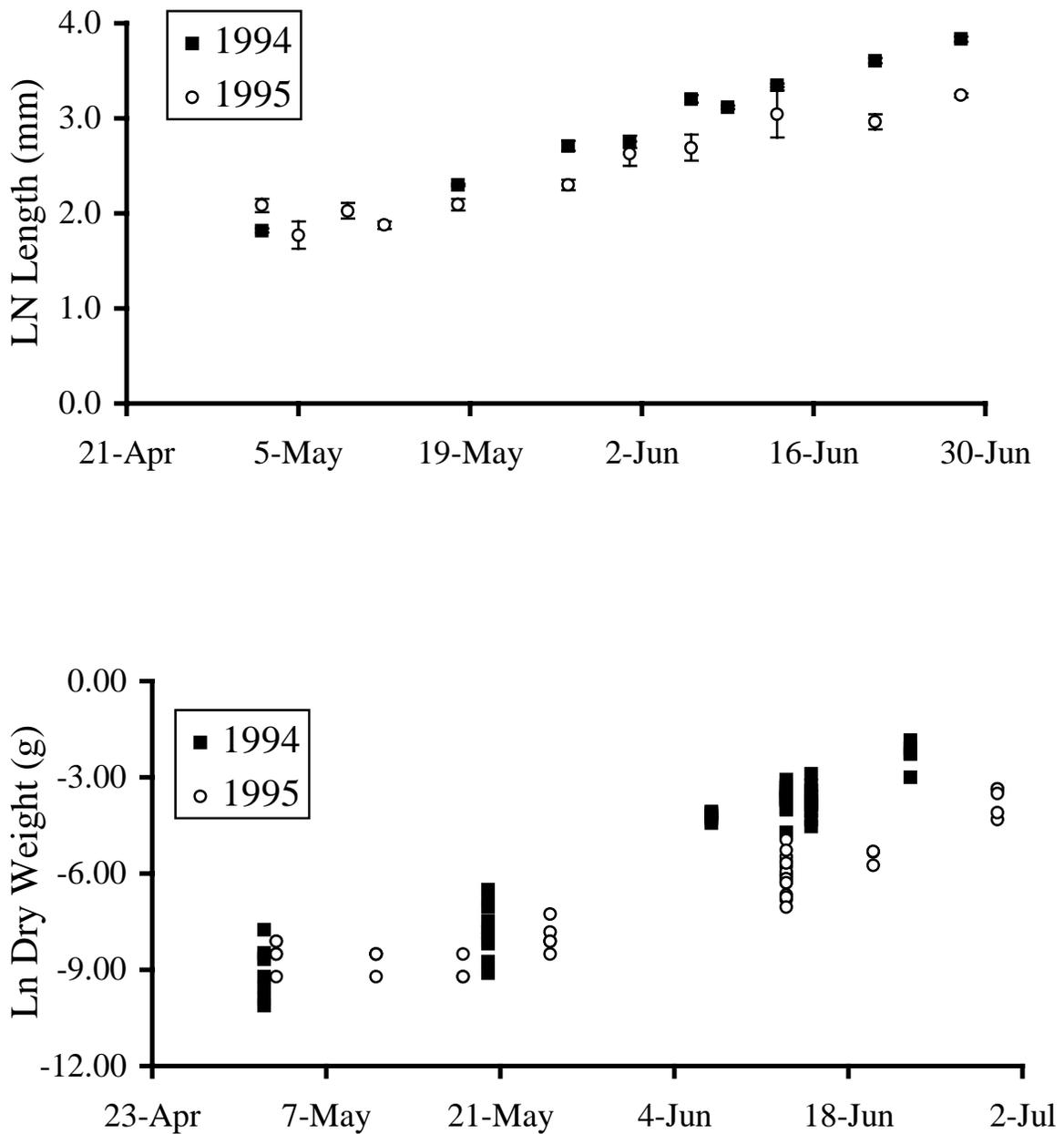
Figure 30. Top panel: Mean lengths (± 1 s.e.) of age-0 walleye collected in neuston nets and bottom trawls (after 9 June) in western Lake Erie in the spring of 1994 and 1995. Bottom panel: Dry-weights (g) of age-0 walleye collected in neuston samplers and bottom trawls (after 9 June) in western Lake Erie in the spring of 1994 and 1995.
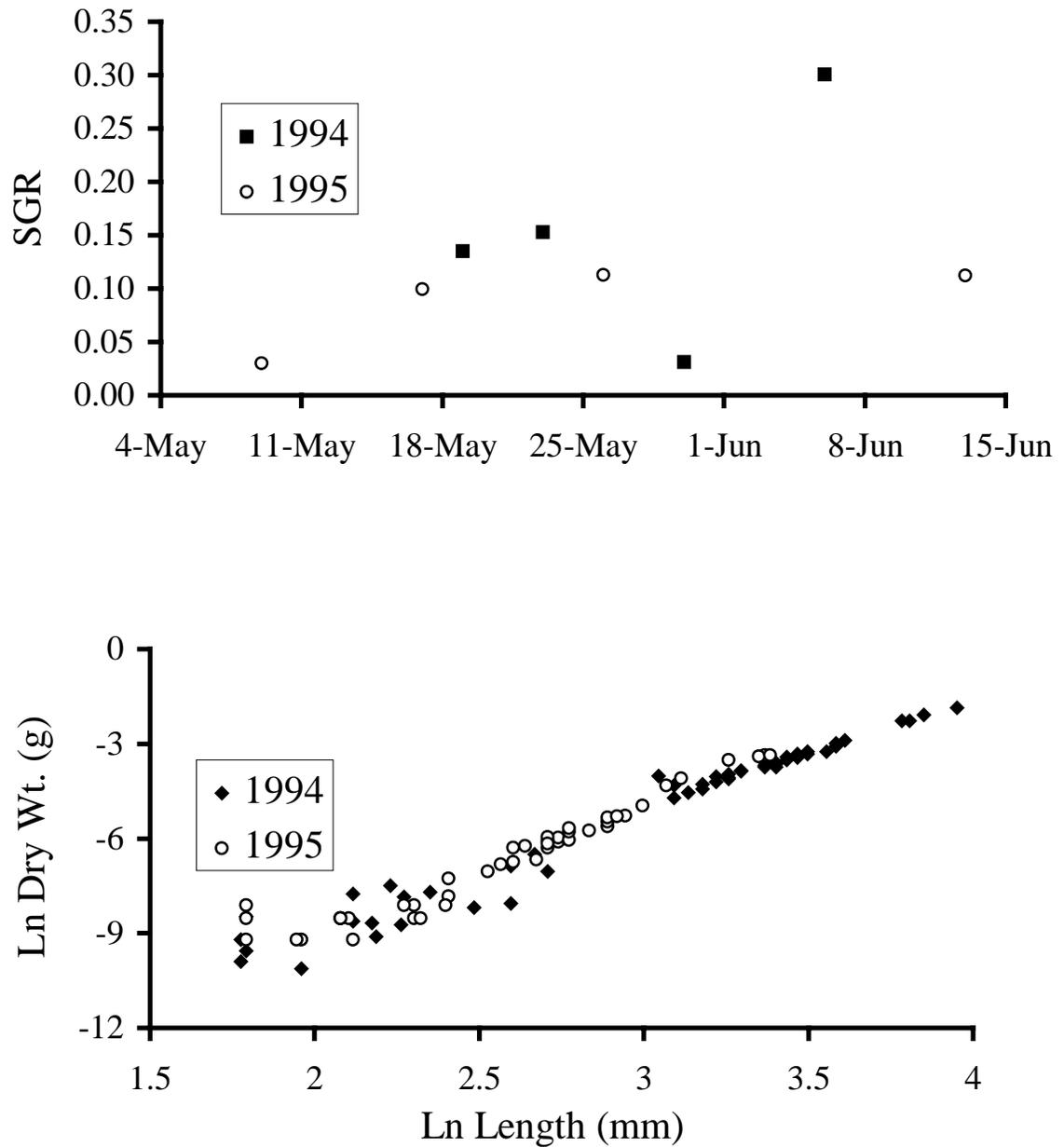
Figure 31. Top panel: Specific growth rates (g dry-weight) of pelagic age-0 walleye collected in neuston samplers in western Lake Erie in the spring of 1994 and 1995. Bottom panel: Relationship between log transformed total length (mm) and dry-weight (g) of age-0 walleye collected from western Lake Erie in the spring of 1994 and 1995.

mm TL in both years but the 1994 cohort averaged 46.2 mm TL by the end of June where the 1995 cohort was over 20 mm shorter at 25.6 mm TL (Figure 30).

Growth in terms of dry-weight was also significantly greater in 1994 than 1995. Sac-fry larvae weighed about 0.0002 g at hatch in both years and increased to an average of 0.1305 g by the end of June 1994 but only 0.0321 g by the same time in 1995 (Figure 31). The regression equation estimating the growth of each cohort over time is Ln DW = 0.1332 (DOY) - 25.7987 for 1994 and Ln DW = 0.0853 (DOY) - 19.8747 for 1995. The slopes of these regression equations are significantly different (ANCOVA; p<0.01) indicating that the growth rate in terms of dry-weight was greater in 1994 than in 1995.

I calculated specific growth rates (SGR) (Ricker 1975) for pelagic walleye larvae only using the dry-weight data. I excluded sac-fry from the first SGR in 1995 to avoid bias of newly hatched fish entering the population and falsely depreciating the SGR estimate. The highest SGR estimates were calculated for 1994 but these data show no obvious trend with time (Figure 31). SGR estimates were generally lower in 1995 than 1994 (Figure 31).

I calculated the sample correlation coefficients (Snedecor and Cochran 1989) between SGR and environmental variables of water temperature, zooplankton biomass, ichthyoplankton biomass, biomass of walleye gut contents, and walleye density to discern the closeness of the relationships between these variables. I used the environmental variables and gut contents biomass observed on the last day of the growth stanza to calculate the correlation coefficients. I pooled the data from both years to increase the

degrees of freedom. While I found no significant correlation's ($r \geq 0.602$; 8 d.f.; $\alpha =$ 0.05) among the variables examined, I did find less than significant positive relationships between SGR and zooplankton biomass ($r = 0.51$) and SGR and gut content biomass ($r = 0.39$). All other correlation's were extremely close to zero.

The length-dry-weight relationship for age-0 walleye in 1994 and 1995 is plotted in Figure 31. The regression of log transformed dry-weight against log transformed total length between years had slopes which did not significantly differ (ANCOVA; $p > 0.3$). The regression equation for the 1994 length-dry-weight data is Ln DW = 3.8182 (TL) - 16.649 and the regression equation for the 1995 data is Ln DW = 3.8833 (TL) - 16.629.

Age-0 Walleye Mortality Rates

I estimated the mortality rate in 1994 using catch data from 19 May - 6 June (Figure 14) for fish ranging in size from 9.9 mm on 19 May to 25 mm on 6 June (Figure 29). In 1995 I used catch data from 25 May - 13 June (Figure 14) when fish size ranged from 9.9 mm on 25 May to 21 mm on 13 June (Figure 29). These time periods defined the descending limb of the catch curves for pelagic larvae. Instantaneous mortality rates estimated for the period 19 May - 6 June 1994 and 25 May - 13 June 1995 were 0.078/day and 0.053/day respectively. The 95% confidence limits for these estimates are $0.191 \geq Z \geq -0.035$ for 1994 and $0.098 \geq Z \geq 0.009$ for 1995. These instantaneous estimates translate into total mortality rates of 75.4% and 73.4% for 1994 and 1995 respectively. Only the 1995 regression equation used to estimates Z is significant ($p = 0.017$); the 1994 regression is not significantly different from zero. Despite this result,

the ANCOVA test indicated that the slopes of these regression equations do not differ

from each other (Type III sums of squares; $p = 0.2371$).

Index of Year-Class Strength

Catch rate in Ohio Division of Wildlife August bottom trawl assessments indicate

that the 1994 walleye year-class is larger than that developing in 1995. The catch rate in

August 1994 was 18.2 age-0 walleye per hour of trawling but only 1.9 age-0 walleye per

hour in August 1995 (Ohio Division of Wildlife 1996).

Discussion

Age-0 Walleye Distribution and Abundance

My study is the first comprehensive examination of the dispersal and abundance of reef-spawned walleye larvae conducted in western Lake Erie. Fish (1932) provides perhaps the earliest study of larval fishes in Lake Erie, but did not include the western basin in her sampling. She does report that walleye larvae were found primarily in "the western part of the lake" from the middle of May until mid-June of 1928 and 1929. She also reported that walleye were a very common fish in Lake Erie and notes that young walleye may be seined in abundance in protected areas alongshore (Fish 1932).

More recent studies of the ichthyoplankton community in western Lake Erie originate from studies conducted by the Center for Lake Erie Area Research. Heniken (1977) reported that walleye larvae were most abundant ($0.1/1000$ m^3) in early May 1976 while Mizera et al. (1981) reported a peak density of $0.75/1,000$ m^3 on 30 April 1977. Heniken's (1977) sampling design was quite comprehensive both spatially and temporally. He sampled 25 to 60 sites at 10-day intervals in western Lake Erie including Maumee and Sandusky Bays and areas within the Bass Islands archipelago from mid-April through August in 1975 and 1976. Mizera et al. (1981) sampled only nearshore (< 5 m) sites along the MI and OH shores and in Maumee Bay.

My peak density estimates for 1994 and 1995 exceed all of the previously mentioned values. These differences may be attributed to differences in spawning stock

size between the sampling periods. Stock size averaged only 4-9 million adults in 1975-77 (Deriso et al. 1988) but exceeded 40 million in 1994 and 1995 (Lake Erie Walleye Task Group 1995). Differences in sampling design and gear are also likely to influence the comparability of these estimates. I used a larger sampler (2.0 m^2 mouth) than Heniken (1977) and Mizera et al.(1981) who both employed a 0.75 m^2 mouth opening. The larger mouth opening allowed me to sample greater volumes of water than smaller samplers which is a more effective means of collecting small pelagic walleye fry.

Based on abundance estimates from Ohio Division of Wildlife index bottom trawls in August, the 1994 walleye year class is the third strongest year class since 1982 with a mean catch per effort of 19 fish/hour of trawling. The 1995 year class is the second weakest year class since 1983 with a mean catch of only 1.9 fish/hour of trawling (Ohio Division of Wildlife 1996). I used the sample correlation coefficient to determine the strength and significance of the relationship between larval peak abundance and abundance estimates in August bottom trawls. I used peak larval abundance estimates from Heniken (1977), Mizera et al. (1981) and this study and catch data from August bottom trawls reported by Ohio Division of Wildlife (1996). I found a positive, though insignificant at $\alpha = 0.05$, correlation (r = 0.699) between peak larval abundance and August catch per unit effort in bottom trawls. This relationship is significant at $\alpha = 0.10$ and could become significant at $\alpha = 0.05$ with only one more data point to increase the degrees of freedom.

The positive relationship between peak larval abundance and August abundance suggests that larval abundance does indeed forecast walleye year class strength in western

Lake Erie. I should also point out that the 1970's bottom trawl values are from inshore stations only and may not represent the entire year-class in these years. The Ohio Division of Wildlife implemented a comprehensive sampling program in the mid 1980's increasing sampling effort and covering a broader range of habitats in western Lake Erie. This sample design provides a more accurate estimate of walleye year-class strength as well as the Lake Erie fish community in general (Ohio Division of Wildlife 1996).

I found age-0 walleye to become concentrated in the nearshore areas southwest and southeast of the mid-lake reef complex in both years of this study. Because larval walleye are principally limnetic (Faber 1967) they are subject to passive transport by water currents in western Lake Erie (Houde 1969; Houde and Forney 1970). The generalized current patterns during the spring in the western basin explain the dispersal patterns observed in 1994 and 1995. Herdendorf and Braidech (1970) illustrate generalized surface current patterns in western Lake Erie in relation to predominant wind forces experienced in the spring. The general flow of water in western Lake Erie is from west to east (Herdendorf and Braidech 1970) and winds over western Lake Erie in the spring are predominately from the west/northwest or east/northeast (Table 3). These combinations of forces direct current patterns over the midlake reef complex in similar direction explaining how walleye larvae became distributed in the nearshore areas south and southeast of the reefs. I would expect a different dispersal and distribution pattern only if spring winds were strong (>20 km/hr) and from the south for the majority of the period when walleye larvae emerge from the reefs. This would cause water currents to

flow from south to north (Herdendorf and Braidech 1970) and move reef-spawned larvae out towards the open waters of western Lake Erie north of the reef complex.

In 1994 I observed 56% of all pelagic age-0 walleye collected to come from sites west of the reefs near Maumee Bay. Only 39% of the pelagic walleye collected in 1994 came from sites on and to the south-southeast of the reef complex. Because the majority of my catch in 1994 came from sites far to the west of the reefs, this may suggest that a large part of this relatively large walleye year-class originated in the Maumee River. In contrast, the weak 1995 year-class may be composed primarily of reef fish as 64% of all pelagic age-0 walleye collected in that year came from sites on the reef complex or south-southeast of it where prevailing water currents would have transported them.

Heniken (1977) reported concentrations of larval walleye at nearshore sites near Metzger Marsh and west of Catawba Island in 1976 (see Figure 13 for locations). Similarly, Parsons (1972) found large numbers of demersal age-0 walleye at inshore sites south and southwest of the reef complex during a bottom trawl survey conducted in July, 1959. His catches of age-0 walleye were highest at inshore sites 3-7 m deep from mid-June through mid-August. Parsons also reported high densities of age-0 walleye in bottom trawls taken along the Michigan shore from the mouth of the Detroit River south to the Raisin River and at the mouth of Sandusky Bay (Parsons 1972).

More recent bottom trawl sampling conducted by the Ohio Division of Wildlife Lake Erie Fisheries Unit from 1982 through 1995 indicate no substantial differences in the catch rates of age-0 walleye between inshore ($\leq$ 6 m) and offshore (> 6 m) sampling stations in August and October (Ohio Division of Wildlife 1996). However, bottom trawl

catches of age-0 walleye were generally higher near Maumee Bay and in areas of low water clarity (Lake Erie Fisheries Unit, Sandusky OH, unpublished data). It should be noted, however, that the Lake Erie Fisheries Unit does not sample in the nearshore area southeast and southwest of the reef complex from Port Clinton west to Bono (see Figure 13 for locations).

Age-0 Walleye Diets

I observed calanoid copepods and large cladocerans to be the mainstay of pelagic age-0 walleye diets in both years. Fish became increasingly prevalent in diets as larvae grew and transformed to demersal juveniles. The increased occurrence of fish in age-0 walleye diets is also associated with increased abundance of ichthyoplankton in the environment. Age-0 walleye became primarily piscivorous by early June in 1994 but zooplankton remained an important part of the age-0 walleye diet until mid June in 1995.

Studies by Hohn (1966) and Paulus (1969) indicated that the first food of walleye larvae less than 9.0 mm TL in western Lake Erie in the 1960's was diatoms. Both of these authors indicated that zooplankton, primarily cyclopoid copepods, became increasingly abundant in larval diets as growth exceeded 9.0 mm. While I found no diatoms or phytoplankton of any kind in walleye diets, I did observe small cladocerans, rotifers, and copepod nauplii in the diets of some small (<11.0 mm TL) walleye larvae while calanoid copepods and large cladocerans dominated the diet above this size range. I also found *Leptodora kindtii*, a large cladoceran, among the stomach contents of age-0

walleye in late May and June. Hurley (1986) observed *Leptodora kindtii* to be the dominant component of age-0 walleye diets in the Bay of Quinte, Ontario.

Changes in the phytoplankton and zooplankton community associated with changes in the trophic status of western Lake Erie are probably responsible for the observed differences in larval walleye diets between the 1960's results and this study. Western Lake Erie was considered hyper-eutrophic in the 1960's due to excessive phosphorous loading and is more recently classified as mesotrophic (Makarewicz and Bertram 1991). Hohn (1966) reported that diatoms accounted for nearly 100% of the total phytoplankton during his study of larval walleye diets and that *Fragilaria capucina*, an eutrophic indicator species was highly abundant. The abundance of this species of diatom has decreased by over 90% since the 1960's and the overall number of dominant eutrophic diatoms has decreased dramatically in western Lake Erie (Makarewicz and Bertram 1991).

The species composition and abundance of zooplankton also reflects the trophic status of lakes. Eutrophic systems typically contain higher cyclopoid copepod and cladoceran biomass than oligotrophic systems (Gannon and Stemberger 1978). Watson (1976) found that cyclopoid copepods were the most abundant crustacean zooplankton species in Lake Erie in 1970 whereas I observed more calanoid copepods in both years of this study. Paulus (1969) found that *Cyclops bicuspidatus* was the dominant species in the zooplankton community and reports no calanoid species at all during his investigation in 1964 and 1965.

I found a variety of items in pelagic larval walleye diets but electivity index values indicated selection for calanoid copepods and large cladocerans having a mean body size of about 1 mm. Houde (1967) and Graham and Sprules (1992) found that first-feeding walleye larvae in Oneida Lake, NY actively selected copepods as prey and Spykerman (1974) found similar results for walleye larvae in Clear Lake, IA. Mathias and Li (1982) concluded that most postlarval walleye are primarily zooplanktivorous. Walleye larvae are gape-limited predators and observations indicate a less than 5% capture success rate when feeding on 1.2 mm Daphnia in a closed system (Mathias and Li 1982). Feeding success of walleye larvae depends on vision and their ability to pursue and capture prey as well as prey size and escape mechanisms (Mathias and Li 1982; Raisanen and Applegate 1983; Graham and Sprules 1992).

Rapid growth during the larval stage is critical for survival of age-0 fish (Miller et al. 1988) so consumption of the most energetically profitable prey type is essential. Researchers seem to disagree on whether prey size or species is most important to young fish in prey selection. Mathias and Li (1982) and Fox (1989) concur that the size of the prey item is important in optimizing larval growth while Confer and Lake (1987) found that fish grow at different rates when fed the same biomass of different prey species. My results indicate that walleye larvae from western Lake Erie select taxonomic groups of zooplankton prey but the size structure of the prey ingested does not differ greatly from that observed in the zooplankton community.

Piscivory in walleye begins with cohort cannibalism (Li and Mathias 1982) and cannibalism has been shown to cause high mortality in walleye culture operations

(Nickum 1978). The incidence of cannibalism is low among age-0 walleye in lakes (Mathias and Li 1982). In support of this, I observed no evidence of cannibalism by age-0 walleye in this study.

Many studies have surmised that size of prey fish relative to the size of walleye is an important factor in regulating the success of a year-class, particularly when stocking age-0 walleye into a system (Madenjian et al. 1991; Jensen 1992). Therefore, it also makes sense that the sooner walleye larvae can grow to a size where piscivory is possible, both growth and survival potential will be increased. I observed faster growth and an earlier onset of piscivory in 1994 than 1995. Ichthyoplankton prey were also much more abundant in May and early June of 1994 potentially increasing the encounter rate with age-0 walleye.

Fish were uncommon in pelagic age-0 walleye diets in 1994 and 1995 but increased in importance in June when the walleye cohorts became demersal. Age-0 walleye were almost exclusively piscivorous by the end of June, and except for the occasional benthic invertebrate, remained piscivorous through fall of 1994. Soft rayed prey occurred more frequently in age-0 walleye diets but I did observe changes in prey use throughout the summer and fall of 1994. Hartman and Margraf (1992) found age-0 walleye in western Lake Erie to be exclusively piscivorous in late June of 1986, 1987, and 1988 with *Morone* species comprising > 50% of their diet in all 3 years. In contrast, Knight et al. (1984) found that age-0 walleye were primarily piscivorous after July in 1979, 1980 and 1981 and that soft rayed fish species dominated the diets in these years.

Age-0 Walleye Growth

Age-0 walleye grew faster in 1994 than 1995, reaching 46 mm TL by the end of

June in 1994 and only 25 mm by the same time in 1995. Differences in water warming

rate and prey abundance between the two years readily explain these differences in

growth rate. Slower water warming rates during egg incubation resulted in later hatching

in 1995 (Roseman et al. 1996; also see Chapter 1). Water warming rates are positively

related to age-0 walleye growth in many systems, especially for pelagic larvae (Forney

1976; Serns 1982). Water temperature dictates physiological function rates in walleye by

limiting fish activity and digestive rates (Kitchell et al. 1977). Not only is water

temperature directly related to physiological rates in fish, but it also influences the timing

and production of prey biomass. Phytoplankton and zooplankton production rates are

positively related to water temperature (Mills and Forney 1988). The timing of spawning

and the duration of incubation periods influence the production of ichthyoplankton in

western Lake Erie (Hamley et al. 1983) and thus the availability of prey for piscivores.

Slower water warming rates can delay spawning and embryonic development resulting in

low prey abundance.

Food limitation also affects the growth of young walleye. Age-0 walleye growth

has been positively related to the abundance of young yellow perch in many lakes

(Carlander and Payne 1977; Kempinger and Churchill 1972; Mills and Forney 1988).

Fox (1989) discovered that walleye growth rate was influenced by chironomid density in

the benthos and, to a lesser degree, zooplankton biomass. Similarly, Kelso's (1972)

experiments showed a positive relationship between ration and walleye growth rate.

Madenjian's (1991) individual-based model of age-0 walleye growth found that fish in

Lake Erie encountered prey at a much higher rate than in Oneida Lake, NY explaining the

greater growth observed for Lake Erie fish.

Comparisons of the total lengths of age-0 walleye in late June that I observed with

previous observations from other studies indicate that fish grew slower in both 1994 and

1995 than in many previous years. I found walleye lengths averaging 40 and 28 mm TL

in late June of 1994 and 1995 respectively. Parsons (1972) reported a mean length of 63

mm in late June for the 1959 year class while Wolfert (1966) reported a mean length of

55 mm in late June 1962. Hatch et al. (1987) described factors causing the decline in

mean length of age-0 walleye in fall and Knight and Vondracek (1993) described changes

in prey fish populations in relation to walleye growth and predation in western Lake Erie.

Both studies attribute the decline in first year growth of walleye to increased walleye

stock size and reductions in phosphorous loading.

Age-0 Walleye Mortality Rates

My survival estimates are for three week periods during the larval period when the

fish are pelagic and vulnerable to my sampling gear. At present, these are the best values

I can estimate pending further study. My estimates are plagued with potential bias from

several sources. First, I currently have no estimates of size-selective avoidance and

therefore have not adjusted my catches accordingly. Noble (1972) adjusted his catches of

larval walleye collected in Miller samplers by employing an electric grid to incapacitate

and disorient fish and adjusted his catches accordingly. I attempted to sample at night to

create an adjustment factor for Lake Erie walleye collected in the neuston net, but my

night sampling produced no more walleye than the day sampling. If they had, I would

wonder if the increased catch was due to a lack of avoidance or vertical migration by the

fish.

Another factor potentially influencing my survival estimates is the immigration of

river-spawned walleye larvae into my population of reef spawned fish. This would tend to

artificially deflate my estimates of mortality. I sampled the Toussaint and Portage Rivers

in 1995 during the time I observed pelagic walleye in the lake and found no walleye

larvae. Upon investigation, these rivers proved to have no suitable spawning areas for

walleye. Researchers at Ohio State University are currently examining outmigration

patterns of river-spawned walleye from the Maumee and Sandusky River. A comparison

of dispersal patterns between reef- and river-spawned larvae is planned and may elucidate

relative contributions of each spawning stock to the general Lake Erie population.

The relative strength of the year classes developed in 1994 and 1995 differed by a

factor of 14 during the pelagic larval period. This factor was reduced to 9.6 according to

relative abundance estimates from August bottom trawls. This could be due to greater

mortality occurring during the summer of 1994, an influx of river-spawned fish in 1995,

or a combination of the two.

Studies in other systems and culture ponds show wide variability in mortality rates

and my mortality estimates fit into the range of reported values found in the literature.

Instantaneous mortality rates ranged from 0.201 to 0.310 for stocked walleye fry in

Oneida Lake, NY (Noble 1972; Forney 1975). Fox (1989) found instantaneous mortality

rates to range from 0.0055/day to 0.087/day for fish stocked in ponds as sac-fry and recovered at 46 mm TL. Te Brugge and McQueen (1991) reported instantaneous mortality rates ranging from 0.016/day to 0.028/day for walleye over a 50 day period (9.3 to 30 mm TL) in enclosures placed in Lake St. George, Ontario. Instantaneous mortality rates ranged from 0.067/day to 0.26/day for stocked sac-fry to 20 days poststocking in Rathbun Lake, IA (Mitzner 1992).

THESIS SUMMARY

Great disparity in year-class strength of reef spawned walleye in Lake Erie is apparent in the egg stage. Egg density in 1994 was approximately twice that observed in 1995 and egg survival was 2.8 times better in 1994. The product of these factors provides an initial year-class disparity factor of nearly 6. I observed pelagic walleye larvae to be 14 times more abundant in 1994 than 1995. Because white perch were present on the reefs during late April and May 1995, the walleye hatch period, significant numbers of walleye larvae may have been removed by predation. The year-class disparity was reduced to a factor of 9.6 by August as estimated by relative abundance in bottom trawls indicating that either mortality was greater during the summer months in 1994 or more river-spawned walleye entered the population in 1995.

The rate of water warming in the spring during both the egg and larval stages appears to be the driving force behind survival of these life stages. Slower warming rates prolong incubation increasing egg vulnerability to adverse conditions. The frequent intense wind events during the incubation period are largely responsible for removing walleye eggs from reefs while predation by fishes is probably detrimental to a lesser degree. Slower warming rates also delay prey production inhibiting walleye growth and

lengthening the duration of the larval stage and the walleye's dependence on zooplankton

prey.

APPENDICES

Appendix 1. Walleye larval and egg sample site coordinates and depths (m).

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Larval Sample Sites

Site #	Latitude	Longitude	Depth
1	41º 37.7'	83º 01.4'	4
2	41º 39.8'	82º 58.2'	4
3	41º 37.4'	82º 59.8'	7
4	41º 39.8'	82º 56.2'	11
5	41º 37.2'	83º 01.7'	6
6	41º 40.3'	82º 59.6'	10
7	41º 38.6'	83º 01.3'	7
8	41º 40.8'	82º 58.4'	10
9	41º 38.2'	82º 57.7'	7
10	41º 36.8'	82º 58.3'	9
11	41º 39.5'	82º 53.8'	10
12	41º 38.1'	82º 55.2'	9
13	41º 39.6'	83º 03.0'	7
14	41º 40.8'	83º 01.6'	10
15	41º 41.8'	82º 55.2'	11
16	41º 42.5'	83º 01.2'	11
17	41º 40.1'	83º 05.0'	8
18	41º 42.5'	83º 03.8'	10
19	41º 38.0'	83º 05.8'	4
19-I	41º 37.6'	83º 05.8'	3
20	41º 38.3'	83º 09.7'	6
20-I	41º 37.9'	83º 09.7'	3
21	41º 40.5'	83º 09.7'	8
22	41º 42.8'	83º 09.7'	9
23	41º 41.2'	83º 14.8'	6
24	41º 43.1'	83º 14.8'	8
25	41º 38.1'	82º 52.0'	10
25-I	41º 38.2'	82º 51.6'	4
26	41º 35.8'	82º 54.7'	9
27	41º 33.9'	82º 56.0'	7
28	41º 32.0'	82º 55.5'	5
29	41º 32.9'	82º 53.6'	6
29-I	41º 32.7'	82º 53.0'	3
30	41º 35.6'	82º 51.5'	8
31	41º 42.0'	82º 58.5'	11
32	41º 35.0'	83º 02.0'	5

Appendix 1 continued.

Site #	Latitude	Longitude	Depth
32-I	41° 34.7'	83° 02.1'	3
33	41° 33.2'	82° 59.0'	7
34	41° 34.8'	82° 58.0'	5
34-I	41° 34.0'	82° 58.0'	3
35			3
Metzger Marsh			3

Egg Sample Sites

Toussaint Reef

Site #	Latitude	Longitude	Depth
1	41 37.75	83 01.15	<3
2	41 37.85	83 01.07	3-5
3	41 37.92	83 00.80	<3
4	41 37.88	83 00.68	3-5
5	41 38.05	83 01.05	5-7
6	41 37.84	83 01.31	5-7
7	41 37.76	83 00.93	5-7

Niagara Reef

Site #	Latitude	Longitude	Depth
1	41 39.90	82 58.45	<3
2	41 39.85	82 58.55	3-5
3	41 39.95	82 58.45	3-5
4	41 40.05	82 58.41	3-5
5	41 40.00	82 58.80	3-5
6	41 39.95	82 59.00	5-7
7	41 39.80	82 59.00	5-7
8	41 39.85	82 58.75	3-5

Appendix 2. Catch-at-age model predictions. Walleye abundance for individual age-classes and estimates of annual survival rate for 1985 - 1995 used to expand the CAGEAN model through age-11 for fecundity estimates (data from Walleye Task Group 1995).

Year	Age-6	Age-7	Age-8	Age-9	Age-10	Age-11	Survival
1989	2,282,695						0.6587
1990	6,189,432	1,503,611					0.6724
1991	6,076,526	4,161,774	1,011,028				0.6734
1992	1,2403,136	4,091,933	2,802,539	680,826			0.6628
1993	3,138,270	8,220,799	2,712,133	1,857,523	451,252		0.6310
1994	2,599,297	1,980,248	5,187,324	1,711,356	1,172,097	284,740	0.6254
1995	1,086,000	1,625,600	1,238,447	3,244,152	1,070,282	733,029	0.6606

Appendix 3. Length-dry weight relationships for species collected in western Lake Erie, 1994 and 1995. Relationship equation is simple linear regression of Ln transformed standard lengths (SL) and dry weights (DW(g)) for species listed; N = sample size; CL = carapace length for amphipods.

Species	Size Range (mm SL)	Relationship Ln DW=m(SL)+b	N	p-value	R^2
1994					
Alewife	29.0 - 95.0	3.450 (SL)-14.365	55	< 0.001	0.98
Amphipoda	4.0 - 12.2	0.00052 (CL) - 0.00235	26	< 0.001	0.87
Clupeidae Larvae	8.5 - 25.5	6.193 (SL) - 23.532	60	< 0.001	0.97
Cyrpinidae Larvae	7.0 - 18.1	3.063 (SL) - 14.227	116	< 0.001	0.76
Emerald Shiner	21.0 - 43.0	2.649 (SL) - 11.749	26	< 0.001	0.95
Freshwater Drum	8.0 - 50.0	3.457 (SL) - 14.471	8	< 0.001	0.95
Gizzard Shad	11.0 - 111.0	4.277 (SL) - 17.915	89	< 0.001	0.99
Johnny Darter	49.0 - 60.0	4.582 (SL) - 18.902	5	0.001	0.97
Logperch	35.0 - 69.0	3.359 (SL) - 14.083	12	< 0.001	0.95
Morone sp. Larvae	6.0 - 80.0	3.765 (SL) - 15.146	418	<0.001	0.98
Rainbow Smelt	16.0 - 53.0	3.085 (SL) - 13.6842	66	<0.001	0.76
Spottail Shiner	30.0 - 93.0	3.411 (SL) - 14.170	62	< 0.001	0.97
Troutperch	12.5 - 87.0	3.310 (SL) - 13.8511	106	<0.001	0.99
Yellow Perch	11.0 - 80.0	3.295 (SL) - 13.829	269	<0.001	0.99

Appendix 3, continued.

Species	Size Range (mm SL)	Relationship LN DW=m(SL)+b	N	p-value	R^2
1995					
Catastomidae Larvae	5.0 - 6.5	3.035 (SL) - 14.359	6	0.103	0.53
Channel Catfish	32.0 - 96	3.267 (SL) - 14.557	14	< 0.001	0.99
Clupiedae Larvae	6.0 - 46.5	4.875 (SL) - 19.773	111	< 0.001	0.96
Cyprinidae Larvae	4.5 - 9.0	1.221 (SL) - 11.297	9	0.124	0.30
Emerald Shiner	44.0 - 71.0	3.385 (SL) - 14.350	26	<0.001	0.95
Freshwater Drum	5.0 - 94.0	3.485 (SL) - 14.425	31	<0.001	0.99
Gizzard Shad	54.0 - 104.0	0.033 (SL) - 2.963	32	< 0.001	0.98
Johnny Darter	30.0 - 36.0	3.158 (SL) - 13.359	6	0.016	0.80
Morone sp. Larvae	6.5 - 72.0	3.950 (SL) - 15.677	112	< 0.001	0.95
Rainbow Smelt	19.0 - 45.0	4.076 (SL) - 17.741	38	<0.001	0.88
Spottail Shiner	19.0 - 99.0	3.390 (SL) - 14.057	103	<0.001	0.99
Troutperch	8.0 - 77.0	3.552 (SL) - 14.729	63	< 0.001	0.99
White Perch	35.0 - 73.0	3.509 (SL) - 14.241	63	< 0.001	0.97
Yellow Perch	8.5 - 62.0	3.926 (SL) - 16.005	76	< 0.001	0.95

Appendix 4. List of genera and families included in functional prey groups.

Functional Prey Group	Species
Rotifers	Rotatoria
Small Cladocerans	Bosminidae, Chydoridae, *Sida crystallina, Ceriodaphnia sp.*
Cyclopoid Copepods	*Acanthocyclops vernalis, Eurytemora affinis, Diacyclops thomasi, Mesocyclops edax, Tropocyclops prasinus mexicanus*
Calanoid Copepods	*Epischura lacustris, Leptodiaptomus sicilis, Leptodiaptomus minutus, Skistodiaptomus oregonensis*
Large Cladocerans	*Daphnia galeata mendotae, Daphnia retrocurva, Leptodora kindtii, Diaphanosoma birgei*
Benthic Prey	Chironomidae, Hexagenia
Spiny Rayed Fish	*Aplodinotus grunniens, Morone spp., Perca flavescens, Percina caprodes, Percopsis omiscomaycus*
Soft Rayed Fish	Catastomidae, Clupeidae, Cyprinidae, Osmeridae

Appendix 5. Densities (#/1,000 m^3) of larval fishes collected in neuston nets at each site in 1994 and 1995.

1994 Burbot (*Lota lota*)

Site #	2 May
1	1.9
2	0.0
3	0.0
4	3.5
5	1.9
6	0.0
7	0.0
8	2.2
9	0.0
10	0.0
11	0.0
12	0.0
13	0.0
14	0.0
15	0.0
17	0.0
18	0.0
19	0.0
20	5.5
21	0.0
22	0.0
23	0.0
24	0.0
25	0.0
26	0.0
27	0.0
28	0.0
29	0.0
30	0.0
31	0.0
32	2.3
33	0.0
34	0.0
MM	0.0

Appendix 5, continued.

1994 Catastomidae

Site #	19 May	23 May	30 May	6 Jun
1	0.0	0.0	2.0	0.0
2	0.0	0.0	0.0	0.0
7	0.0	0.0	0.0	0.0
8	0.0	0.0	5.5	0.0
9	0.0	0.0	0.0	
10	0.0	0.0	0.0	
11	0.0	0.0	0.0	1.7
12	0.0	0.0		
13	0.0	0.0		0.0
14	0.0	0.0	0.0	0.0
15	0.0	0.0	0.0	
17	0.0	0.0	0.0	0.0
18	0.0	0.0	0.0	
19	0.0	2.5	0.0	0.0
19I			0.0	0.0
20	0.0	0.0	0.0	0.0
21	0.0	0.0		
22	0.0	0.0	0.0	0.0
23	3.1	0.0	0.0	0.0
24	0.0	0.0	0.0	
25	0.0	0.0	0.0	
25I			0.0	0.0
26	0.0	0.0	0.0	0.0
27	0.0	0.0	0.0	0.0
28	0.0	0.0	0.0	0.0
29	0.0	0.0	0.0	0.0
29I			0.0	0.0
30	0.0	0.0	0.0	1.6
30I			0.0	0.0
31	0.0			
32	0.0	0.0	0.0	0.0
32I			0.0	0.0
33	0.0	0.0	0.0	
34	0.0	0.0	2.0	1.7
34I			0.0	0.0
MM	0.0	0.0	22.8	0.0

Appendix 5, continued.

1994 Centrarchidae

Site #	23 May
1	0.0
2	0.0
7	0.0
8	0.0
9	0.0
10	0.0
11	0.0
12	0.0
13	0.0
14	0.0
15	0.0
17	0.0
18	0.0
19	0.0
20	0.0
21	0.0
22	0.0
23	0.0
24	0.0
25	0.0
26	0.0
27	0.0
28	0.0
29	0.0
30	0.0
32	13.4
33	0.0
34	0.0
MM	0.0

Appendix 5, continued.

1994 Cluepidae

Site #	19 May	23 May	30 May	6 Jun	9 Jun	13 Jun	28 Jun
1	0.0	0.0	74.8	0.0	27.9	1.5	0.0
2	0.0	0.0	0.0	1.6	4.6	1.5	1.6
7	0.0	0.0	51.0	0.0	5.6	1.6	
8	0.0	0.0	103.8	0.0	42.5	3.1	
9	0.0	0.0	0.0				
10	0.0	0.0	0.0		124.6	0.0	111.9
11	0.0	0.0	0.0	1.7			
12	10.6	0.0					
13	0.0	0.0		0.0			
14	0.0	0.0	5.3	0.0			
15	0.0	0.0	0.0				
17	0.0	0.0	0.0	0.0			
18	0.0	0.0	2.2				
19	0.0	2.5	280.1	19.7	46.2	6.2	256.9
19I			28.4	0.0			
20	0.0	0.0	0.0	1.6		13.7	
21	7.0	0.0			2536.9	1339.6	
22	0.0	0.0	0.0	0.0	576.9		
23	389.6	111.4	18.6	0.0		166.0	
24	0.0	0.0	7.1			4.7	
25	0.0	0.0	57.2			1.5	
25I			0.0	0.0		0.0	0.0
26	0.0	0.0	2.1	0.0		15.3	
27	0.0	0.0	8.8	0.0			
28	0.0	0.0	121.0	860.4			1584.8
29	0.0	0.0	6.9	0.0		23.0	1.6
29I			16.5	0.0		0.0	
30	0.0	0.0	2271.7	0.0			
30I			0.0	0.0		3.2	
31	0.0						
32	0.0	827.2	6.7	309.2		1697.2	
32I			0.0	1.8		67.1	462.0
33	0.0	4.9	2.0				
34	0.0	0.0	8.1	5.1	183.7		34.8
34I			2.0	0.0		75.0	
MM	0.0	33.2	1351.9	117.3	6912.3	54.0	

Appendix 5, continued.

1994 Cyprinidae

Site #	2 May	30 May	6 Jun	9 Jun	13 Jun	20 Jun	28 Jun
1	0.0	13.8	1.8	1.5	27.7	0.0	0.0
2	0.0	15.3	0.0	0.0	19.1	0.0	140.5
3	0.0						
4	0.0						
5	0.0						
6	0.0						
7	0.0	4.1	0.0	0.0	171.4	0.0	
8	2.2	0.0	0.0	0.0	241.1	0.0	
9	0.0	8.5					
10	0.0	0.0		0.0	449.0	0.0	24.3
11	0.0	0.0	0.0			0.0	
12	0.0						
13	0.0		0.0				
14	0.0	0.0	0.0				
15	0.0	0.0					
17	0.0	0.0	0.0				
18	0.0	0.0					
19	0.0	4.3	1.1	0.0	45.1	1530.2	115.1
19I		30.6	0.0			0.0	
20	0.0	2.5	0.0		71.4	0.0	
21	0.0			0.0	1.6		
22	0.0	0.0	0.0	81.4			
23	0.0	4.6	0.0		1.6		
24	0.0	0.0			4.7	0.0	
25	0.0	0.0			429.5	1037.9	
25I		0.0	0.0		0.0	0.0	23.6
26	0.0	0.0	1.6		15.3	3.2	
27	0.0	0.0	0.0			0.0	
28	0.0	2.0	18.7			0.0	19391.7
29	0.0	20.8	0.0		21.5	8.3	365.6
29I		0.0	0.0		16.5	0.0	
30	0.0	29.2	12.6				
30I		0.0	1.5		1.6	0.0	
31	0.0						
32	0.0	0.0	1.8		392.4		
32I		0.0	3.6		191.6	34.7	0.0
33	0.0	2.0					
34	0.0	8.1	0.0	0.0			1027.2
34I		0.0	1.4		106.5	0.0	
MM		37.3	8.3	0.0	20.0	205.8	

Appendix 5, continued.

1994 Freshwater Drum

Site #	19 May	9 Jun	13 Jun	20 Jun	28 Jun
1	0.0	0.0	0.0	0.0	0.0
2	0.0	0.0	0.0	0.0	0.0
7	0.0	0.0	0.0	0.0	
8	0.0	0.0	0.0	0.0	
9	0.0				
10	0.0	0.0	0.0	0.0	0.0
11	0.0				
12	0.0				
13	0.0				
14	0.0				
15	0.0				
17	0.0				
18	0.0				
19	0.0	0.0	0.0	3.7	0.0
19I				0.0	
20	0.0		0.0	0.0	
21	0.0	0.0	0.0		
22	0.0	0.0			
23	0.0		0.0		
24	0.0		0.0	0.0	
25	0.0		0.0	0.0	
25I			0.0	0.0	0.0
26	0.0		0.0	0.0	
27	0.0			0.0	
28	0.0			0.0	0.0
29	0.0		0.0	0.0	1.6
29I			0.0	0.0	
30	0.0				
31	0.0				
32	0.0		6.2		
32I			0.0	0.0	0.0
33	0.0				
34	24.4	15.2			0.0
34I			0.0	0.0	
MM	0.0	0.0	0.0	0.0	

Appendix 5, continued.

1994 Channel Catfish

Site #	13 Jun
1	0.0
2	0.0
7	0.0
8	0.0
10	0.0
19	0.0
20	0.0
21	0.0
23	0.0
24	0.0
25	0.0
25I	0.0
26	0.0
29	0.0
29I	0.0
30I	0.0
32	1.5
32I	0.0
34I	0.0
MM	0.0

Appendix 5, continued.

1994 Logperch

Site #	19 May	6 Jun	9 Jun	13 Jun
1	0.0	0.0	0.0	0.0
2	0.0	0.0	0.0	0.0
7	0.0	0.0	0.0	0.0
8	0.0	0.0	9.1	0.0
9	0.0			
10	0.0		0.0	0.0
11	0.0	0.0		
12	0.0			
13	0.0	0.0		
14	0.0	0.0		
15	0.0			
17	0.0	0.0		
18	0.0			
19	0.0	0.0	0.0	0.0
19I		0.0		
20	0.0	0.0		0.0
21	0.0		6.1	0.0
22	0.0	0.0	0.0	
23	15.5	0.0		17.2
24	0.0			0.0
25	0.0			0.0
25I		0.0		0.0
26	0.0	0.0		0.0
27	0.0	0.0		
28	0.0	0.0		
29	0.0	0.0		0.0
29I		0.0		0.0
30	0.0	0.0		
30I		0.0		0.0
31	0.0			
32	0.0	1.8		3.1
32I		0.0		0.0
33	0.0			
34	0.0	0.0	0.0	
34I		0.0		0.0
MM	3.1	0.0	0.0	4.0

Appendix 5, continued.

1994 Lake Whitefish.

Site #	4 Apr	29 Apr	2 May	19 May
1		62.0	13.0	0.0
2			7.8	0.0
3			7.1	
4			0.0	
5		36.5	24.1	
6			0.0	
7			0.0	0.0
8			4.3	0.0
9			1.9	0.0
10			1.8	0.0
11			0.0	0.0
12			0.0	0.0
13			6.9	0.0
14			5.3	0.0
15			0.0	0.0
17			12.5	0.0
18			9.4	0.0
19	1.7		12.4	0.0
20			23.9	0.0
21			9.6	0.0
22			0.0	0.0
23			55.5	0.0
24			13.3	0.0
25			3.1	0.0
26			0.0	8.3
27			14.0	0.0
28			11.8	2.4
29			0.0	0.0
30			70.0	0.0
31			3.2	0.0
32		154.3	36.2	0.0
33		41.5	7.4	0.0
34		8.1	2.3	0.0
MM				6.2

Appendix 5, continued.

1994 Morone spp.

Site #	19 May	23 May	30 May	6 Jun	9 Jun	13 Jun	20 Jun	28 Jun
1	0.0	5.8	78.7	28.6	6.2	4.6	0.0	1.7
2	0.0	175.9	13.1	13.1	1.5	1.5	0.0	0.0
7	0.0	0.0	142.7	1.8	2.8	3.2	0.0	
8	0.0	0.0	0.0	0.0	1.5	12.3	0.0	
9	0.0	8.3	2.1					
10	0.0	14.7	6.8		6.2	13.8	0.0	0.0
11	0.0	0.0	0.0	0.0			0.0	
12	0.0	0.0						
13	0.0	0.0		0.0				
14	0.0	0.0	0.0	0.0				
15	0.0	6.3	0.0					
17	0.0	0.0	0.0	6.1				
18	0.0	0.0	0.0					
19	36.6	5.0	157.3	28.5	6.2	4.7	5.6	12.6
19I			238.3	0.0			0.0	
20	6.7	0.0	427.4	6.5		0.0	0.0	
21	7.0	14.6			457.5	42.4		
22	29.4	0.0	4.1	0.0	109.0			
23	408.2	0.0	315.5	9.5		0.0		
24	114.3	0.0	7.1			1.6	0.0	
25	0.0	0.0	45.8			16.6	0.0	
25I			0.0	0.0		0.0	0.0	0.0
26	0.0	0.0	2.1	0.0		0.0	0.0	
27	0.0	6.2	4.4	0.0			0.0	
28	2.4	4.2	62.5	297.6			0.0	88.0
29	2.6	45.7	85.5	0.0		3.1	165.7	0.0
29I			0.0	0.0		0.0	0.0	
30	18.1	0.0	43.8	0.0				
30I			0.0	0.0			4.8	0.0
31	0.0							
32	5.0	3.4	250.3	126.9		2386.5		
32I			0.0	5.3		27.8	173.6	357.3
33	5.1	0.0	5.9					
34	0.0	0.0	264.1	17.0	2209.2			0.0
34I			21.7	0.0		225.1	1.8	
MM	0.0	0.0	740.2	82.8	2950.8	431.8	3212.7	

Appendix 5, continued.

1994 Northern Pike (*Esox lucious*)

Site #	19 May
1	0.0
2	0.0
7	0.0
8	0.0
9	0.0
10	0.0
11	0.0
12	0.0
13	0.0
14	0.0
15	0.0
17	0.0
18	0.0
19	0.0
20	0.0
21	0.0
22	0.0
23	0.0
24	0.0
25	0.0
26	0.0
27	0.0
28	0.0
29	0.0
30	0.0
31	0.0
32	0.0
33	0.0
34	0.0
MM	3.1

Appendix 5, continued.

1994 Rainbow smelt (*Osmeris mordax*)

Site #	13 Jun	20 Jun
1	0.0	0.0
2	0.0	0.0
7	0.0	0.0
8	0.0	0.0
10	0.0	0.0
19	0.0	0.0
19I		0.0
20	0.0	0.0
21	1.6	
23	0.0	
24	0.0	0.0
25	0.0	0.0
25I	0.0	0.0
26	0.0	1.6
27		0.0
28		0.0
29	0.0	0.0
29I	0.0	0.0
30I	0.0	0.0
32	0.0	
32I	0.0	0.0
34I	0.0	0.0
MM	0.0	3.8

Appendix 5, continued.

1994 Troutperch

Site #	28 Jun
1	0.0
2	0.0
10	0.0
19	0.0
25I	0.0
28	0.0
29	6.5
32I	0.0
34	0.0

Appendix 5, continued.

1994 Walleye

Site #	29 Apr	2 May	19 May	23 May	30 May	6 Jun	9 Jun	20 Jun
1	43.5	88.9	0.0	17.5	0.0	0.0	0.0	0.0
2		23.5	0.0	94.7	0.0	0.0	0.0	0.0
3		7.1						
5	26.9	20.4						
7			2.4	0.0	0.0	0.0	0.0	0.0
8			0.0	22.5	0.0	0.0	0.0	0.0
9		3.9	0.0	0.0	0.0			
10		32.2	8.0	0.0	0.0		0.0	0.0
11			0.0	0.0	0.0	0.0		
12			0.0	0.0				
13		3.4	0.0	0.0		0.0		
14			0.0	0.0	0.0	0.0		
15			0.0	0.0	0.0			
17		2.1	0.0	0.0	0.0	0.0		
18			0.0	0.0	0.0			
19		88.7	0.0	0.0	4.3	0.0	0.0	0.0
19I					0.0	0.0		
20		273.4	20.2	0.0	0.0	0.0		
21		23.0	0.0	0.0			112.5	0.0
22		2.2	0.0	3.3	0.0	0.0	1.5	
23		318.7	9.3	0.0	4.6	0.0		0.0
24		247.4	28.6	27.9	0.0			0.0
25		6.1	0.0	0.0	0.0			0.0
25I						0.0		0.0
26		25.7	99.8	0.0	0.0	0.0		0.0
27		39.8	192.2	15.4	0.0	0.0		
28		165.3	583.3	0.0	2.0	0.0		
29		357.3	26.3	91.4	2.3	0.0		0.0
29I					0.0	0.0		0.0
30		242.5	9.0	0.0	0.0	0.0		
30I					0.0	0.0		0.0
31		0.0	0.0					
32	73.7	488.9	29.8	16.8	2.2	1.8		0.0
32I			0.0		0.0	0.0		0.0
33	5.7	17.3	0.0	17.3	0.0			
34	0.0	563.1	0.0	2.8	0.0	0.0	141.2	
34I					0.0	0.0		0.0
MM		93.7	438.8	0.0	2.1	143.5	37.5	4.0

Appendix 5, continued.

1994 Yellow perch.

Site #	2 May	19 May	23 May	30 May	6 Jun	9 Jun	13 Jun	20 Jun
1	0.0	11.7	23.4	0.0	0.0	0.0	0.0	0.0
2	0.0	769.2	121.8	0.0	0.0	0.0	0.0	0.0
3	0.0							
4	0.0							
5	0.0							
6	0.0							
7	0.0	74.1	0.0	0.0	0.0	0.0	0.0	0.0
8	0.0	742.4	22.5	0.0	0.0	0.0	0.0	0.0
9	0.0	164.6	37.4	0.0				
10	0.0	140.5	32.4	2.3		50.7	0.0	0.0
11	0.0	17.4	0.0	0.0	0.0			0.0
12	0.0	105.7	0.0					
13	0.0		0.0		0.0			
14	0.0	656.1	0.0	0.0	0.0			
15	0.0	9.4	0.0	0.0				
17	0.0	2.5	0.0	0.0	0.0			
18	0.0	61.3	2.9	0.0				
19	0.0	256.4	0.0	2.2	0.0	21.5	0.0	0.0
19I				2.2	0.0			0.0
20	5.5	431.0	0.0	0.0	0.0		0.0	0.0
21	0.0	42.1	0.0.			65.4	106.7	
22	0.0	147.1	6.6	0.0	0.0	17.4		
23	9.0	52.6	0.0	0.0	1.2		3.1	
24	0.0	1142.9	27.9	2.4			0.0	0.0
25	0.0	280.9	9.7	0.0			0.0	0.0
25I					0.0		0.0	0.0
26	0.0	63.7	22.0	0.0	0.0		0.0	84.0
27	0.0	0.0	18.5	0.0	0.0			0.0
28	0.0	28.9	0.0	0.0	0.0			0.0
29	0.0	102.4	19.6	0.0	0.0		0.0	0.0
29I				0.0	0.0		0.0	0.0
30	0.0	153.7	0.0	14.6	0.0			
30I				0.0	0.0		0.0	0.0
31	0.0	185.0						
32	0.0	486.6	30.3	4.5	3.6		0.0	
32I			23.5	28.4	3.6		0.0	0.0
33	0.0	40.9	19.7	0.0				
34	0.0	0.0	0.0	0.0	0.0	56.2		
34I				0.0	0.0		0.0	0.0
MM	93.7	49.8	0.0	35.2	0.0	106.0	0.0	34.3

Appendix 5, continued.

1995 Catastomidae

Site #	19 May	26 May	30 May	5 Jun	13 Jun	19 Jun
1	0.0	0.0	0.0	0.0	0.0	17.5
2		0.0	0.0		0.0	
4	0.0					
5	0.0	0.0	1.6			
7	0.0	0.0	0.0			65.6
8		0.0				
10	0.0	0.0	0.0			
11	0.0	0.0	0.0			
12	0.0		0.0			
13	0.0	0.0				
14	0.0	0.0		0.0		
17	0.0	0.0		0.0	0.0	
18	0.0	0.0	0.0			
19		0.0		0.0	1.5	0.0
19I		0.0	0.0	0.0	0.0	0.0
20				0.0	0.0	1.5
20I		0.0	0.0	0.0	0.0	0.0
21		0.0		0.0		
22			0.0			
23				0.0	0.0	
24			0.0			
25	0.0					
25I	0.0	0.0	0.0	0.0		
26	0.0	0.0	0.0			
27	0.0	0.0	0.0			
28	1.9	0.0	0.0	0.0		
28I						0.0
29	0.0	0.0	0.0			3.3
29I	0.0	0.0	0.0	0.0		
30	0.0					3.3
30I		0.0		0.0	0.0	0.0
32	1.9	4.3	1.5			
32I	0.0	0.0	0.0			0.0
33	0.0	0.0	0.0			
34	1.8	1.8		0.0		
34I	0.0	0.0	0.0	0.0	0.0	0.0
35	0.0	0.0	0.0	1.9	7.8	0.0
MM	4.0		0.0	0.0	1.6	0.0

Appendix 5, continued.

1995 Centrarchidae

Site #	13 Jun
1	0.0
2	0.0
17	0.0
19	0.0
19I	0.0
20	0.0
20I	0.0
23	0.0
29I	0.0
30	1.5
34I	0.0
35	0.0
MM	0.0

Appendix 5, continued.

1995 Clupeidae.

Site #	12 May	19 May	26 May	30 May	5 Jun	13 Jun	19 Jun	26 Jun
1	0.0	0.0	16.4	4.6	3.5	5.9	1.6	
2	0.0		0.0	0.0		0.0		
3	0.0	0.0						
4	0.0	0.0						
5	0.0	0.0	0.0	0.0				
6	0.0							
7	0.0	0.0	0.0	0.0			55.5	
8	0.0		0.0					
9	0.0							
10	0.0	0.0	219.5	0.0				
11	0.0	0.0	0.0	0.0				
12	0.0	0.0		0.0				
13	0.0	3.8	1.9					
14	0.0	0.0	0.0		0.0			
15	0.0							
17	0.0	0.0	40.0		0.0	1.6		
18	0.0	0.0	0.0	0.0				
19	0.0	0.0	13.4		15.2	1.5	1.6	
19I	0.0	0.0	184.0	6.1	197.5	496.8	9.2	28.6
20		0.0			3.1	307.7	6.1	
20I	0.0	0.0	40.6	0.0	0.0	0.0	260.7	25.5
21	0.0	0.0	22.2		4.0			
22	0.0	0.0		0.0				
23	21.7	0.0			0.0	1.4		
24	1.8			8.3				
25	0.0	0.0						
25I	0.0	0.0	20.9	0.0	0.0			
26	0.0	0.0	104.4	13.6				
27	0.0	0.0	81.8	0.0				
28	0.0	0.0	15.8	0.0	5.4			
28I							3.1	
29	0.0	1.9	3.6	154.0				
29I		0.0	14.6	0.0	9.0	126.0	6.7	
30	0.0	0.0						
30I	0.0		13.9	9.0		0.0	4.7	
31	0.0							
31I	0.0							
32	0.0	26.6	176.4	1.5	49.9	311.8	70.0	
32I	0.0	31.6	349.1	194.5			36.8	
33	0.0	0.0	1344.8	1.6				
34	0.0	0.0	104.4	0.0	15.9			
34I		0.0	18.3	21.7	34.6	96.6	0.0	
35		0.0	14.8	355.5	7.5	12.5	0.0	
MM	0.0	0.0			4.5	1.6	9.8	7.8

Appendix 5, continued.

1995 Cyprinidae.

Site #	19 May	26 May	30 May	5 Jun	13 Jun	19 Jun
1	0.0	0.0	0.0	0.0	7.3	46.2
2		0.0	0.0		1.5	
3	0.0					
4	0.0					
5	0.0	0.0	0.0			
7	0.0	0.0	0.0			
8		0.0				
10	0.0	8.7	0.0			
11	0.0	0.0	0.0			
12	0.0		0.0			
13	0.0	0.0				
14	0.0	0.0		0.0		
17	0.0	0.0		0.0	0.0	
18	0.0	0.0	0.0			
19	0.0	13.4		0.0	0.0	3.2
19I	0.0	0.0	0.0	0.0	0.0	7.7
20	0.0			0.0	1.5	24.3
20I	0.0	0.0	0.0	0.0	3.1	46.3
21	0.0	3.7		0.0		
22	0.0		0.0			
23	0.0			0.0	1.4	
24			0.0			
25	0.0		4.7			
25I	0.0	0.0	0.0	0.0		
26	0.0	0.0	0.0			
27	0.0	0.0	0.0			
28	0.0	3.5	0.0	0.0		
28I						56.2
29	1.9	1.8	3.0			
29I	0.0	22.9	0.0	0.0	0.0	1.7
30	0.0					
30I		9.9		0.0	1.5	7.9
32	1.9	6.4	1.5			41.1
32I	0.0	4.0	0.0			12.7
33	0.0	0.0	1.6			
34	0.0	3.7		1.8		
34I	0.0	1.8	0.0	0.0	0.0	106.7
35	2.0	1.9	0.0	1.9	0.0	1.6
MM	0.0		0.0	0.0	1.6	4.7

Appendix 5, continued.

1995 Deepwater Sculpin.

Site #	30 Apr	12 May
1	1.8	0.0
2	0.0	0.0
3		0.0
4	0.0	0.0
5	0.0	0.0
6		0.0
7		0.0
8		0.0
9		0.0
10		0.0
11		0.0
12	0.0	0.0
13	0.0	0.0
14	0.0	0.0
15		0.0
17	0.0	0.0
18		0.0
19		0.0
19I		0.0
20I		0.0
21		0.0
22		0.0
23		0.0
25		1.8
25I		0.0
26		0.0
27		0.0
28		0.0
29		0.0
30		0.0
30I		0.0
31		0.0
31I		0.0
32		0.0
32I		0.0
33		0.0
34		0.0
MM		0.0

Appendix 5, continued.

1995 Freshwater Drum.

Site #	26 May	13 Jun	19 Jun
1	0.0	1.5	0.0
2	0.0	0.0	0.0
5	0.0		
7	0.0		
8	0.0		
10	0.0		
11	0.0		
13	0.0		
14	0.0		
17	0.0	0.0	
18	0.0		
19	0.0	0.0	1.6
19I	0.0	0.0	0.0
20		0.0	0.0
20I	0.0	0.0	0.0
21	0.0		
23		0.0	0.0
25I	0.0		
26	0.0		
27	0.0		
28	0.0		
28I			0.0
29	0.0		
29I	0.0	0.0	0.0
30I	0.0	0.0	1.6
31			
32	0.0		
32I	0.0		0.0
33	0.0		
34	3.7		
34I	0.0	0.0	0.0
35	3.7	0.0	0.0
MM		0.0	0.0

Appendix 5, continued.

1995 Lake Whitefish.

Site #	28 Mar	5 Apr	10 Apr	18 Apr	21 Apr	24 Apr	28 Apr	30 Apr	3 May
1		5.2	9.1	7.1	7.1	11.4	21.6	1.8	12.8
2			6.7		6.5	15.8		37.2	13.8
3									0.0
4								7.1	3.5
5								12.9	0.0
6						12.4			3.5
7							45.3		0.0
8					7.4	19.8			6.9
10		3.5				25.3	23.7		
11									0.0
12								3.7	1.9
13								16.5	1.7
14						0.0		16.4	10.2
17						58.2		12.9	47.2
18									17.6
19						22.6	25.5		29.7
19I	8.9	3.5	9.2						0.0
20									
20I				17.2					
21									
22									12.8
23				27.2					26.0
24									7.3
25									1.8
26									0.0
27									
28				0.0					8.9
29									3.6
30									
31									0.0
32									
32I				143.7		53.0	0.0		
33						10.4	32.1		0.0
34				10.9			7.2		1.8
34I		3.6	0.0						
MM				93.4					35.8

Appendix 5, continued.

1995 Lake Whitefish, continued.

Site #	9 May	12 May	19 May	26 May
1	1.9	3.6	0.0	0.0
2	0.0	0.0		0.0
3		0.0	11.4	
4		2.0	2.0	
5		4.7	0.0	0.0
6	2.4	0.0		
7		0.0	3.5	1.8
8	0.0	4.2		0.0
9		0.0		
10		28.6		
11		11.4	0.0	0.0
12		5.5	0.0	
13		0.0	0.0	0.0
14		0.0	0.0	0.0
15		0.0		
17		0.0	3.7	0.0
18		2.5	0.0	0.0
19	1.9	13.1	0.0	1.9
19I	0.0	0.0	0.0	3.7
20			0.0	
20I		0.0	0.0	1.9
21		21.7	0.0	0.0
22		0.0	1.9	
23		18.1	2.0	
24		3.6		
25		12.5	2.3	
25I		0.0	0.0	0.0
26		1.8	0.0	0.0
27		7.0	0.0	0.0
28		0.0	3.7	0.0
29		0.0	0.0	0.0
29I			0.0	0.0
30		5.4	0.0	
30I		0.0		0.0
31		0.0		
31I		0.0		
32		0.0	1.9	0.0
32I		0.0	0.0	0.0
33		1.8	0.0	0.0
34		1.7	0.0	0.0
34I			0.0	0.0
35			0.0	0.0
MM		2.5	0.0	

Appendix 5, continued.

1995 Morone spp.

Site #	12 May	19 May	26 May	30 May	5 Jun	13 Jun	19 Jun
1	0.0	3.7	25.5	0.0	3.5	11.7	1.6
2	0.0		0.0	0.0		0.0	
3	0.0	0.0					
4	0.0	0.0					
5	0.0	0.0	0.0	0.0			
6	0.0						
7	0.0	1.8	5.5	0.0			5.0
8	0.0		0.0				
9	0.0						
10	0.0	0.0	0.0	0.0			
11	0.0	0.0	0.0	0.0			
12	0.0	0.0		0.0			
13	0.0	1.9	3.8				
14	0.0	0.0	15.4		0.0		
15	0.0						
17	0.0	0.0	40.0		0.0	3.1	
18	0.0	2.3	77.1	0.0			
19	0.0	1.8	11.5		3.0	21.6	1.6
19I	0.0	0.0	38.6	1.5	0.0	0.0	36.9
20		0.0			0.0	1.5	10.6
20I	0.0	0.0	29.0	0.0	0.0	7.8	260.7
21	1.8	0.0	7.4		0.0		
22	0.0	0.0		0.0			
23	10.9	0.0			0.0	1.4	
24				0.0			
25	0.0	0.0					
25I	0.0	0.0	81.8	0.0	0.0		
26	0.0	4.5	6.0	0.0			
27	0.0	18.3	8.4	0.0			
28	0.0	1.9	0.0	0.0	0.0		
28I							7.8
29	0.0	21.3	5.4	11.6			
29I		34.6	0.0	0.0	0.0	2.3	0.0
30	0.0	0.0					
30I	0.0		2.0		0.0	1.5	6.2
31	0.0						
32	5.7	26.6	85.0	1.5		54.5	
32I	0.0	154.2	82.7	0.0			11.3
33	0.0	4.3	186.7	0.0			
34	0.0	0.0	5.5		0.0		
34I		0.0	9.1	1.5	0.0	4.9	17.3
35		2.0	14.8	1.6	0.0	0.0	0.0
MM	0.0	0.0		1.5	0.0	0.0	6.2

Appendix 5, continued.

1995 Troutperch.

Site #	26 May
1	1.8
2	0.0
5	0.0
7	0.0
8	0.0
10	0.0
11	0.0
13	0.0
14	0.0
17	0.0
18	0.0
19	0.0
19I	0.0
20I	0.0
21	0.0
25I	0.0
26	0.0
27	2.1
28	0.0
29	0.0
29I	0.0
30	0.0
30I	2.0
32	0.0
32I	0.0
33	0.0
34	0.0
34I	0.0
35	0.0

Appendix 5, continued.

1995 Log Perch

Site #	12 May	19 May	26 May	30 May	5 Jun	19 Jun
1	0.0	0.0	0.0	0.0	0.0	0.0
2	0.0		0.0	0.0		
3	0.0	0.0				
4	0.0	0.0				
5	0.0	0.0	0.0	0.0		
6	0.0					
7	0.0	0.0	0.0	0.0		0.0
8	0.0		0.0			
9	0.0					
10	0.0	0.0	0.0	0.0		
11	0.0	0.0	0.0	0.0		
12	0.0	0.0		0.0		
13	0.0	0.0	0.0		0.0	
14	0.0	0.0	0.0			
15	0.0					
17	0.0	0.0	0.0		0.0	
18	0.0	0.0	0.0	0.0		
19	0.0	0.0	0.0		1.5	0.0
19I	0.0	0.0	0.0	0.0	0.0	0.0
20		0.0			0.0	0.0
20I	0.0	0.0	0.0	0.0	0.0	0.0
21	12.6	0.0	0.0		0.0	
22	0.0	0.0		0.0		
23	0.0	0.0			0.0	
24				0.0		
25	0.0	0.0				
25I	0.0	0.0	0.0	0.0	0.0	
26	0.0	0.0	0.0	0.0		
27	0.0	0.0	0.0	0.0		
28	0.0	0.0	0.0	0.0	0.0	
28I						0.0
29	0.0	0.0	1.8	5.8		
29I		0.0	0.0	0.0	0.0	0.0
30	0.0	0.0				
30I	0.0		0.0		0.0	0.0
31	0.0					
31I	0.0					
32	0.0	1.9	2.1	1.5		
32I	0.0	0.0	0.0	4.6		4.2
33	0.0	0.0	0.0	0.0		
34	0.0	0.0	0.0		0.0	
34I			0.0	0.0	0.0	0.0
35		0.0	1.9	0.0	0.0	0.0
MM	0.0			0.0	0.0	0.0

Appendix 5, continued.

1995 Walleye.

Site #	3 May	9 May	12 May	19 May	26 May	30 May	5 Jun	13 Jun
1	11.0	5.7	8.9	0.0	0.0	0.0	0.0	0.0
2	0.0	2.2	3.8		0.0	0.0		0.0
3	0.0		0.0	0.0				
4	0.0		0.0	0.0				
5	0.0		23.5	0.0	0.0	0.0		
6	0.0	0.0	0.0					
7	1.7		0.0	3.5	0.0	0.0		
8	0.0	0.0	0.0		0.0			
9			0.0					
10			0.0	0.0	0.0	0.0		
11	0.0		0.0	0.0	0.0	0.0		
12	0.0		0.0	0.0		0.0		
13	0.0		4.0	5.8	0.0			
14	0.0		0.0	4.3	0.0		0.0	
15			0.0					
17	0.0		0.0	5.5	0.0		0.0	0.0
18	0.0		0.0	0.0	0.0	0.0		
19	0.0	23.1	11.5	0.0	1.9		1.5	1.5
19I		0.0	0.0	0.0	12.9	0.0	0.0	0.0
20	1.7		15.6	0.0			0.0	0.0
20I			3.8	0.0	11.6	0.0	0.0	0.0
21			5.4	0.0	1.8		0.0	
22	0.0		0.0	0.0		0.0		
23	0.0		7.2	0.0			0.0	0.0
24	0.0					1.7		
25	0.0		1.7	0.0				
25I			0.0	0.0	0.0	0.0	0.0	
26	0.0		0.0	0.0	3.0	0.0		
27			5.2	0.0	0.0	0.0		
28	0.0		1.8	0.0	0.0	0.0	0.0	
29	0.0		5.2	0.0	0.0	2.9		
29I				0.0	0.0	0.0	0.0	0.0
30			0.0	0.0				
30I			0.0		0.0		0.0	0.0
31	0.0		0.0					
31I			0.0					
32			18.9	9.4	6.4	9.0		
32I			5.9	0.0	0.0	0.0		
33	0.0		3.6	0.0	10.9			
34	0.0		3.5	0.0	1.8		0.0	
34I			8.7	0.0	23.8	0.0	0.0	0.0
35				2.0	0.0	1.6	0.0	0.0
MM	25.5		32.7	8.0		1.5	0.0	0.0

Appendix 5, continued.

1995 Yellow Perch.

Site #	9 May	12 May	19 May	26 May	30 May	5 Jun	13 Jun
1	0.0	0.0	0.0	1.8	0.0	0.0	0.0
2	0.0	0.0		0.0	6.1		0.0
3		0.0	0.0				
4		0.0	0.0				
5		0.0	0.0	6.0	0.0		
6	0.0	0.0					
7		0.0	0.0	3.7	0.0		
8	0.0	0.0		0.0			
9		0.0					
10		0.0	0.0	0.0	0.0		
11		0.0	0.0	0.0	0.0		
12		0.0	0.0		0.0		
13		0.0	0.0	3.8			
14		0.0	0.0	5.8		0.0	
15		0.0					
17		0.0	0.0	4.0		0.0	0.0
18		0.0	0.0	2.0	0.0		
19	3.8	0.0	0.0	11.5		1.5	3.1
19I	0.0	3.9	0.0	5.5	0.0	0.0	0.0
20			0.0			0.0	3.1
20I		3.8	0.0	1.9	0.0	0.0	0.0
21		0.0	0.0	1.8		0.0	
22		5.4	0.0		0.0		
23		0.0	0.0			0.0	0.0
24					0.0		
25		0.0	0.0				
25I		0.0	0.0	0.0	0.0	0.0	
26		0.0	0.0	3.0	0.0		
27		0.0	0.0	4.2	0.0		
28		0.0	0.0	0.0	0.0	0.0	
29		3.5	0.0	5.4	8.7		
29I			0.0	0.0	0.0	0.0	0.0
30		0.0	0.0				
30I		0.0		0.0		1.6	0.0
31		0.0					
31I		0.0					
32		0.0	3.8	6.4	18.1		
32I		0.0	1.9	24.2	0.0		
33		0.0	0.0	7.2	0.0		
34		3.5	3.7	0.0		0.0	
34I			0.0	0.0	0.0	0.0	3.3
35			0.0	1.9	3.3	0.0	0.0
MM		0.0	0.0		4.5	0.0	0.0

Appendix 6. Area, volume estimates, and percent of walleye larvae collected from each depth zone in western Lake Erie.

Depth Range (m)	Area (km^2)	Volume (m^3)	% of Catch 1994	1995
0 - 4	103.12	2.66×10^8	58	60
4 - 8	235.88	13.93×10^8	29	35
8 - 12	52.57	4.73×10^8	13	5

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