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Edward Francis Roseman

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PHYSICAL AND BIOLOGICAL PROCESSES INFLUENCING WALLEYE EARLY LIFE HISTORY IN WESTERN LAKE ERIE

By

Edward Francis Roseman

AN ABSTRACT OF A DISSERTATION

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ABSTRACT

PHYSICAL AND BIOLOGICAL PROCESSES INFLUENCING WALLEYE EARLY LIFE HISTORY IN WESTERN LAKE ERIE

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Edward Francis Roseman

Walleye (*Stizostedion vitreum*) are the dominant piscivore in western Lake Erie and provide valuable sport and commercial fisheries in Canada and the United States. Historical records of their abundance reflect unstable levels of recruitment primarily due to highly variable year-class formation. To investigate the mechanisms underlying variable year-class strength formation of reef-spawned walleye in western Lake Erie, I sampled walleye eggs on mid-lake reefs (Cone, Crib, Locust Pt., Niagara, Round and Toussaint) and larvae on and adjacent to the reefs from 1994 through 1999. Reefs varied in depth and size and egg sampling was stratified by depth. Larval sampling sites extended from Maumee Bay to the Bass Islands complex and were stratified by depth and distance from shore. The initiation of spawning was generally consistent, beginning in the first week of April, although spawning began noticeably earlier in mid-March 1998. Egg abundance varied among reefs and between years. Shallow sites on reefs had higher egg relative abundance early in the incubation period but this trend reversed later in April and early May as eggs were removed from exposed shallow areas on reefs by currents and predators. Egg viability was generally lowest early in egg incubation periods and showed an increasing trend as incubation progressed. Abundance of egg predators increased after peak egg abundance occurred. Egg survival was generally highest in years when lake waters warmed quickly and few wind events occurred during incubation periods. Egg survival was also higher for cohorts of eggs spawned later in the spawning season due to quicker incubation rates. Analysis of recruitment indices from 1960 - 1997 indicate that a water warming of at least 0.2 °C/day during egg incubation periods is necessary for good year-classes to form.

Abundance, growth, and survival of larval walleye varied between years and was positively related to egg abundance and survival, water temperature, and prey abundance. Larvae became concentrated in shallow nearshore areas of western Lake Erie. These areas were warmer, darker, and had higher abundance of zooplankton and ichthyoplankton prey than offshore areas. Abundance of demersal age-0 walleye in October index bottom trawl surveys was highest in 1996 (30.8/h trawling), a year with moderately high egg abundance (7,230/tow), good egg survival (21%), moderately high larval abundance (8.1/1,000 m^3), good larval growth (0.34 mm/day), and exceptional larval survival (72%). The weakest year class was formed in 1995 when the October bottom trawl index was only 0.2/hour of trawling. This year had low egg abundance (3,610/tow), low egg survival (0.105), low larval abundance (3.5/1,000 m^3), slow larval growth (0.31 mm/day), and low larval survival (36.5%). This research emphasizes the importance of physical processes like wind and water warming rate in tempering the environmental setting that biological processes take place. Further, this study exposed specific nearshore areas in western Lake Erie important as nursery zones for walleye.

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Dissertation Introduction

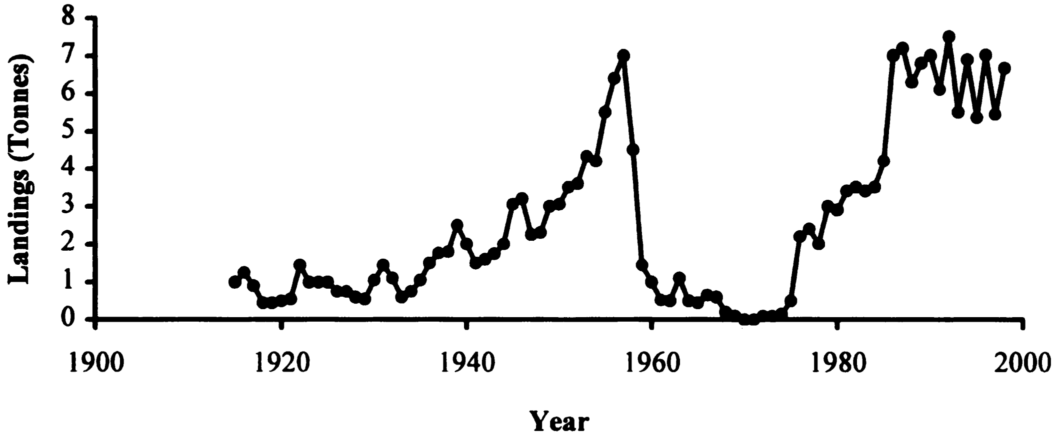
Walleye (*Stizostedion vitreum*) have supported important sport and commercial fisheries in Lake Erie for over 150 years (Regier et al. 1969, Knight 1997). Commercial landings of walleye increased steadily through the early part of the 20th century exceeding 6.8 million kg in the mid 1950's (Figure 1). Catches declined dramatically in the late 1950's when the population diminished due to exploitation, pollution, eutrophication, and degraded spawning habitat. The discovery of high levels of mercury in the tissue of walleye prompted closure of the fishery in 1970, offering the exploited population a reprieve from harvest. Following the 1972 adoption of the Great Lakes Water Quality Agreement, basin-wide management strategies focused on reducing organic inputs to the lake in efforts to improve fish habitat and rehabilitate populations (Burns 1985, Makarewicz and Bertram 1991). The fishable stock increased from about 83,000 walleye in 1970 to over 14 million in 1976 (Hatch et al. 1987) and landings increased accordingly (Figure 1). Adult population abundance peaked in 1988 when population estimates exceeded 99 million fish age-2 and older. The current population is estimated to exceed 60 million fish (Ohio Division of Wildlife 2000).

Because walleye are the dominant predator in Lake Erie and support important sport and commercial fisheries, fluctuations in their population size and structure can have direct implications for the entire Lake Erie ecosystem. For example, Knight and Vondracek (1993) found that increases in the abundance of walleye in the late 1970's and 1980's played a major role in the decline in abundance of soft-rayed species such as emerald shiner (*Notropis atherinoides*), spottail shiner (*N. hudsonius*) and alewife (*Alosa pseudoharengus*). They concluded that management goals focusing primarily on walleye affected not only the targeted species but the entire fish community of western Lake Erie. Further, Nicholls (1999) hypothesized that the changes in the fish community documented by Knight and Vondracek were partially responsible for reductions in total phosphorous in western Lake Erie prior to the invasion of Dreissenidae. Nicholls suggested that the increase in piscivorous walleye reduced planktivore biomass thereby increasing phytoplankton grazing by zooplankton allowing increased levels of phosphorous to be transferred into the foodweb.

After the fishery recuperated, abundant walleye populations attracted interest of anglers throughout the midwestern United States and led to the development of a substantial sportfishing industry in the states bordering the lake as well as a rejuvenated commercial gillnet fishery in Canada. Consequently, fluctuations in the walleye population have resulted in direct economic consequences to businesses and families relying on these fisheries (Knight 1997, Lichtkoppler 1997). The Lake Erie walleye population is currently managed under a quota system allocating portions of the stock to 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).

Despite its large adult population size, the Lake Erie walleye population exhibits wide fluctuations in recruitment. The abundance of age-2 fish entering the stock has varied as much as 60-fold since 1977 (Figure 1). Although causes of Lake Erie walleye recruitment variation are speculative, interannual variation in egg and larval survival are considered the principal source of recruitment variability for walleye populations in other lakes (Carlander and Payne 1977; Koonce et al. 1977; Ney 1978; Forney 1980). For most fish species in large systems, 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.

Density-independent physical processes and density-dependent biological factors that affect egg survival, and the growth and survival of individual larval walleye may be the driving force behind walleye year-class strength formation in western Lake Erie. Preliminary studies performed in 1994 and 1995 indicated that physical processes (water warming rate and wind events that created strong water currents) and biological processes (prey density, growth) played important roles in structuring year-class strength during early life history stages (Roseman et al. 1996, Roseman 1997). My dissertation research examines more closely the interactions and influence of physical and biological processes occurring in western Lake Erie on age-0 walleye demographics. Specifically, my research examines the linkages between life stages and habitats as well as the degree of spatial and temporal overlap between age-0 walleye and habitat conditions conducive to good walleye development, growth, and survival.



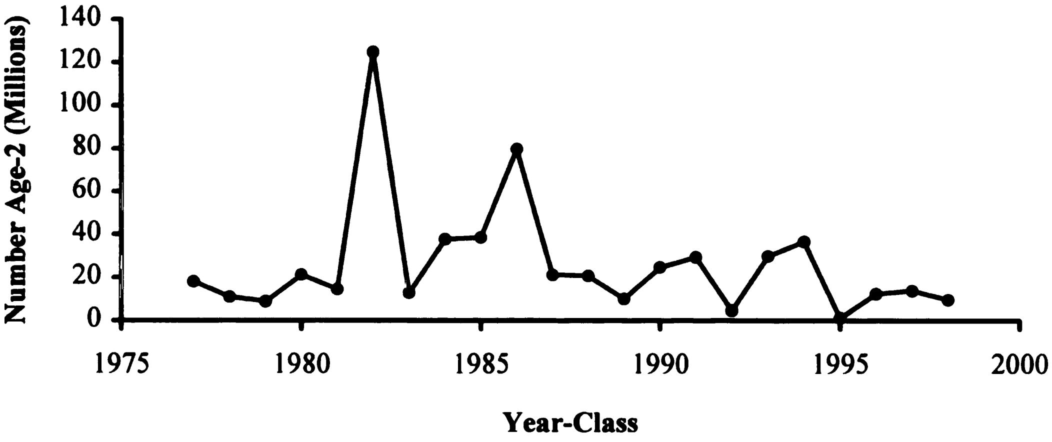


Figure 1. (Top) Landings of walleye from United States and Ontario waters of Lake Erie, 1915-1994. (Bottom) Number of age-2 walleye entering the Lake Erie walleye stock as determined by CAGEAN model estimates for the 1977-1998 year-classes. Data are from the 1999 Lake Erie Walleye Task Group Report.

Many naturally spawning walleye populations experience high levels of mortality during the egg stage (Priegel 1970; Forney 1976, 1980). Processes such as water warming rate have prolonged indirect effects on development rate and survival of fish embryos by determining the duration of incubation periods. Optimal egg survival occurred in laboratory experiments when water temperature increased at a rate of 1°C/day from a starting temperature of 5 °C (Smith and Koenst 1975). Incubation periods are prolonged when water warms more slowly, thereby increasing vulnerability of eggs to predation, disease, and removal by wind generated currents (Wolfert *et al.* 1975, Koonce et al. 1977; Roseman et al. 1996). Other processes such as catastrophic storms can produce immediate devastation of complete cohorts of fish (Martin et al. 1992; Letourneur et al. 1993). 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; Roseman et al. 1996).

Predation by fishes and invertebrates may also contribute to egg mortality (Carlander et al. 1960; Wolfert et al. 1975; Roseman et al. 1996). In western Lake Erie tributaries, exotic white perch (*Morone americana*) were found to consume large quantities of walleye and white bass (*Morone chrysops*) eggs in 1981-83 (Schaefer and Margraf 1987) while Wolfert et al. (1975) found yellow perch (*Perca flavescens*) to be the most important predator of walleye eggs on Kelly's Island Shoal in western Lake Erie from 1969-71. The recent invasion of Lake Erie by round gobies (*Neogobius melanostomus*, Jude et al. 1992) creates increased concern about fish recruitment variability as this species is suspected to be a major predator on fish eggs on Lake Erie reefs (DeSorcie and Edsall 1995).

Pelagic walleye larvae are poor swimmers (Houde 1969) and consequently are subject to transport by water currents. These currents serve as the mechanism by which larvae move from spawning areas to nursery areas both in rivers and on reefs (Houde and Forney 1970, Mion et al. 1998, Roseman 1997). Walleye spawned on reefs in western Lake Erie rely on current patterns in the spring to transport the larvae to the warmer and more productive nearshore nursery habitats (Roseman 1997). Ichthyoplankton samples collected in 1994 and 1995 showed high densities of walleye larvae and other ichthyoplankton in nearshore areas of western Lake Erie suggesting that current patterns during this time of year act to transport pelagic larvae to these areas (Mion 1996, Roseman et al. 1996, Roseman 1997). These nearshore areas warm quickly in the spring and are known to have higher densities of prey than offshore areas providing habitat conditions favorable to larval walleye growth and survival (Roseman 1997).

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. He 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 post-larvae 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 appropriate 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 slower 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 year-class strength (Houde 1987). Both episodic events (weather-related events) and subtle variability (temperature dependent development) in early life history vital rates can significantly effect the year-class development of fishes. Episodic events are usually catastrophic in nature, removing large numbers of individuals from the population (Houde 1989). Such events may relieve survivors of density-dependent regulatory mechanisms (i.e. competition) and shorten the duration of vulnerable early life history stages, allowing good growth and survival of the remaining cohort. Conversely, decelerated development and larval growth rates precipitated by unfavorable temperatures or low prey availability can lead to substantially longer early life history stage duration over which high mortality rates can operate resulting in fewer recruits (Houde 1987).

My hypotheses is that a combination of abiotic physical processes and biotic factors occurring during the egg 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 of walleye in western Lake Erie to allow for the identification of causal mechanisms controlling year-class formation. I also strive to identify areas in western Lake Erie that are important for age-0 walleye recruitment (i.e. spawning and nursery areas) to assist fishery managers in the rehabilitation and conservation of the Lake Erie walleye fishery. My specific objectives were to:

1. Determine spatial and temporal patterns in spawning, larval hatching, abundance, growth, and survival of reef-spawned walleye in western Lake Erie.

2. Evaluate the timing of larval dispersal from reefs and their subsequent distributions in relation to the distribution of zooplankton and ichthyoplankton prey resources.

3. Evaluate interactions between selected lacustrine processes (water temperature and currents), abundance of prey resources, and growth and survival of walleye larvae.

4. Assess the importance of various lake habitats to walleye growth, survival and recruitment.

Study Area

My 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 2). 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 the Appendix.

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 (Herdendorf and Braidech 1972).

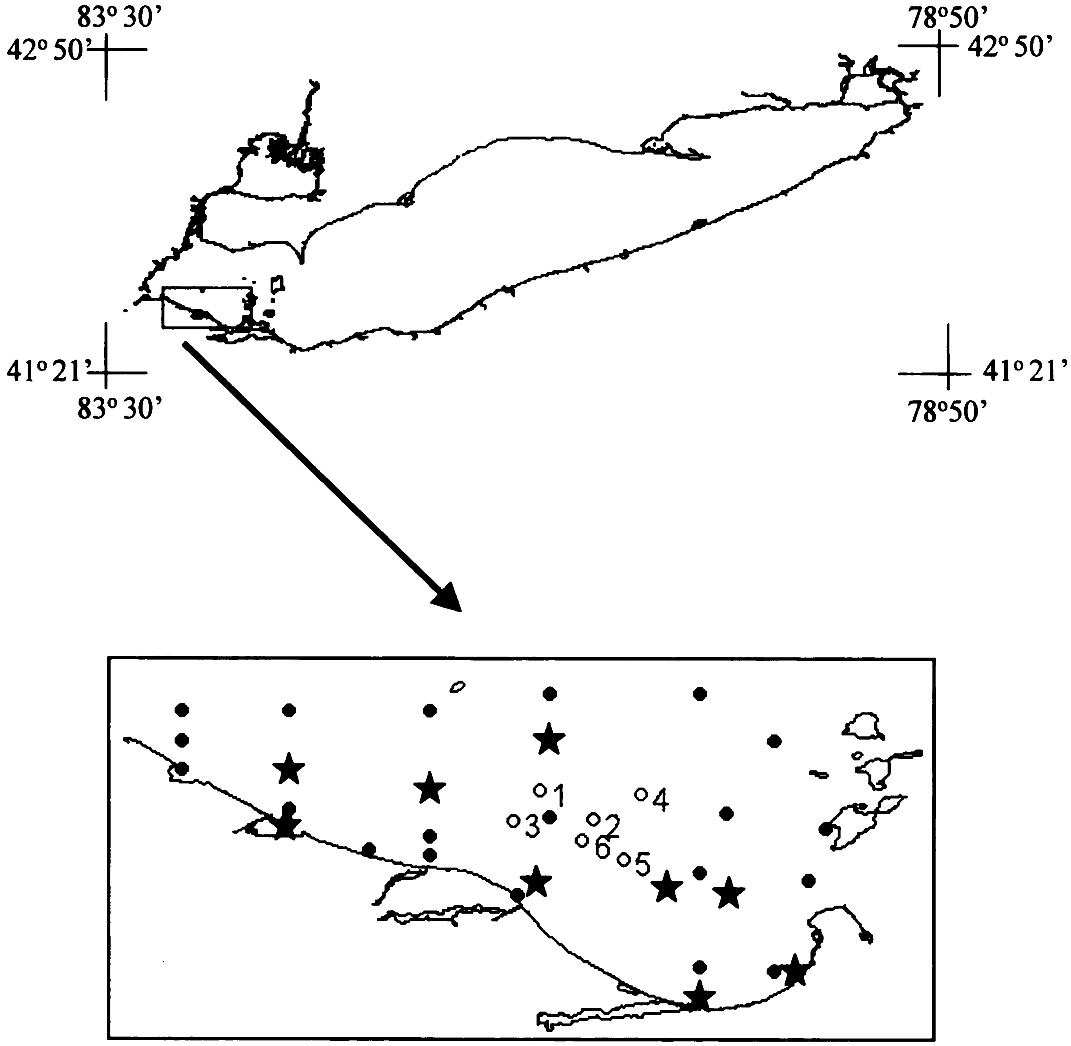


Figure 2. Western Lake Erie study area. Numbers indicate reef locations: 1 - Cone reef, 2 - Crib reef, 3 - Locust Pt. reef, 4 - Niagara reef, 5 - Round reef, 6 - Toussaint reef. Filled circles (•) indicate larval sampling sites. Stars indicate larval sampling sites that are also bottom trawl sites. Reef sites 2, 3, 4, and 5 are also larval sampling sites.

Walleye are the dominant predator in the western basin supported by a prey base of gizzard shad (*Dorosoma cepedianum*), alewife , shiners, white perch, white bass, and yellow perch. Other common fish species include carp (*Cyprinus carpio*), freshwater drum (*Aplodinotus grunniens*), rainbow smelt (*Osmerus mordax*), channel catfish (*Ictalurus punctatus*), and suckers (Catostomidae) (Trautman 1957, Knight and Vondracek 1993).

Several invasive exotic species of fish and invertebrates have also become established in western Lake Erie in the past decade. Many of these species have the potential to alter fish community and trophic dynamics (Mills et al. 1993). For example exotic dreissenid mussels are well established in western Lake Erie (Mills et al. 1999) and are altering nutrient dynamics by shifting energy from pelagic to benthic pathways. These mussels also alter substrate morphology which may have important ramifications to walleye egg incubation on reefs. Round goby abundance has increased dramatically in western Lake Erie since 1996, and, as mentioned earlier, these fish may be important predators on fish eggs (DeSorcie and Edsall 1995).

Walleye Life History

In western Lake Erie, walleye spawn on mid-lake reefs in the western basin as well as in tributaries such as the Maumee, Sandusky, and Detroit rivers. Spawning typically begins shortly after ice-out and peaks around the middle of April (Baker and Manz 1971, Roseman et al. 1996). Walleye broadcast their eggs over hard substrates and provide no direct parental protection. Eggs typically hatch in 7 to 15 days depending on water temperature (Hurley 1972, Nepszy et al. 1991, Roseman et al. 1996). Small interstitial spaces in the substrate provide the benthic eggs some protection from predation and displacement but eggs remain vulnerable to physical processes such as water warming rate, wind induced wave and current action, and sedimentation that can influence the duration of incubation, egg abundance, and survival (Roseman et al. 1996).

In Lake Erie, walleye larvae emerge from the substrate immediately upon hatching and rely on lake currents for transport to nursery areas (Nepszy et al. 1991). The yolk-sac is usually absorbed within 3 to 5 days when the larvae are about 9.5 mm total length (TL). The duration of the pelagic larval stage is temperature dependent and typically lasts from 3 to 4 weeks until the young fish become demersal at about 30 mm TL (McElman and Balon 1979). Due to their small size, limited mobility, and delicate nature, larval walleye are susceptible to a variety of direct and indirect influences from physical processes like water temperature and wind generated currents. These processes can influence the timing and magnitude of larval development, distribution, growth, and survival.

My research examines the interactions between physical and biological processes occurring in western Lake Erie and their role in structuring walleye early life history vital rates and year-class development. I present data I collected from 1994 – 1999 that reveals patterns in egg distribution and survival and larval abundance, distribution, growth, and survival and I relate trends in these data to concurrent physical and biological processes that occurred in western Lake Erie. I conclude my dissertation with a discussion and synthesis of my research that includes some implications for the management of the Lake Erie walleye population and its habitat.

Chapter 1

PHYSICAL AND BIOLOGICAL PROCESSES INFLUENCING WALLEYE EARLY LIFE HISTORY STAGES IN WESTERN LAKE ERIE

Abstract

Walleye are the dominant piscivore in western Lake Erie and also provide valuable sport and commercial fisheries. Historical records in their abundance reflect highly variable recruitment with much of the fluctuations in abundance due to interannual differences in year-class formation. To investigate the mechanisms underlying variable year-class strength formation of reef-spawned walleye in western Lake Erie, I sampled walleye eggs on mid-lake reefs (Cone, Crib, Locust Pt., Niagara, Round and Toussaint) and larvae on and adjacent to the reefs in western Lake Erie from 1994 through 1999. Reefs varied in depth and size and egg sampling was stratified by depth. Larval sampling sites extended from Maumee Bay to the Bass Islands complex and were stratified by depth and distance from shore. Walleye spawning generally began during the first week of April, although spawning began noticeably earlier in mid-March 1998. Egg abundance varied among reefs and between years. Shallow reefs generally had higher egg relative abundance than deep reefs. Shallow sites on reefs had higher egg relative abundance early in the incubation period but this trend reversed later in April and early May as eggs were removed from shallow areas on reefs. Egg viability was generally lowest early in

egg incubation periods showing an increasing trend as incubation progressed. Egg survival was generally highest in years when lake waters warmed quickly and few wind events occurred during incubation periods. Egg survival was also higher for cohorts of eggs spawned later in the spawning season due to quicker incubation rates. Analysis of recruitment indices from 1960 - 1997 indicate that a water warming of at least 0.2 °C/day during egg incubation periods is necessary for good year-classes to form.

Abundance, growth, and survival of larval walleye varied between years and was positively related to egg abundance and survival, water temperature, and prey abundance. Larvae became concentrated in shallow nearshore areas of western Lake Erie. These areas were warmer, darker, and had higher zooplankton and ichthyoplankton prey abundance than offshore areas. Demersal age-0 walleye abundance in October index bottom trawl surveys was highest in 1996 (30.8/h trawling), a year with moderately high egg abundance (7,230/tow), good egg survival (21%), moderately high larval abundance (8.1/1,000 m^3), good larval growth (0.34 mm/day), and exceptional larval survival (72%). The weakest year class was formed in 1995 when the October bottom trawl index was only 0.2/hour of trawling. This year also had low egg abundance (3,610/tow), low egg survival (0.105), low larval abundance (3.5/1,000 m^3), slow larval growth (0.31 mm/day), and low larval survival (36.5%). This research emphasizes the importance of physical processes like wind and water warming rate in tempering the environmental setting that biological processes take place. Further, this study exposed specific nearshore areas in western Lake Erie important as nursery zones for walleye.

Introduction

Lake Erie supports the world's largest naturally reproducing population of walleye providing valuable sport and commercial fisheries in the United States and Canada. Like most natural populations, Lake Erie walleye have exhibited significant variation in year-class strength over the past 20 years. The abundance of age-2 fish entering the stock has fluctuated nearly 60 fold since 1977 (Figure 1) and the causes of this recruitment variability have been unclear (Henderson and Nepszy 1994, Madenjian et al. 1996). Recent field research in western Lake Erie, however, reveals the importance of density-independent physical processes in walleye year-class formation with the strongest year-classes occurring in years with fast water warming rates and few storm events during egg incubation and larval dispersal periods (Mion et al. 1998, Roseman et al. 1996). These studies concluded that variability in environmental conditions influenced the timing of life history events and caused differential survival rates during the egg and larval stages which translated into variability in year-class strength and recruitment to the adult stock.

Physical processes and other abiotic factors can have powerful, although usually indirect effects on fish population and community dynamics by tempering the environmental conditions in which many important biological processes operate (Dunson and Travis 1991). For example, water temperature has been shown to be one of the most influential physical factors in walleye egg development and survival (Allbaugh and Manz

1964, Hurley 1972). In western Lake Erie, Busch et al. (1975) and Roseman et al. (1999) found a positive relationship between water warming rate and walleye year class strength. Egg incubation periods are lengthened when waters warm more slowly, thereby increasing the amount of time eggs are exposed to predation, disease, and severe wind events (Wolfert et al. 1975, Roseman et al. 1996). Further, water temperature mediates larval walleye activity including metabolism, feeding rate, growth rate, and survival (Hokanson and Koenst 1986, Santucci and Wahl 1993, Mion et al. 1998, Roseman 1997).

Water clarity is another important physical characteristic of walleye habitat. Walleye possess a special layer in the eye, the *Tapetum lucidum*, which reflects light within the eye and allows the fish to feed and perform other activities in low light conditions (e.g., turbid waters, crepuscular periods). The *Tapetum lucidum* makes walleye sensitive to bright light intensities and the fish actively seek darker conditions (i.e., secchi < 2 m) to avoid the brightness (Scott and Crossman 1973). Laboratory studies have further revealed that growth and survival rates of larval walleye are higher in turbid waters than in clear waters (Bristow et al. 1996, Rieger and Summerfelt 1997).

A final physical process of great importance to reef-spawning fish in western Lake Erie is storm-related wind and wave action. Because of the east-west orientation of the lake, the western basin is susceptible to the effects of storm generated waves and currents, especially those originating from easterly direction which have long fetches and carry high wave energy (Gedney and Lick 1972). Several studies have documented the storm-induced mortality and disappearance of cohorts of fish in marine and estuarine systems as the result of single catastrophic events (Peterman and Bradford 1987; Walker et al. 1991; Moring 1996). The effects of similar storm events on freshwater fish communities, especially in large lakes, is not as well documented though still considered important to fish population dynamics (Shuter and Post 1990). Storm events on large lakes like Lake Erie can create strong wind-driven currents and strong wave action (Gedney and Lick 1972; Hamblin 1979) and some studies have inferred that such processes cause mortality during the early life history stages of fish thereby reducing year-class strength and limiting recruitment (Busch et al. 1975, Houde 1989).

Because walleye are broadcast spawners, their eggs are vulnerable to mortality caused by dislodging from severe wind and wave action during spawning and incubation periods (Johnson 1961; Serns 1982). Prolonged strong wind events create wave and current conditions that can transport fish large distances (Martin et al. 1992) as well as cause damage to delicate larvae (Cordone and Kelley 1961, Mion et al. 1998). Further, heavy wave action is known to stir up sediments causing increased turbidity associated with sediment transport (Gedney and Lick 1972). Increased turbidity reduces the phototrophic zone thereby reducing primary productivity (Wetzel 1975) which can translate to reductions in fish growth (Carpenter and Kitchell 1993). These processes can have significant negative effects on walleye year-class development by reducing egg and larval abundance and survival.

While many physical processes are difficult to predict (i.e. weather), we can gain insight into the response of fish populations to such factors by understanding how physical processes influence fish and their habitat. Some factors such as water warming rate have gradual effects on development rate and survival of fish embryos (Koonce et al. 1977), whereas other factors such as severe and catastrophic storms can produce immediate devastation of complete cohorts of fish (Martin et al. 1992; Letourneur et al.

1993). Therefore, it is important to identify and understand the various physical processes that structure fish populations and determine how physical processes influence the biological processes involved in fish population dynamics. In this chapter, I use data I collected from 1994 through 1999 to evaluate the relationship between physical processes and the distribution, abundance, and survival of reef-spawned walleye eggs and larvae in western Lake Erie. Specifically, I will 1) assess the relationship between water temperature and walleye egg development, larval distribution, and larval growth; 2) assess the relationship between water clarity and larval walleye distribution; 3) demonstrate the effects of severe wind events on reef-spawned walleye egg abundance and survival.

Methods

Egg Collection

I combined data on egg abundance and survival collected on Toussaint and Niagara reefs in 1994 and 1995 (Roseman 1997) with new information collected from 1996 – 1999. From 1996-1999 I sampled eggs on Cone, Crib, Locust Pt., Niagara, Round, and Toussaint reefs which are located among a bedrock reef complex in the western basin of Lake Erie (Figure 2). Area and depth of the study reefs varied. Total reef surface area ranged from 0.67 km^2 to 2.49 km^2 but surface area above the 5 m contour, where the majority of walleye spawning occurs (Baker and Manz 1971; Roseman et al. 1996), ranged from 0.0 km^2 to 1.5 km^2 (Table 1; Bolsenga and Herdendorf 1993). 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 which provide incubation sites for walleye eggs (Herdendorf and Braidech 1972; Roseman et al. 1996). The shallowness of the reefs allows the reef surface to be scoured by ice movements as well as by wind-generated waves and currents. 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 1972; Bolsenga and Herdendorf 1993).

Walleye egg sampling on reefs typically began in mid to late March shortly after ice-out and continued through to mid-May when spawning ceased and catches of walleye eggs were negligible. Egg sampling was stratified by depth to examine egg deposition density; depths of 0-5 m, and 5-7 m were sampled. These depth strata encompass the range of depths where walleye eggs were collected in previous studies (Baker & Manz 1971, Roseman et al. 1996, Roseman 1997). Three samples were taken at each depth on each sampling day. I located sample sites by global positioning system coordinates and marked them with an anchored buoy. I used a 39-kg iron sled (Stauffer 1981) attached to a diaphragm pump at the surface by a flexible hose 5 cm in diameter for egg collections. For each sample, the sled was towed for 2 min at 0.5 m/s.

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 acclimated and refrigerated at 5 °C until they could be sorted at the laboratory which typically took from 2.5 to 24 h. I found no indication that delays in processing of up to 24 h influenced egg viability or survival estimates.

At the laboratory, samples were weighed then 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 acclimated 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 (s) was estimated as

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

Day 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.

To compare relative egg density between reefs, I calculated weighted averages of numbers of walleye eggs collected per 2 min tow on each reef. I used the proportion of the reef surface area contributing to both depth strata as weighting factors for each reef. Surface area proportions were estimated from bathymetric maps of the reefs (Herdendorf and Braidech 1972). To examine the effects of a severe storm event that occurred during the egg incubation period in 1998, I used analysis of variance in the form of a general linear model to assess the significance of differences in egg relative density between sampling dates, between reefs, and between depths before and after the storm occurred. Percent loss of eggs was used as the dependent variable and depth and reef were the interacting class variables. I used a significance level of 0.05 for all statistical tests.

Table 1. Surface area of reefs (km^2) in western Lake Erie sampled for walleye eggs (area shallower than 5 m is shown in parentheses).

Reef	Area (km^2)
Cone	0.67 (0.00)
Crib	0.85 (0.65)
Locust Pt.	0.93 (0.80)
Niagara	2.49 (1.50)
Round	0.88 (0.79)
Toussaint	1.23 (1.02)

Larval Sampling

I combined data collected in 1994 and 1995 on the abundance, growth, distribution, and survival of larval walleye in western Lake Erie (Roseman 1997) with new information gathered in 1996 – 1999. From 1996 – 1999, larval walleye were sampled at 30-36 sites on and adjacent to the reefs (Figure 2). Larval sampling typically began in mid-April before eggs hatched on reefs. Pelagic larvae were sampled once per week ending in late June when most age-0 walleye had become demersal. 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. Larval fishes were euthanized with a lethal dose of tricaine methanesulfonate 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. Mean larval density for the period from the first hatch through May 31was used as an index of larval abundance to compare between years. I examined the distribution of larvae for years 1994-99 using a geographic information system (GIS). To create a graphical representation of trends in the distribution of larval fish for each year, I used the GIS to plot the deviations from the overall annual mean density estimate for each sampling site for each year as discrete point samples. I used the natural break function in ArcView to group data into distinct categories. This method minimizes the sum of the variance within each data class (Environmental Systems Research Institute 1999). Estimates of daily walleye densities for 1994 and 1995 are in Roseman (1997). I used the sample correlation coefficient (Snedecor and Cochran 1989) to assess the relationship between lake depth at sample sites and walleye density at that site. I used the geometric mean catch of age-0 walleye collected in bottom trawls in October as an index of walleye year-class strength (Ohio Division of Wildlife 2000).

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 age-0 walleye at 9 sites adjacent to the reef complex (Figure 2). Trawls were towed for 10 min at about 1.5 m/sec at each site beginning the last week of May. Bottom trawl samples were taken weekly from late May through June in all years of the study. Trawls typically sampled a 3,900 m^2 area. Bottom trawl sites were selected based on substrate compatibility with the gear and consistent catch results of age-0 walleye. Fish collected in bottom trawl samples were only used to evaluate growth rates of age-0 walleye.

Larval Growth

Fish total length (TL) was measured to the nearest millimeter. I pooled pelagic and demersal captured fish for my analysis. To compare growth rates of age-0 walleye between years and between periods within years, I calculated the specific growth rates (Ricker 1975) of larval walleye during the zooplanktivorous and piscivorous periods. The period of zooplanktivory typically occurs from May 1 – June 10 and the period when age-0 walleye are primarily piscivorous occurs after June 10 (Roseman 1997). I assessed the relationship between specific growth rates and prey abundance and water warming rates using sample correlation coefficients and regression analysis (Snedecor and Cochran 1989).

Age-0 Walleye Survival

I estimated daily 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). I converted the daily instantaneous rates (Z) to total mortality estimates (A) for the time periods covered by the regression equations as follows:

$$A = 1 - e^{z*t}$$

where e is the constant (2.71828...) and t is the number of days included in the regression.

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. Zooplankton data collected in 1994 and 1995 are reported in Roseman (1997). From 1996-1999, zooplankton samples were collected at each larval fish sampling site concurrent with fish sampling (Figure 2). Samples were immediately preserved in sugar-formalin (Haney and Hall 1973). One to three 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. I calculated average numbers per liter for the pooled zooplankton sample using taxa known to be consumed by young walleye. Based on previous diet studies, I knew that walleye consumed mainly copepopds and large cladocerans (Roseman 1997). To create a graphical representation of trends in the distribution of zooplankton for each year (1996-99), I used the GIS to plot the deviations from the overall annual mean density estimate for each sampling site. I used the natural break function in ArcView to group data into distinct categories (Environmental Systems Research Institute 1999). Because zooplankton are known to occur in patches of high and low abundance (Patalas and Salki 1992), I treated the zooplankton data as discrete point samples.

Water Temperature

To compare with egg development on reefs, water temperatures (C) on Toussaint reef were recorded with continuous monitoring thermographs (Ryan Instruments, Inc.). I calculated the rate of water warming on the reefs for the period 1April through 15 May because this time period typically covers the walleye egg incubation period on the reefs (Roseman et al. 1996). I also recorded water temperature 2 m below the water surface at each larval sampling site using a YSI digital temperature meter. To examine the effects of water temperature on walleye growth rate, I calculated average water warming rates during the period when pelagic larval walleye are primarily zooplanktivorous (May 1- June 10) and primarily piscivorous (June 10 – June 30; Roseman 1997). To create a graphical representation of geographic patterns in water temperature across my study area, I used a GIS to plot the deviations from the overall annual mean water temperature for each sampling site as discrete point samples. I used the natural break function in ArcView to group data into distinct categories (Environmental Systems Research Institute 1999). I used the sample correlation coefficient (Snedecor and Cochran 1989) to assess the relationship between depth and water temperature.

Water Clarity

Secchi disk readings (nearest 0.1 m) were taken at each egg and larval sampling site as a measure of water clarity. To create a graphical representation of patterns in water clarity across my study area, I used GIS to plot the deviations from the overall annual mean secchi disk reading for each sampling site as discrete point samples. I used the natural break function in ArcView to group data into distinct categories (Environmental Systems Research Institute 1999). I used the sample correlation coefficient (Snedecor and Cochran 1989) to assess the relationship between depth and water clarity.

Wind Severity

Wind velocity and direction data recorded at South Bass Island in western Lake Erie were obtained from the National Climatic Data Center web site (National Climatic Data Center 2000). South Bass Island is the nearest weather station and is located approximately 20 km east of the reef complex. I determined the number of days between April 1 and May 15 when wind events having velocities between 25 - 50 km/h and > 50 km/h occurred. This time period typically covers the walleye egg incubation period on reefs in western Lake Erie (Baker and Manz 1971; Roseman et al. 1996; Roseman 1997). Busch et al. (1975) determined that winds exceeding 25 km/h were sufficient to remove incubating eggs from reefs. I separated wind events exceeding 50 km/h from the first category because storm events of this magnitude were rare during my study period (NCDC 2000) and I observed that they had a different impact on incubating eggs than storms of a lesser magnitude. Additionally, I considered only winds originating from directions with fetches > 10 km (260° – 110°) because wave energy increases with fetch (Gedney and Lick 1972) and I observed that southerly offshore winds with shorter fetches produced smaller wave amplitudes and had minimal effects on the abundance of incubating eggs on reefs.

Results

Water Temperature and Warming Rate

Mean daily water temperature on reefs in western Lake Erie are presented in Figure 3. The calculated water warming rates during the egg incubation, zooplanktivorous larval, and piscivorous age-0 periods for each year are listed in Table 2. Waters warmed fastest during the egg incubation period in 1998 at a rate of 0.24 °C/day and slowest in 1995 at a rate of only 0.16 °C/day (Figure 3, Table 2). Lake waters warmed fastest during the zooplanktivorous larval period in 1995 at a rate of 0.25 °C/day and slowest in 1999 at a rate of only 0.12 °C/day (Figure 3, Table 2). Waters warmed fastest during the piscivorous age-0 period in 1997 at a rate of 0.39 °C/day and slowest in 1994 at a rate of only 0.11 °C/day (Figure 3, Table 2).

Table 2. Water warming rates (°C/day) during typical egg incubation (April 1 – May 15), zooplanktivorous larval (May 1 – June 10), and piscivorous juvenile (June 10 – June 30) periods 1994 through 1999.

Year	Incubation Period	Zooplanktivorous Period	Piscivorous Period
1994	0.22	0.24	0.11
1995	0.16	0.25	0.23
1996	0.22	0.22	0.35
1997	0.19	0.18	0.39
1998	0.24	0.19	0.35
1999	0.18	0.12	0.20

Water temperatures were generally warmer at inshore sites than at offshore sites in all years. Figures 4 - 9 display the deviation from the daily average water temperature at my larval sampling sites for 1994 through 1999. Water temperatures consistently exceeded the daily mean water temperature at shallow nearshore sites. I found a significant but weak negative relationship between depth and water temperature across all years of my study (sample correlation coefficient $r = -0.192$, $p < 0.001$, $n = 1,156$).

Water Clarity

Secchi disk readings varied widely between sampling sites and sampling dates but were generally lower (darker water) at nearshore sites than at offshore sites in all years (Figures 4 - 9). I found a weak significant positive relationship between depth and secchi disk depth (sample correlation coefficient $r = 0.109$, $p < 0.001$, $n = 1,156$).

Walleye Egg Abundance and Distribution

Walleye egg relative abundance (mean number of eggs collected per two-minute tow) for years 1994 through 1999 are presented in Figures 10 – 14. In 1994 and 1995 I sampled only Niagara and Toussaint reefs. From 1996-1999 I sampled the six reefs listed in the methods; Cone, Crib, Locust Pt., Niagara, Round, and Toussaint. No eggs were found in samples collected on April 1, 1994. Walleye eggs first appeared in samples from both reefs on April 7. Egg abundance peaked on the reefs on April 21 when and average of over 11,300 walleye eggs were collected in a single 2-minute tow. Sampling frequency on Niagara reef was not sufficient to determine the timing of peak egg density but an average of over 2,300 eggs/tow was collected in a single tow on April 10. Viable eggs persisted in samples at all sites through May 18, 1994 when less than 100 walleye eggs were collected per 2 min tow (Figure 10).

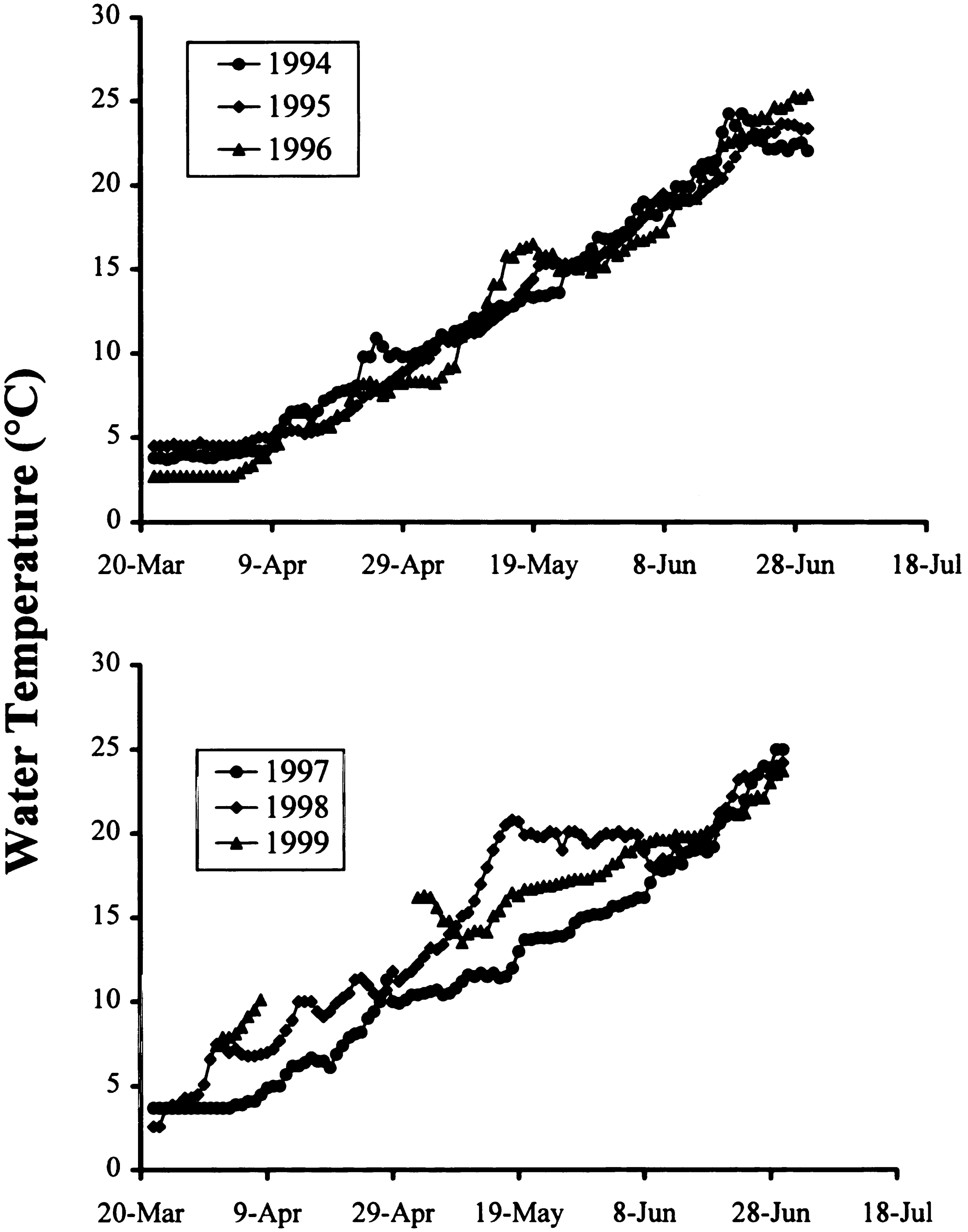


Figure 3. Water temperature on Toussaint reef, 1994-1999.

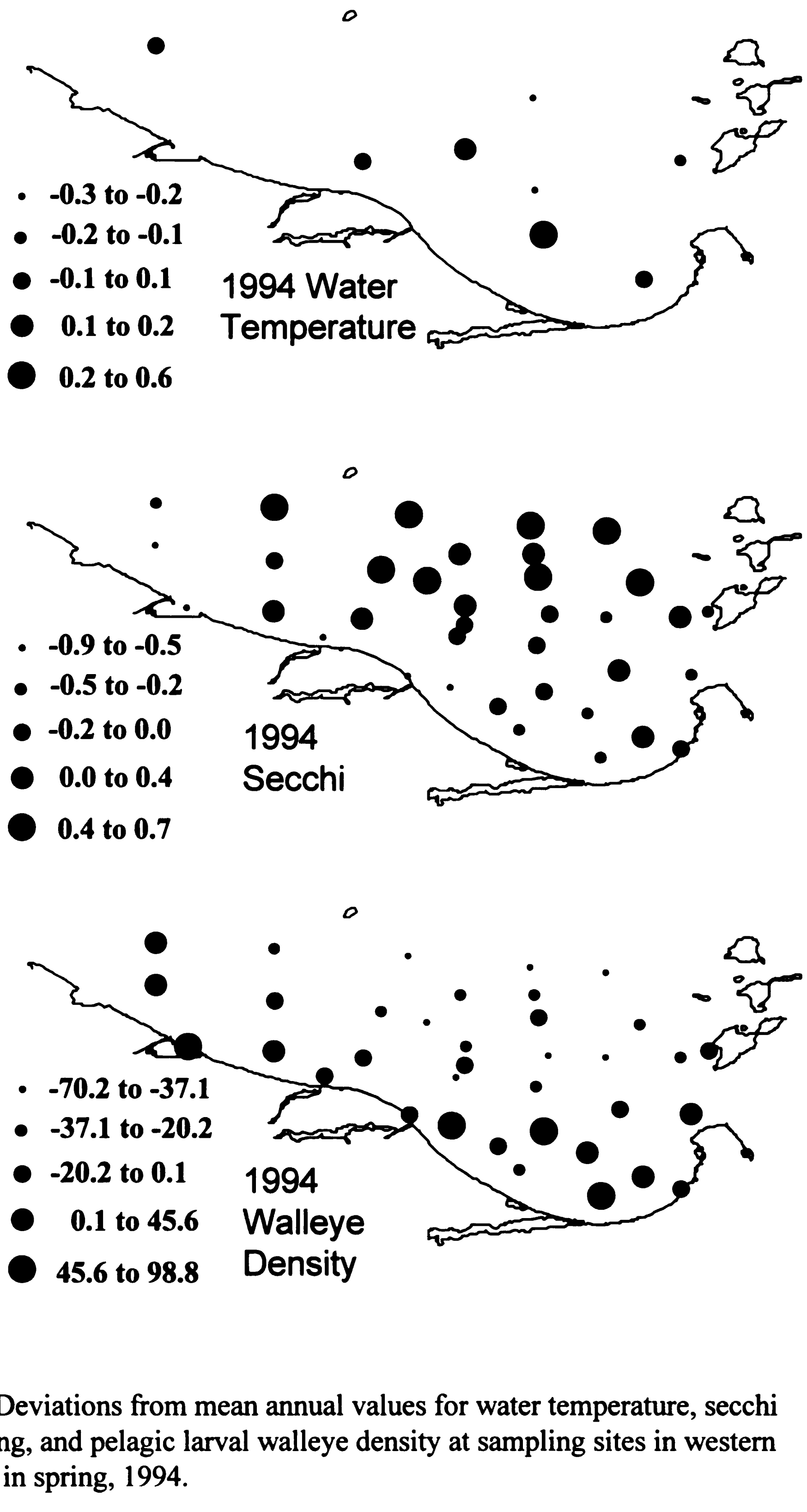


Figure 4. Deviations from mean annual values for water temperature, secchi disk reading, and pelagic larval walleye density at sampling sites in western Lake Erie in spring, 1994.

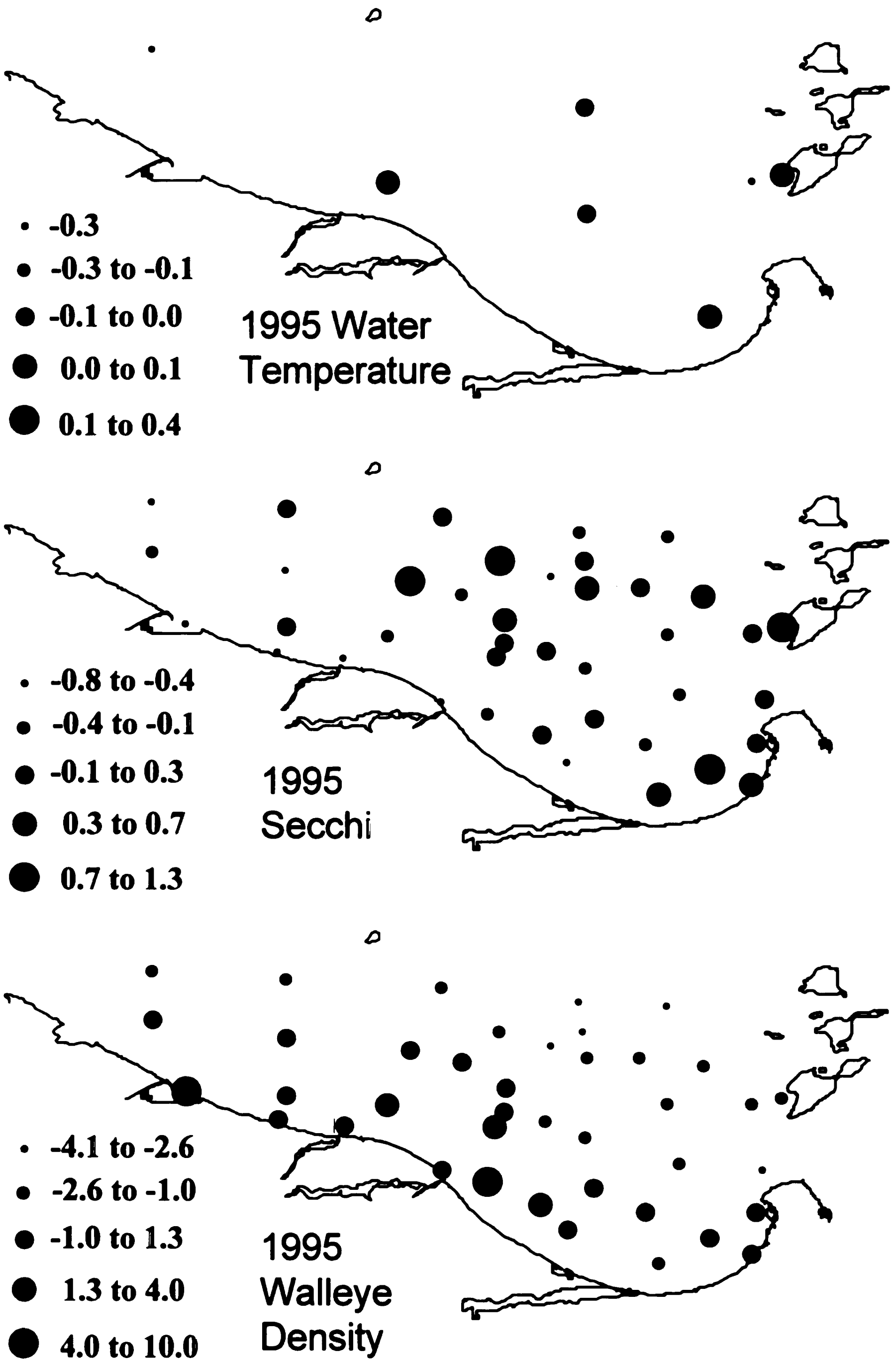


Figure 5. Deviations from mean annual values for water temperature, secchi disk reading, and pelagic larval walleye density at sampling sites in western Lake Erie in spring, 1995.

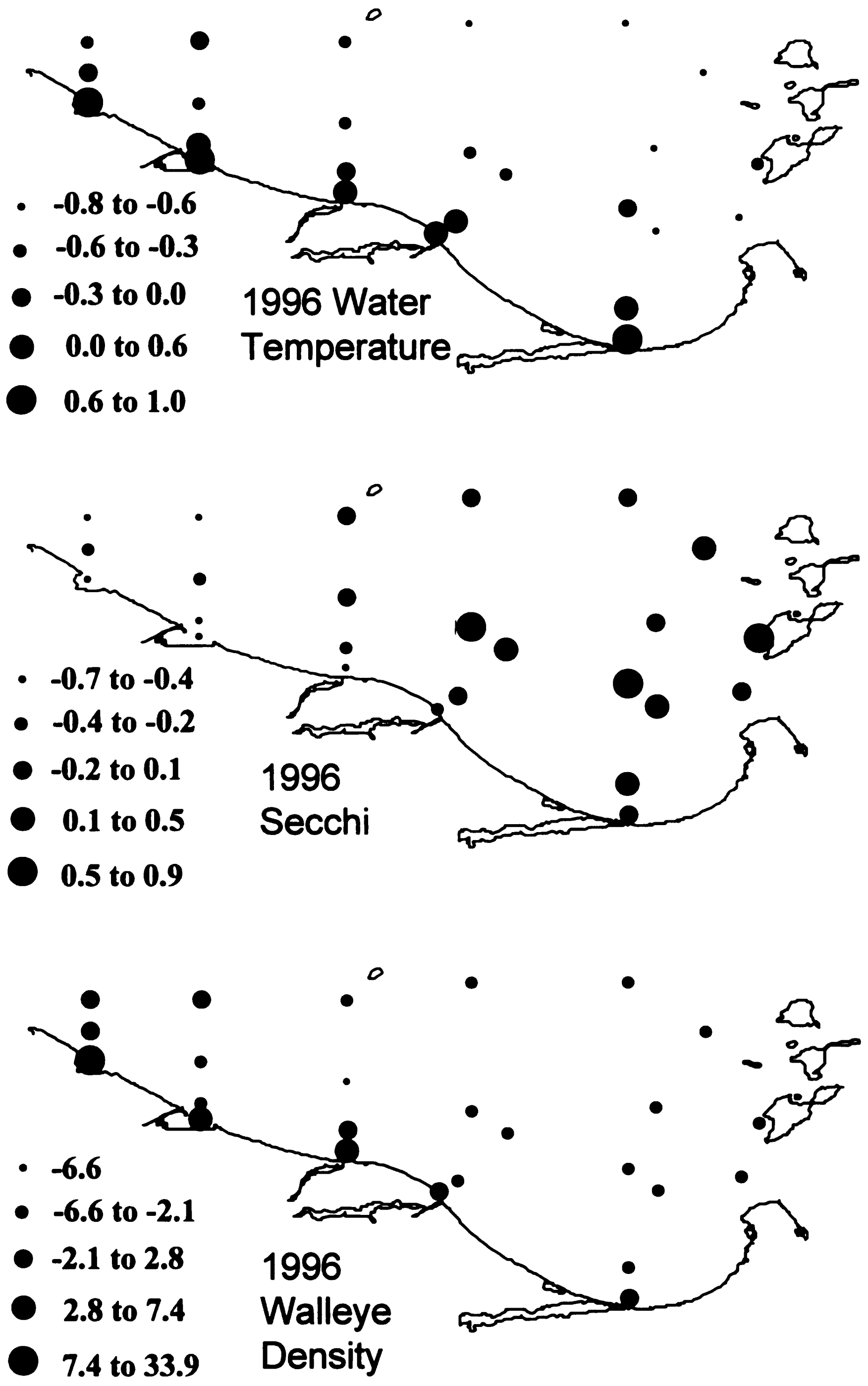


Figure 6. Deviations from mean annual values for water temperature, secchi disk reading, and pelagic larval walleye density at sampling sites in western Lake Erie in spring, 1996.

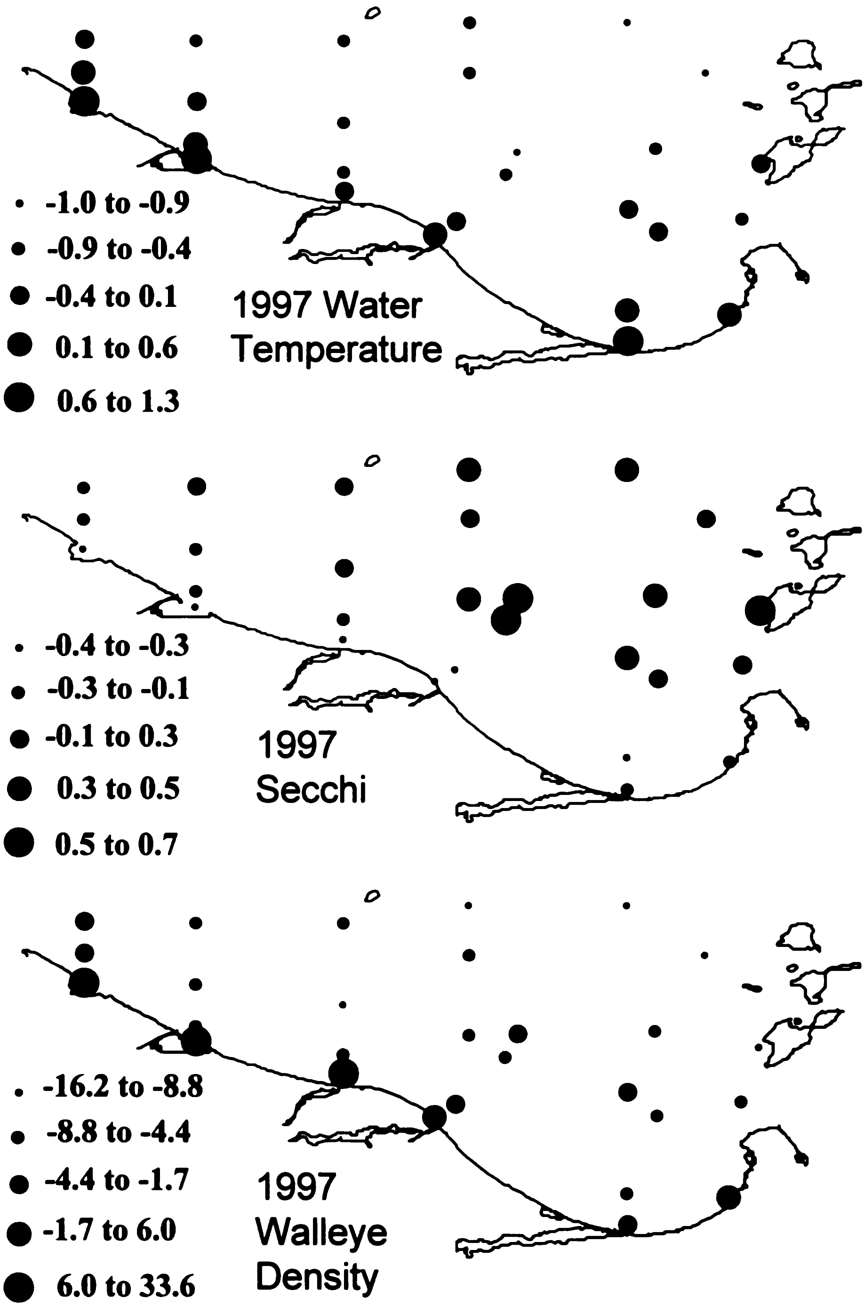


Figure 7. Deviations from mean annual values for water temperature, secchi disk reading, and pelagic larval walleye density at sampling sites in western Lake Erie in spring, 1997.

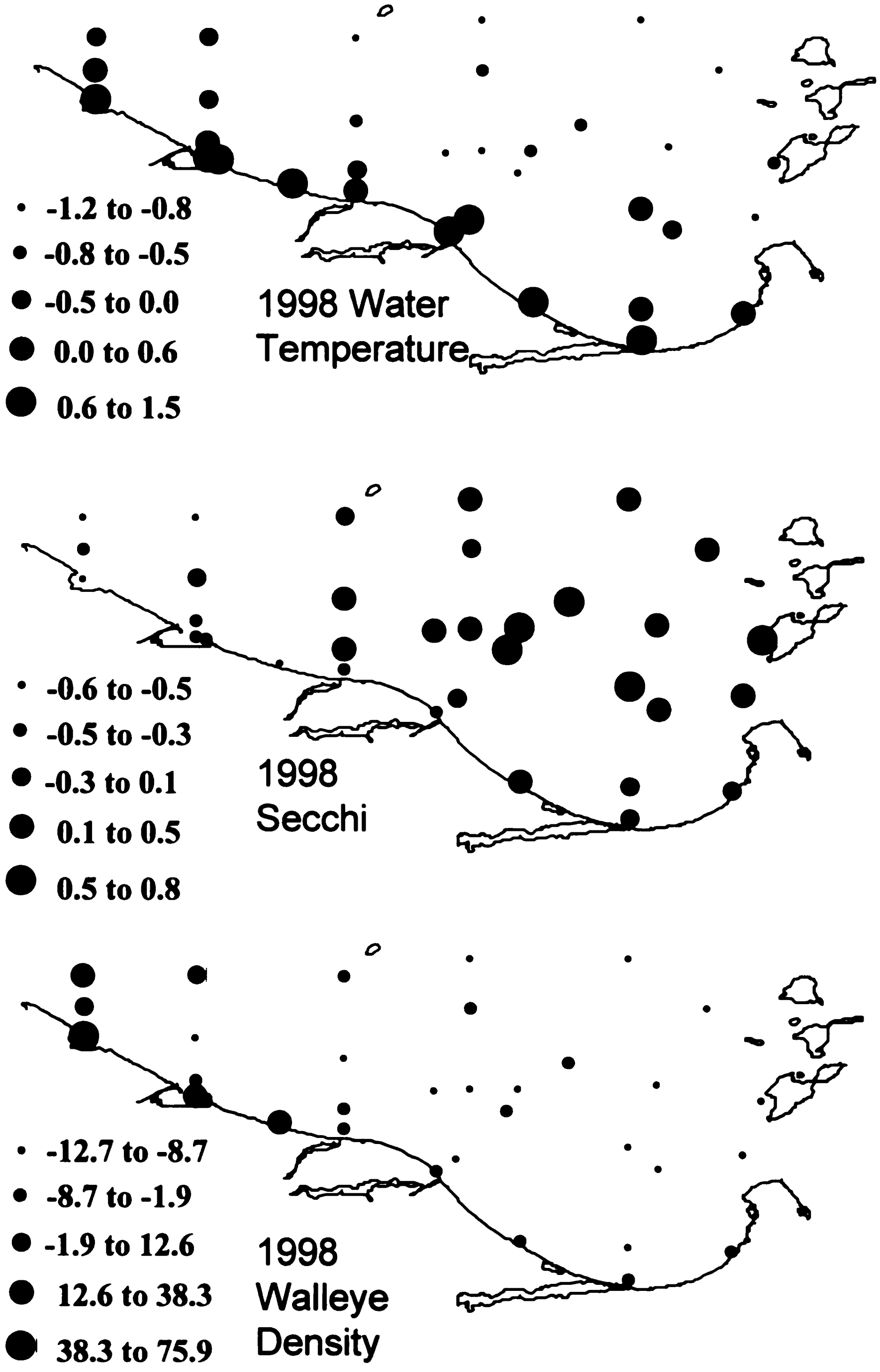


Figure 8. Deviations from mean annual values for water temperature, secchi disk reading, and pelagic larval walleye density at sampling sites in western Lake Erie in spring, 1998.

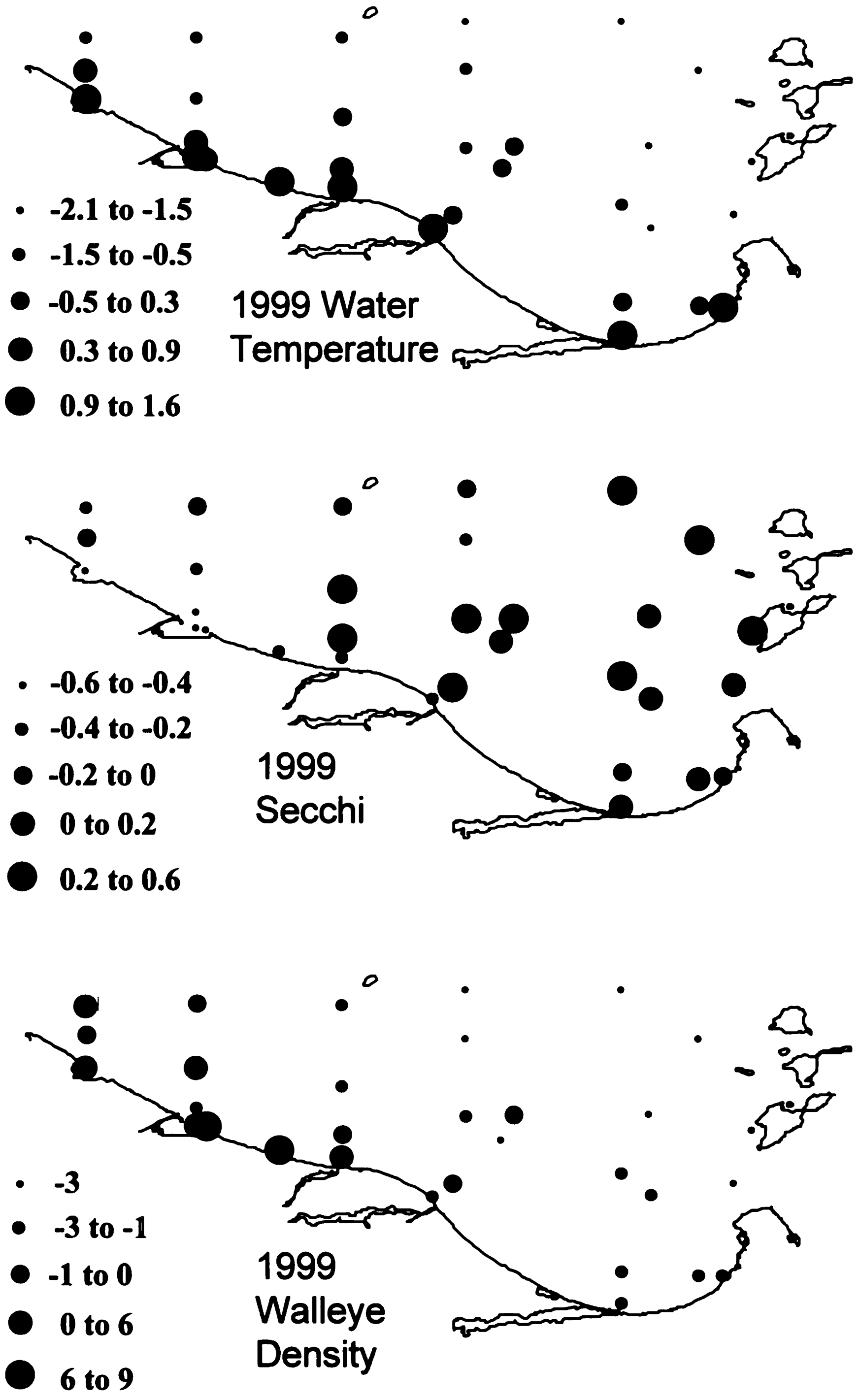


Figure 9. Deviations from mean annual values for water temperature, secchi disk reading, and pelagic larval walleye density at sampling sites in western Lake Erie in spring, 1999.

Egg densities were roughly 50% lower on Toussaint and Niagara reefs in 1995 than in 1994. Eggs were present in low numbers on Toussaint reef on April 1 but didn't appear in samples from Niagara reef until after April 1. Densities peaked on Toussaint reef on April 24 and on April 21 on Niagara reef when 3,300 and 1,900 eggs were collected per 2 min tow from each reef respectively. Viable walleye eggs were collected through May 17, 1995 when less than 50 walleye eggs were collected per 2 min tow from both reefs (Figure 10).

In 1996, no walleye eggs were found in samples collected from reefs on March 31. Walleye eggs first appeared in samples collected from all reefs on April 8. Egg relative abundance peaked on Cone, Crib, Locust Pt., Niagara and Round reefs on April 21 when I collected an average of 3,336, 2,015, 3,338, 2,387, and 2,454 eggs per 2-minute tow from each reef respectively. Egg abundance peaked on Toussaint reef on April 17 when I collected an average of 7,308 eggs per 2-minute tow. Toussaint reef was observed to have the highest egg relative abundance in 1996. Viable walleye eggs persisted in samples through May 13 when eggs numbers in samples became negligible (Figure 11).

Eggs first appeared in samples collected from Niagara and Toussaint reefs on March 30, 1997 and on April 1 from Cone, Crib, Locust Pt., and Round reefs. Egg abundance peaked on April 14 on Locust Pt. Reef when I collected an average of 1,280 eggs per 2-minute tow. Egg abundance peaked on Cone, Crib, Niagara, and Toussaint reefs on April 19 when I collected and average of 1,688, 415, 563, and 1,077 eggs from the four reefs, respectively. Egg abundance peaked on Round reef on April 23 when an average of 2,852 eggs were collected. Viable walleye eggs persisted in samples collected from all reefs through May 11 (Figure 12).

In 1998 I collected the first walleye eggs on March 23 from Locust Pt. and Toussaint reefs, about a week earlier than the other 5 years of my study. Eggs were present on all reefs on March 29. Egg relative abundance peaked on Toussaint reef on April 3 when I collected an average of 2,747 eggs per 2-minute tow. Egg relative abundance peaked on Crib, Locust Pt., Niagara, and Round reefs on April 6 when I collected an average of 540, 1,063, 1,340, and 562 egg per 2-minute tow. Egg abundance peaked on Cone reef on April 15 when I collected 1,164 eggs per 2-minute tow. Viable walleye eggs were collected from all reefs through April 28 while eggs were found on only Locust Pt. and Niagara reefs on May 3 (Figure 13).

Eggs were sampled only three times during 1999 due to equipment failure. Eggs first appeared in samples collected on March 31. Egg abundance averaged 932, 1,928, 674, 1,281 3,437, and 581 on Cone, Crib, Locust Pt., Niagara, Round and Toussaint reefs respectively on April 8. Eggs were still present in low numbers on all reefs on May 5 (Figure 14).

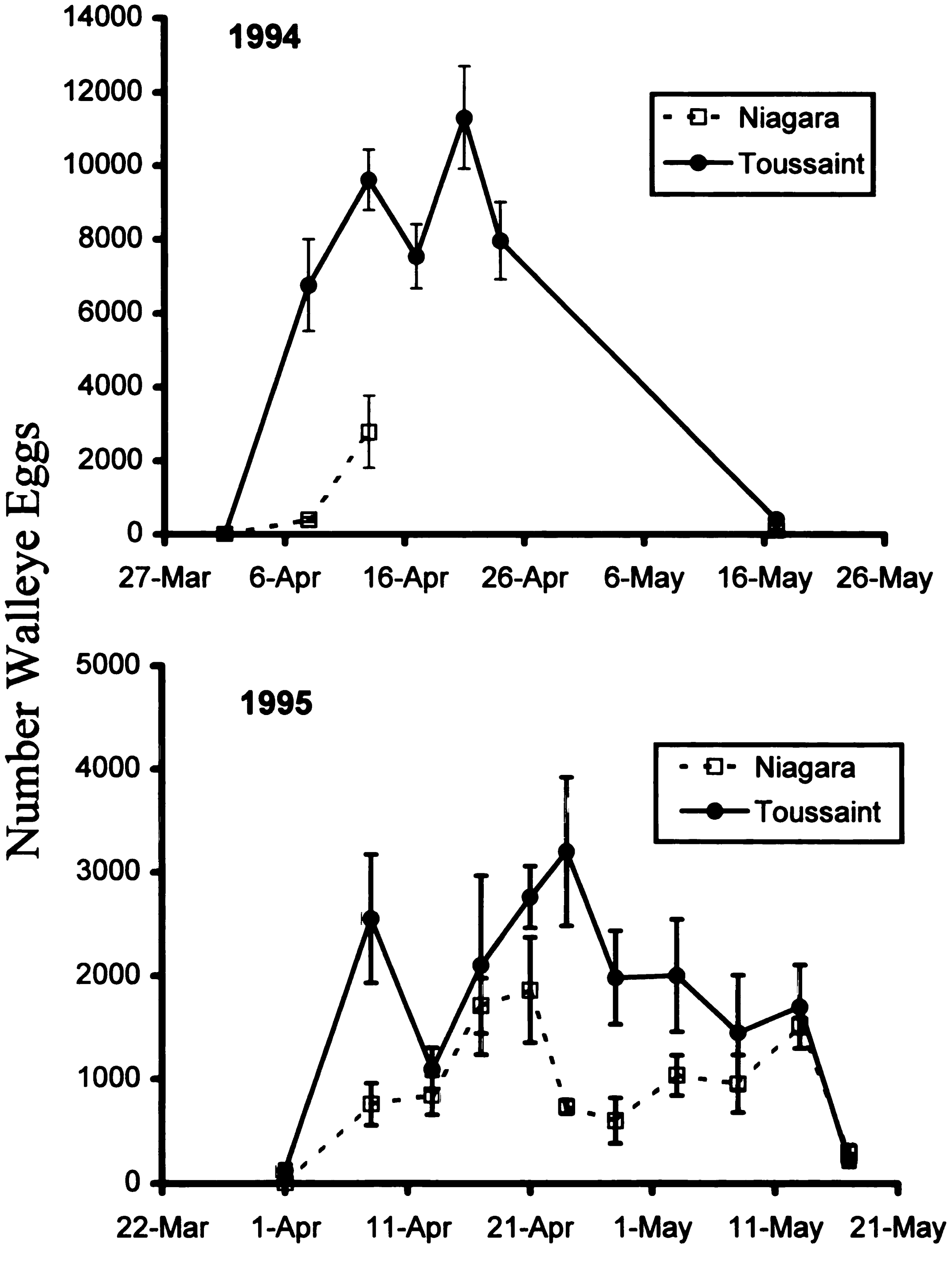


Figure 10. Walleye egg relative abundance (± 1 standard deviation) on reefs in western Lake Erie, 1994 and 1995. Abscissa scales vary.

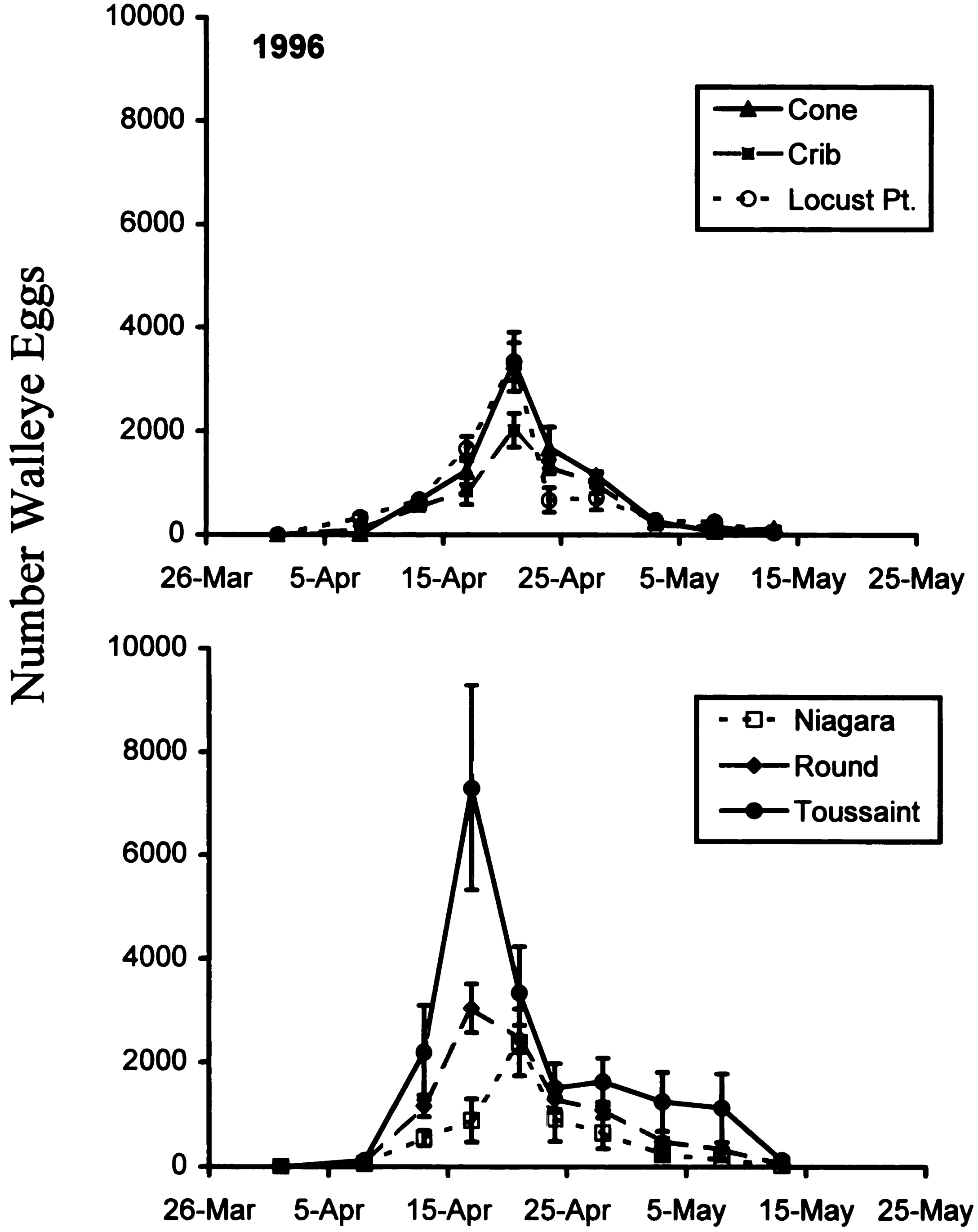


Figure 11. Walleye egg relative abundance (± 1 standard deviation) on reefs in western Lake Erie, 1996.

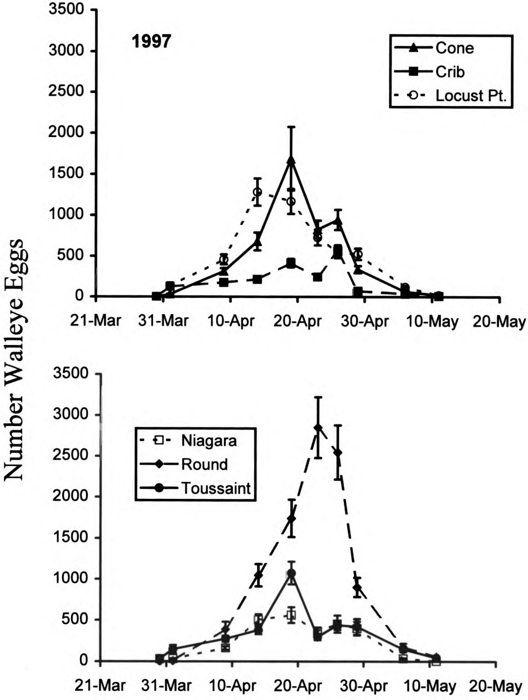


Figure 12. Walleye egg relative abundance (± 1 standard deviation) on reefs in western Lake Erie, 1997.

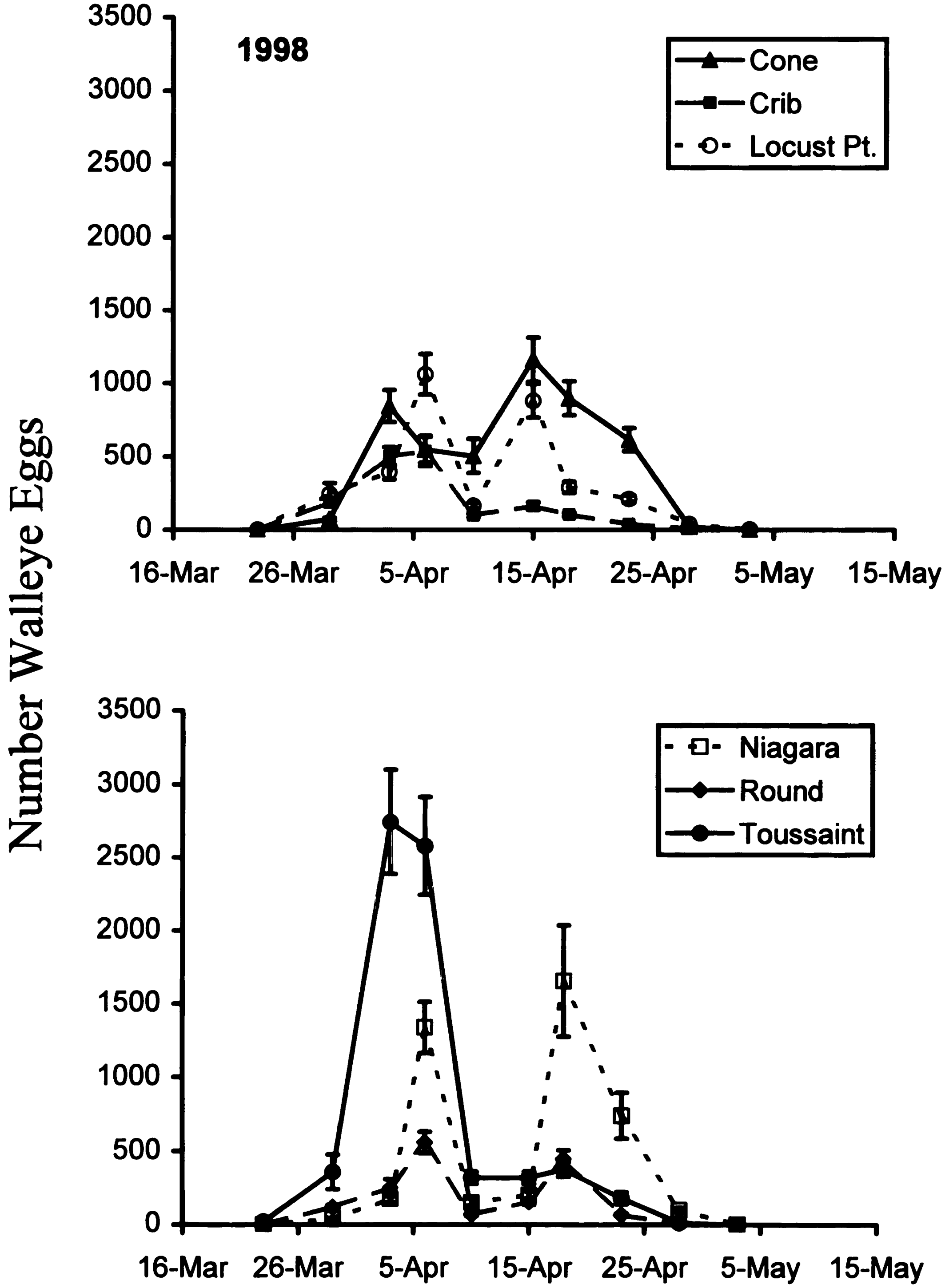


Figure 13. Walleye egg relative abundance (± 1 standard deviation) on reefs in western Lake Erie, 1998.

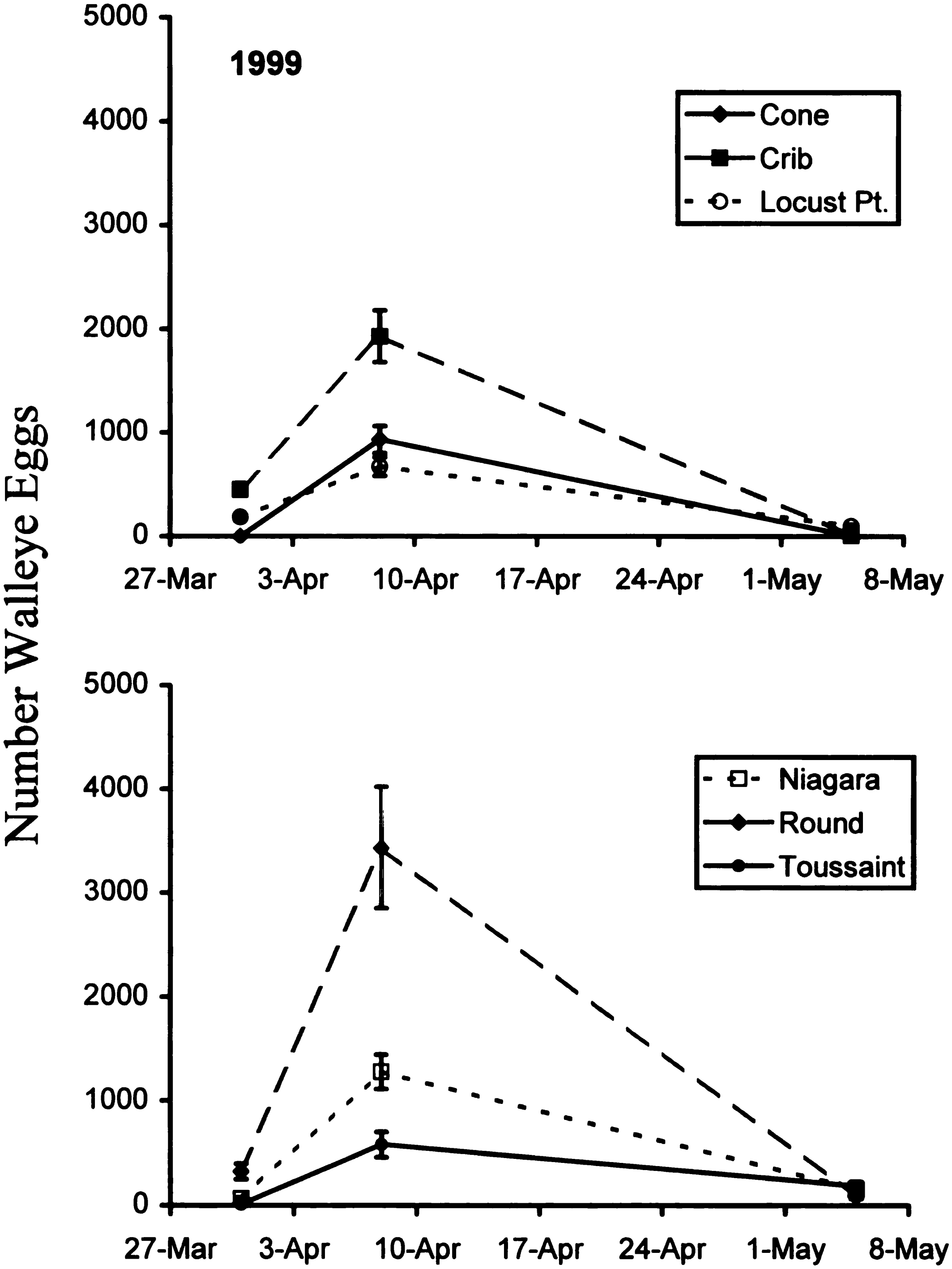


Figure 14. Walleye egg relative abundance (± 1 standard deviation) on reefs in western Lake Erie, 1999.

In general, I found more eggs at shallow sites on reefs than deep sites early in the spawning season of each year. This trend reversed later in the egg incubation period as eggs were removed from shallow sites and displaced to deeper sites on the reefs (Figures 15 - 17).

Egg Viability and Survival

Walleye egg viability did not differ substantially between reefs or depths. In 1994 walleye egg viability remained relatively steady at values ranging between 50 and 60% (Figure 18). In 1995 viability was low on both reefs early in the egg incubation period, increased to over 60% by mid-April, then decreased to about 20 – 30% by late April and May when I noticed large numbers of fungused eggs in the samples (Figure 18). Egg viability increased from values around 20% on all reefs in early April, 1996, 1997, 1998, and 1999 to about 60% by early May in each of those years (Figures 19 and 20).

I estimated egg survival for distinct cohorts of eggs on each reef in each year of the study except 1999. As I reported in my thesis (Roseman 1997), egg survival estimates were higher in 1994 than 1995. My samples allowed for a single egg survival estimate from April 10 to April 21, 1994. Egg survival for pooled depths was 0.430 for Toussaint reef and 0.300 for Niagara reef . I calculated 2 separate estimates for each reef in 1995. Walleye egg survival to stage 3 for the period April 7 to April 29, 1995 was estimated at 0.140 for Toussaint reef and 0.070 for Niagara reef. Estimates for the period April 15 – May 9, 1995 were 0.160 and 0.150 for Toussaint and Niagara reefs respectively.

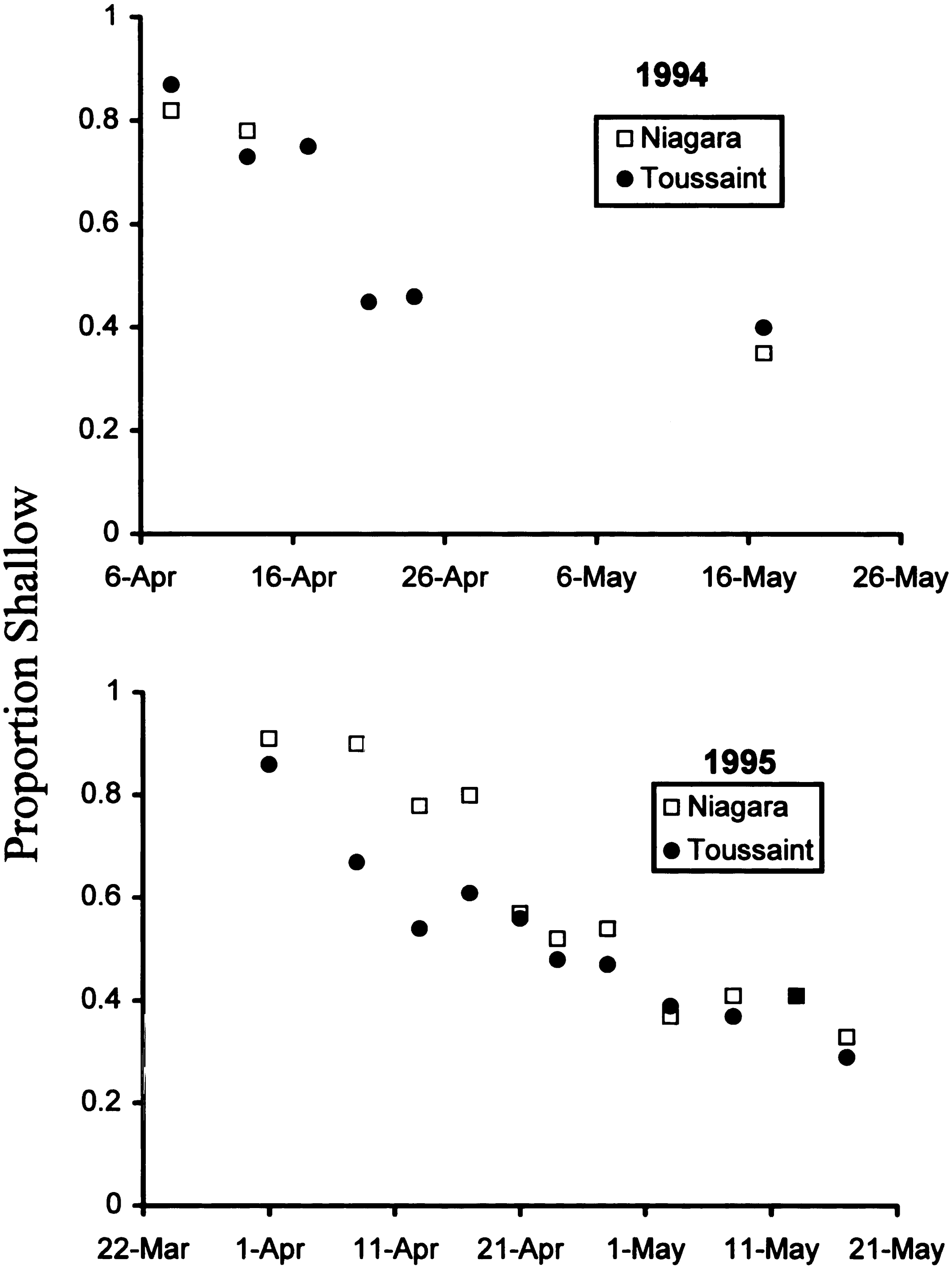


Figure 15. Proportion of walleye eggs collected from shallow sites (< 5m) on reefs in western Lake Erie, 1994 and 1995.

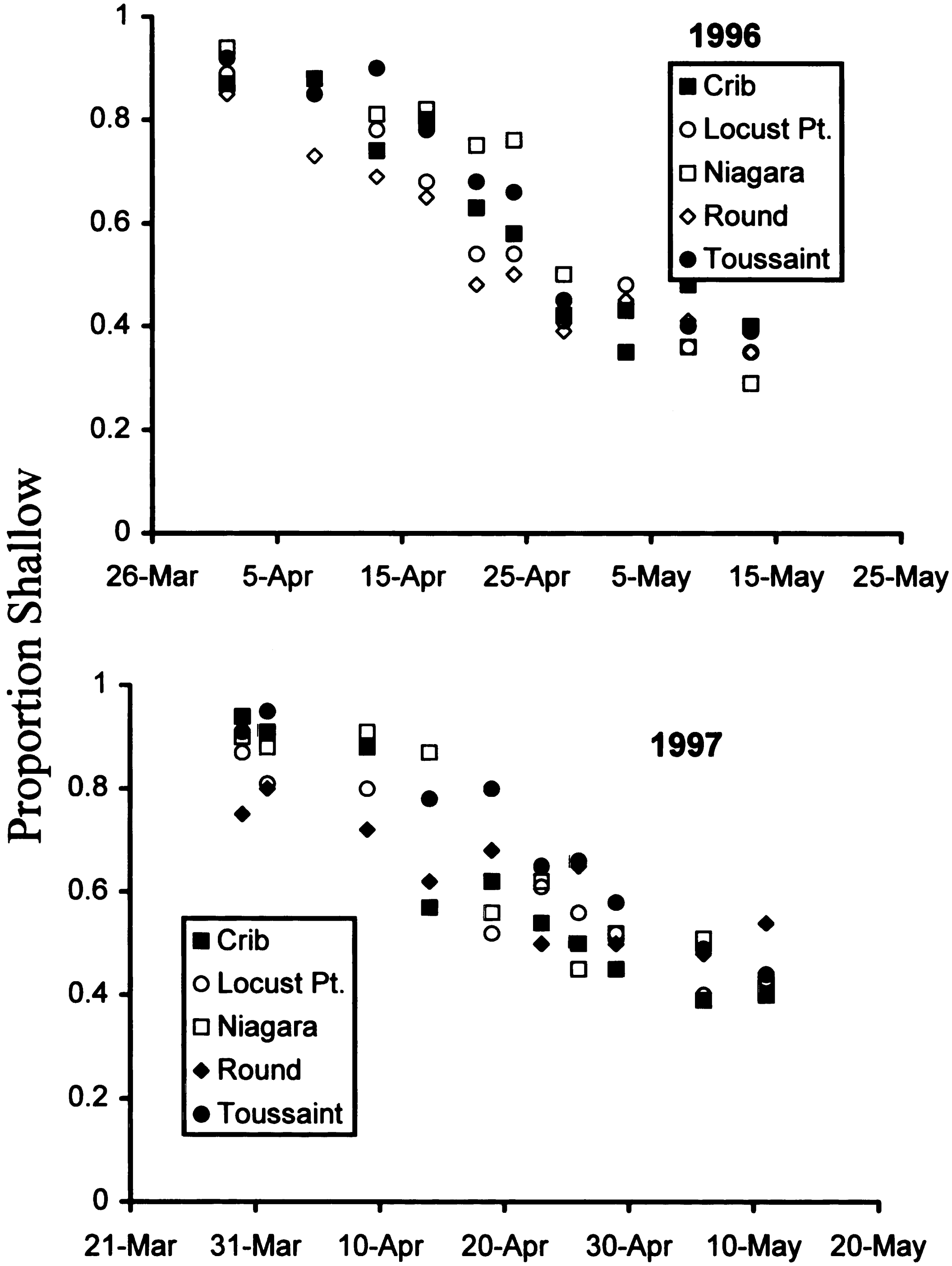


Figure 16. Proportion of eggs collected from shallow sites (< 5m) on reefs in western Lake Erie, 1996 and 1997.

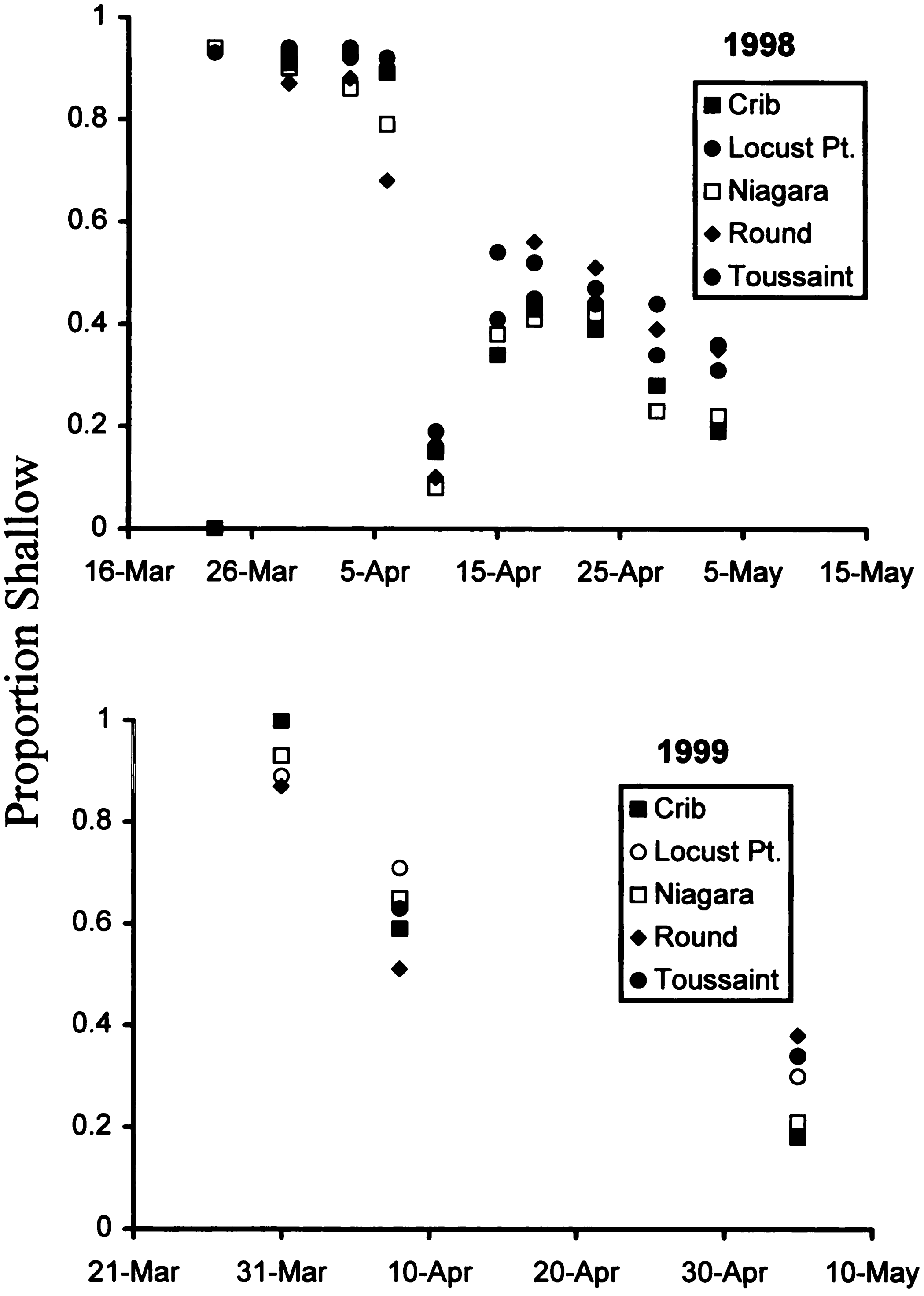


Figure 17. Proportion of eggs collected from shallow sites (< 5m) on reefs in western Lake Erie, 1998 and 1999.

In 1996 I calculated 2 walleye egg survival rates for each of the six reefs sampled. Survival ranged between 0.097 – 0.181 between the six reefs and averaged 0.138 for the period April 17 – April 28, 1996. Survival was significantly higher (paired t-test, 5 d.f., $p = 0.012$) for the period April 24 – May 3, 1996. Estimates ranged between 0.199 and 0.390 and averaged 0.276 (Table 3).

In 1997 I calculated 2 walleye egg survival rates for each of the six reefs sampled. Survival ranged between 0.094 – 0.143 between the six reefs and averaged 0.129 for the period April 9 – April 23, 1997. Survival was significantly higher (paired t-test, 5 d.f., $p < 0.001$) for the period April 19 – April 29, 1997. Estimates ranged between 0.299 and 0.481 and averaged 0.389 (Table 3).

I calculated 3 walleye egg survival values in 1998. Survival ranged between 0.001 – 0.010 on Crib, Locust Pt., Niagara, Round, and Toussaint reef and was substantially higher on Cone reef at 0.185 for the period March 26 – April 10, 1998. Survival averaged 0.019 across all reefs for the first period estimated. Survival was significantly higher on all reefs for the period April 15 – April 28, 1998 ranging from 0.190 – 0.285 and averaging 0.216 (paired t-test, 5 d.f., $p < 0.001$). Survival was also significantly higher for the period April 23 – May 3 than the earliest period (paired t-test, 5 d.f., $p < 0.001$) but did not differ significantly from the second survival estimate ($p = 0.320$). Walleye egg survival averaged 0.395 and ranged between 0.295 and 0.508 for the period April 23 – May 3, 1998 (Table 3).

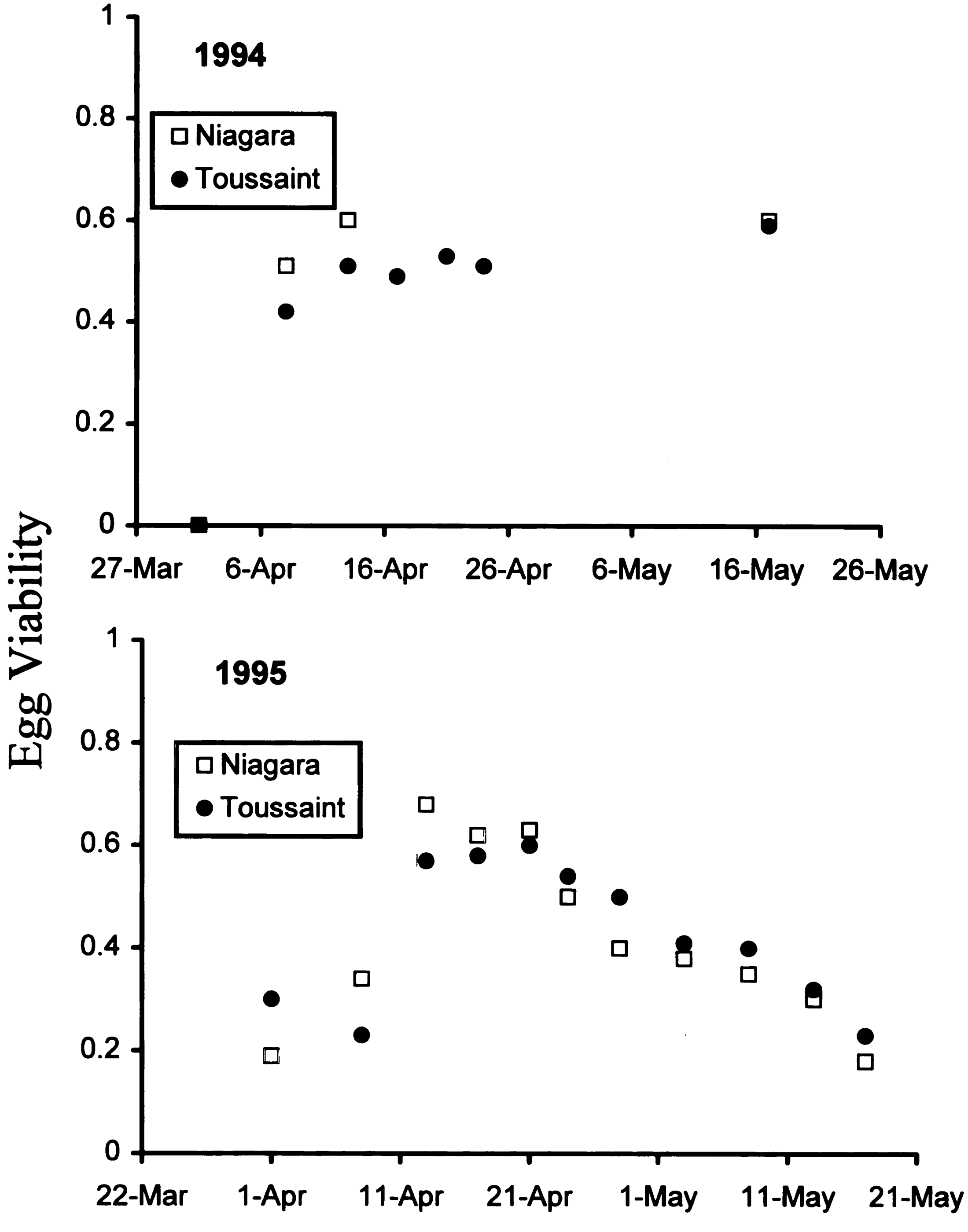


Figure 18. Walleye egg viability on reefs in western Lake Erie, 1994 and 1995.

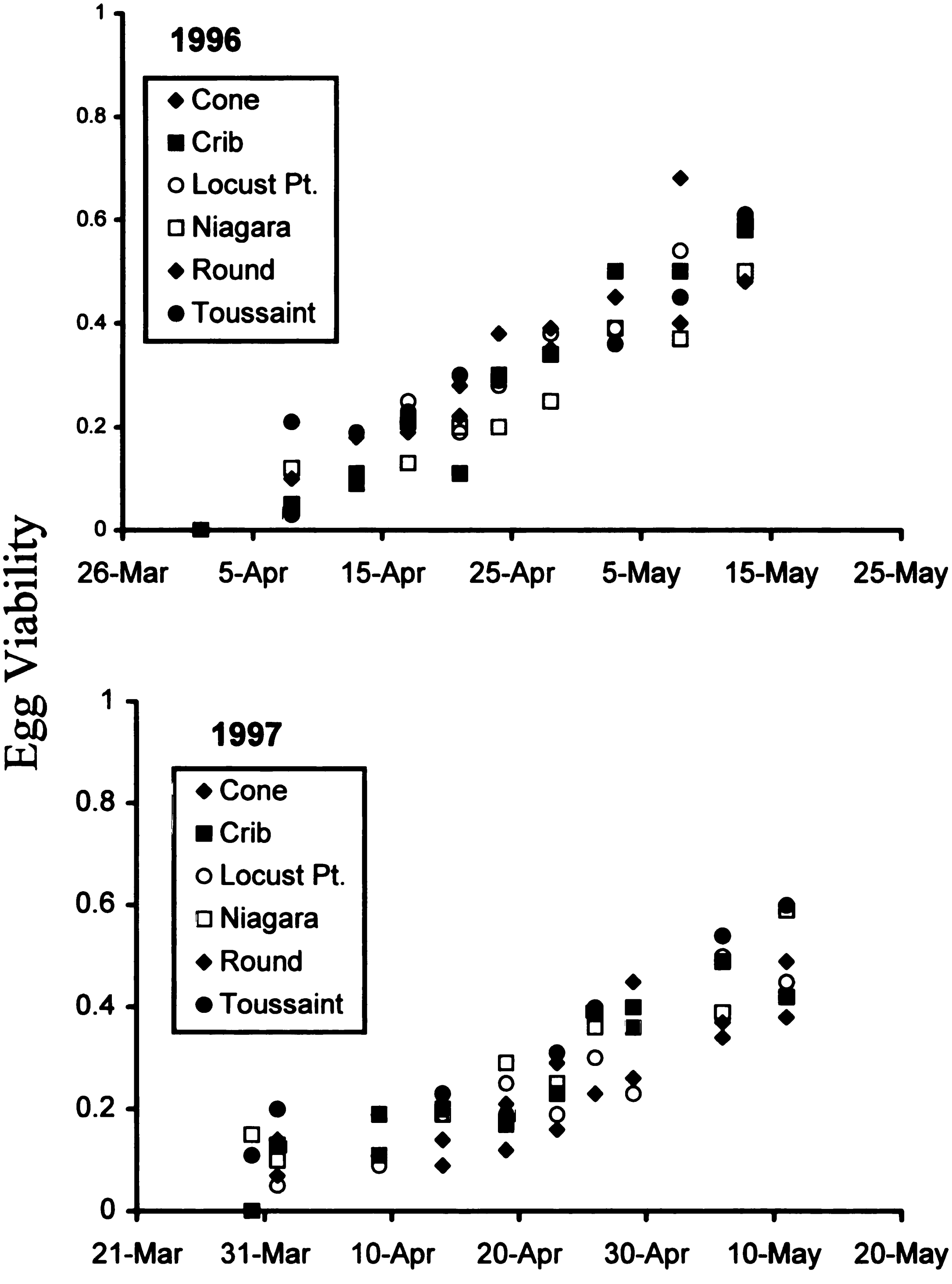


Figure 19. Walleye egg viability on reefs in western Lake Erie, 1996 and 1997.

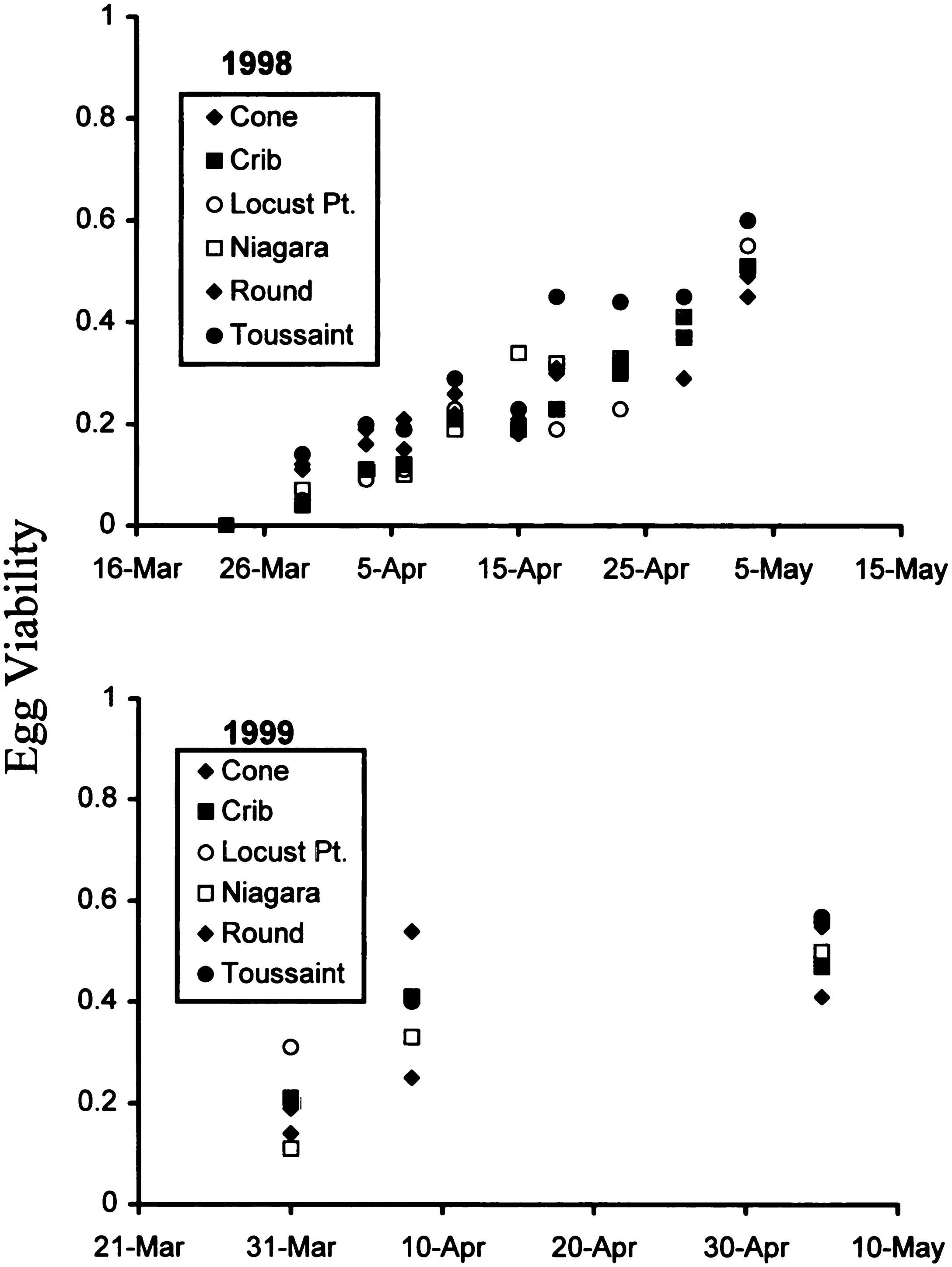


Figure 20. Walleye egg viability on reefs in western Lake Erie, 1998 and 1999.

Table 3. Walleye egg survival estimates for discrete time intervals for reefs in western Lake Erie, 1996 - 1998.

1996	April 17 – April 28	April 24 – May 3	
Cone	0.149	0.199	
Crib	0.197	0.277	
Locust Pt.	0.199	0.277	
Niagara	0.101	0.299	
Round	0.181	0.203	
Toussaint	0.158	0.296	
1997	April 9 – April 23	April 19 – April 29	
Cone	0.131	0.299	
Crib	0.126	0.387	
Locust Pt.	0.143	0.377	
Niagara	0.139	0.391	
Round	0.142	0.399	
Toussaint	0.094	0.481	
1998	March 26 - April 10	April 15 - April 28	April 23 - May 3
Cone	0.185	0.197	0.299
Crib	0.001	0.193	0.295
Locust Pt.	0.010	0.285	0.405
Niagara	0.009	0.235	0.391
Round	0.003	0.194	0.475
Toussaint	0.008	0.190	0.508

Wind and Storm Events

The numbers of days having wind events with velocity and direction sufficient to remove incubating walleye eggs from reefs are listed in Table 4. I observed two different types of effects of wind on egg abundance and survival. First, during the incubation period in 1995, a total of 21 storm events having severe winds (25-50 km/h) occurred which gradually reduced total egg numbers on reefs by about 50% (Figure 10) and substantially increasing egg mortality. These frequent storm events also likely contributed to the slower water warming rate observed on the reefs during the egg incubation period in 1995 (Figure 3, Table 2). I considered the effects of the frequent storms in 1995 on egg abundance and survival to be cumulative, where multiple episodes each contributed to the total loss of eggs from the reefs.

In 1998 I had the unique opportunity to observe the effects of a single gale-force storm event on the relative density, distribution, and survival of walleye eggs on reefs in western Lake Erie. The storm occurred between April 8 and the morning of April 10, well after spawning had begun that year (Figure 12). This storm brought gale force winds in excess of 80 km/h from the east-northeast and persisted for over 36 h (Table 4; NCDC 2000). Resulting waves (some > 4 m in height) scoured western basin reefs. I found about 80% fewer eggs in samples collected on April 10 than on April 6 and this difference was significant (ANOVA, $p < 0.001$). All reefs except Cone experienced a significant decrease in egg relative density between April 6 and April 10. Shallow sites (< 5 m) on reefs lost significantly more eggs (87%) than deep sites (50%) (ANOVA, $p < 0.0001$; Figure 17). Cone reef is a deep reef having no area with depth less than 6 m during my investigation in 1998. I observed a difference in egg relative density of only

8% between April 6 and April 10 on Cone reef and this difference was not statistically significant (p = 0.08).

On average, over 80% of the eggs were collected from shallow sites on the reefs before the storm while only 19% of the eggs were collected from shallow sites after the storm (Figure 17). Egg survival for the period that includes the storm (March 26 – April 10) was quite low ranging from 0.001 – 0.010 on reefs with shallow sampling sites but noticeably higher on Cone reef at 0.185 (Table 3). Walleye continued to spawn on the reefs after the storm, as evidenced by increasing egg relative abundance (Figure 13). Egg survival was much higher on the reefs during mid-April ranging from 0.190 – 0.508 (Table 3).

Table 4. Number of days when wind events occurred over the western Lake Erie reef complex with velocities 25 – 50 km/hr and >50 km/hr during walleye egg incubation periods, 1994 – 1999.

	25 – 50 km/hr.	≥ 50 km/hr.
1994	15	0
1995	21	0
1996	15	0
1997	17	0
1998	12	2
1999	17	0

Larval Walleye Abundance and Distribution

I collected the first pelagic larval walleye on April 28, 1994. The catch peaked on May 1, 1994 when densities averaged 92.5 fish/1,000 m^3 of water. The larval walleye abundance index was 20.7/1,000 m^3 in 1994, the highest I observed during the six years of my study. Pelagic walleye larvae were last collected on June 20, 1994 (Figure 21). Walleye larvae were consistently most abundant at shallow inshore sites west and southeast of the reefs through April, May and early June, 1994 (Figure 4).

In 1995, I collected the first pelagic walleye larvae on May 3. The catch of walleye larvae peaked on May 9, 1995 when catches averaged 5.2 fish/1,000 m^3 of water sampled (Figure 21). The larval walleye abundance index was 3.5/1,000 m^3 in 1995, the lowest observed during my study. Walleye larvae persisted in samples through June 14, 1995. Similar to the distribution of larvae I observed in 1994, the majority of pelagic walleye larvae were collected from shallow inshore sites west and southeast of the reefs (Figure 5).

I collected the first walleye larvae on April 24 in 1996. The catch of walleye larvae peaked on May 26 with an average density of 42.3 fish/1,000 m^3 of water sampled. The larval walleye abundance index estimate was 8.1/1,000 m^3 in 1996. Walleye larvae persisted in samples through June 17, 1996 but catches were low (Figure 22). I collected more pelagic walleye larvae from shallow nearshore sites west of the reefs than elsewhere in 1996 (Figure 6).

I collected the first walleye larvae on April 28 in 1997. The catch of walleye larvae peaked on May 10 with an average density of 30.9 fish/1,000 m^3 of water sampled. The larval walleye abundance index was 13.1/1,000 m^3 in 1997. Walleye larvae persisted in samples through June 20, 1997 but catches were low (Figure 22). I collected the majority of pelagic walleye larvae from nearshore sites west and south of the reefs in 1997 (Figure 7).

I collected the first walleye larvae on April 14 in 1998. The catch of walleye larvae peaked on April 20 with an average density of 27.3 fish/1,000 m^3 of water sampled. The larval abundance index estimate was 16.8/1,000 m^3 in 1998. Walleye larvae persisted in samples through June 3, 1998 (Figure 23). The impact of the loss of walleye eggs from the reefs due to the April 8-10 storm was evident in the distribution and abundance of walleye larvae collected in western Lake Erie in 1998. Larval walleye abundance was consistently low (< 0.01/1,000 m^3) at sampling sites adjacent to reefs during late April and May 1998. Catches of walleye larvae were high at sites near Maumee Bay throughout April and May (densities often > 30/1,000 m^3) while catches on and near the reefs remained low (Figure 8). In fact, over 90% of all walleye larvae collected in my samples came from six sites closest to Maumee Bay suggesting that a large portion of the walleye larvae I collected in western Lake Erie in 1998 were of Maumee River origin.

In 1999 I collected the first pelagic walleye larvae on May 3. Densities of pelagic larvae peaked on May 28 with a mean density of 4.32 fish/1,000 m^3 of water sampled. The larval walleye abundance index was 3.8/1,000 m^3 in 1999. Pelagic walleye larvae persisted in samples through June 7, 1999 (Figure 23). The majority of pelagic walleye were collected from sites west of the reefs in 1999 (Figure 9).

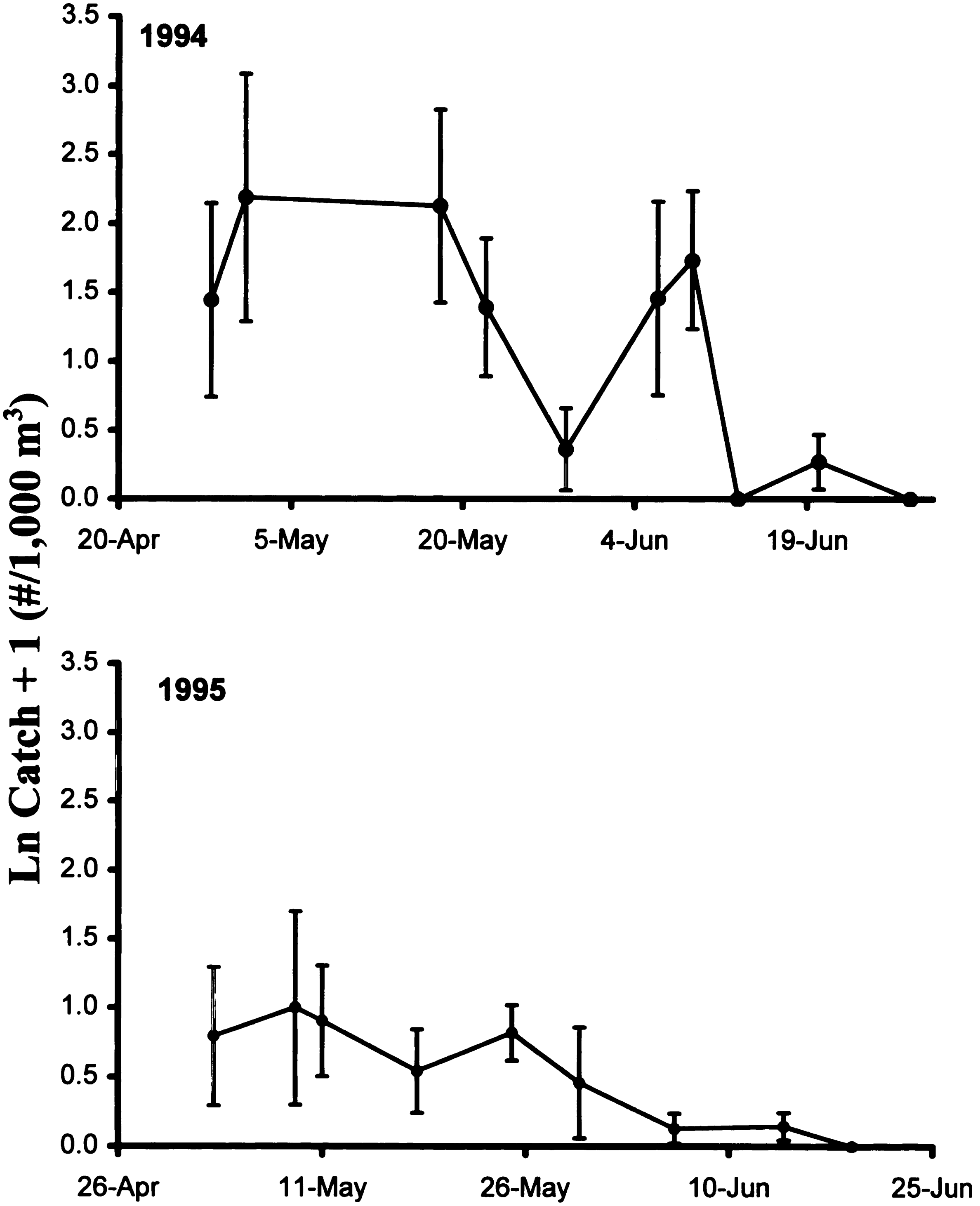


Figure 21. Log-transformed (Ln Catch +1 #/1,000 m) densities of pelagic walleye larvae collected from sites in western Lake Erie, 1994 and 1995.

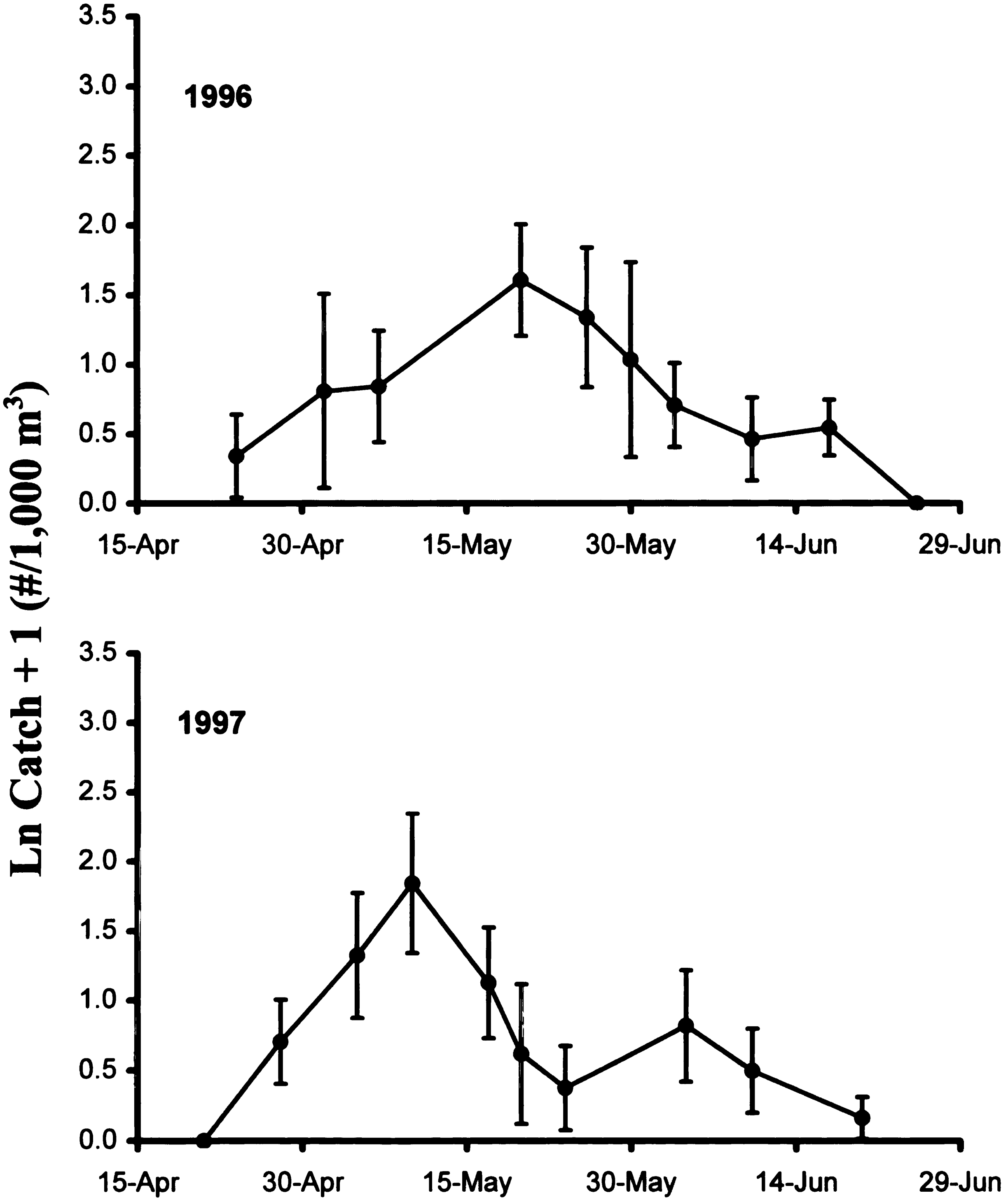


Figure 22. Log-transformed (Ln Catch +1 #/1,000 m) densities of pelagic walleye larvae collected from sites in western Lake Erie, 1996 and 1997.

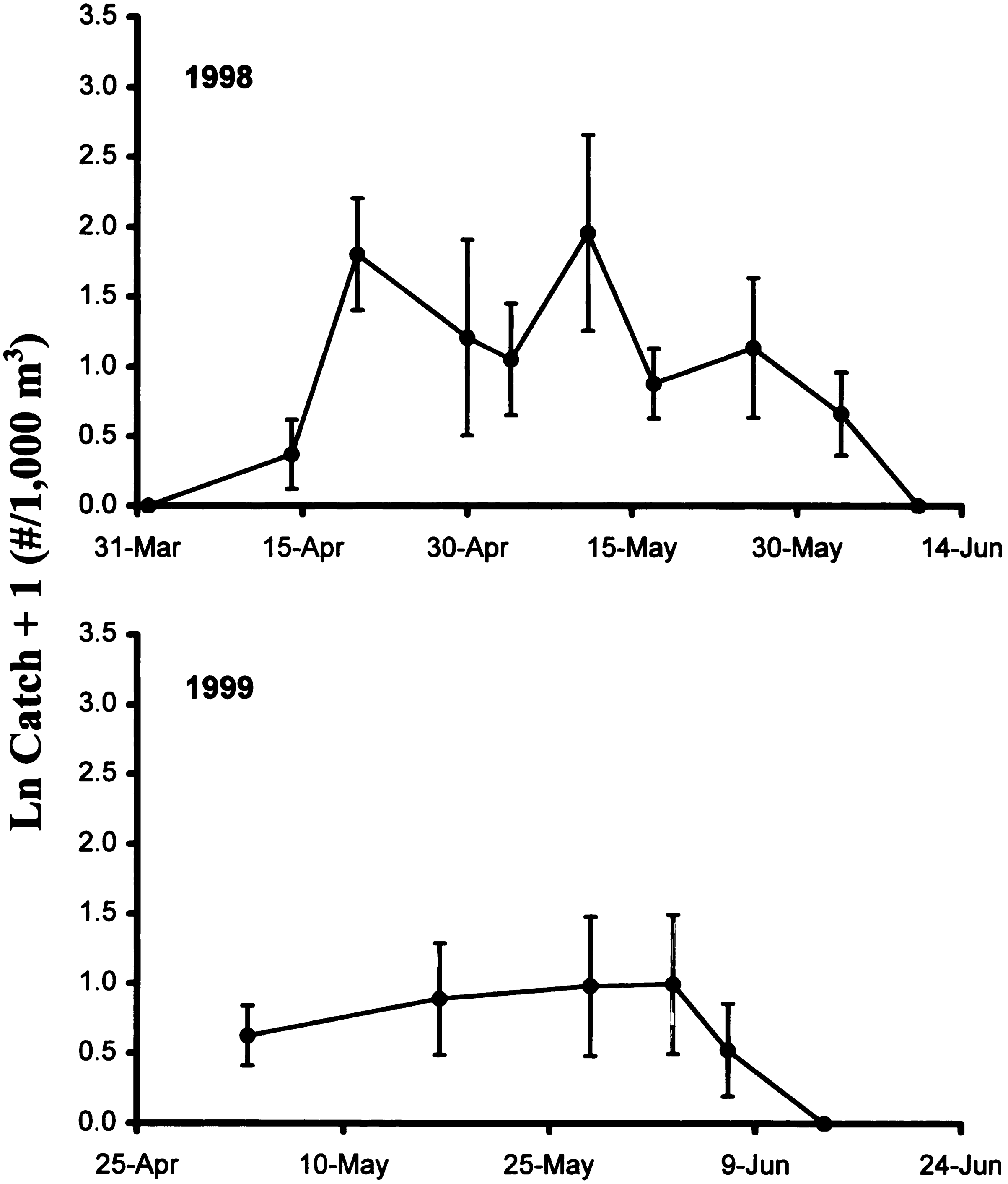


Figure 23. Log-transformed (Ln Catch +1 #/1,000 m) densities of pelagic walleye larvae collected from sites in western Lake Erie, 1998 and 1999.

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Zooplankton Abundance

Zooplankton density was approximately 10 per liter in early May 1994 and increased to over 60 per liter by June 15, 1994. Zooplankton numbers were about 10 per liter in early May of 1995, 1996, and 1998 and increased at a similar rate in all three years to just over 40 individuals per liter by June 15. Zooplankton were most abundant in the spring of 1999 with an initial density of about 10 individuals per liter but a large increase to over 130 per liter by June 15. Zooplankton were least abundant in 1997, not exceeding 20 organisms per liter during May and early June (Figure 24). Zooplankton were generally more abundant at inshore sites in 1996 and 1999 but this trend was not as evident in 1997 and 1998 (Figures 25 and 26).

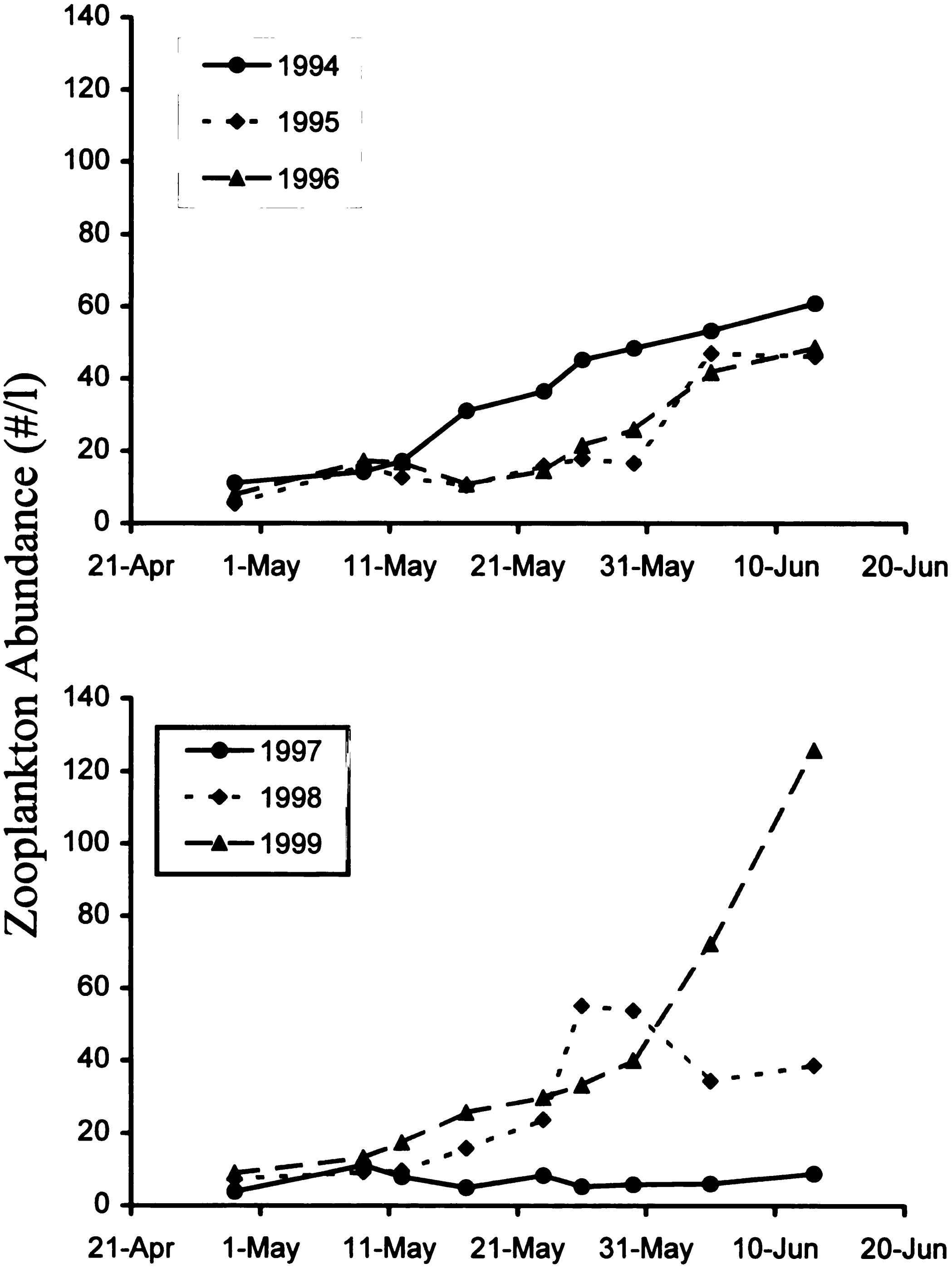


Figure 24. Abundance of zooplankton at nearshore sites in western Lake Erie during the period from May 1 – June 10, 1994 – 1999.

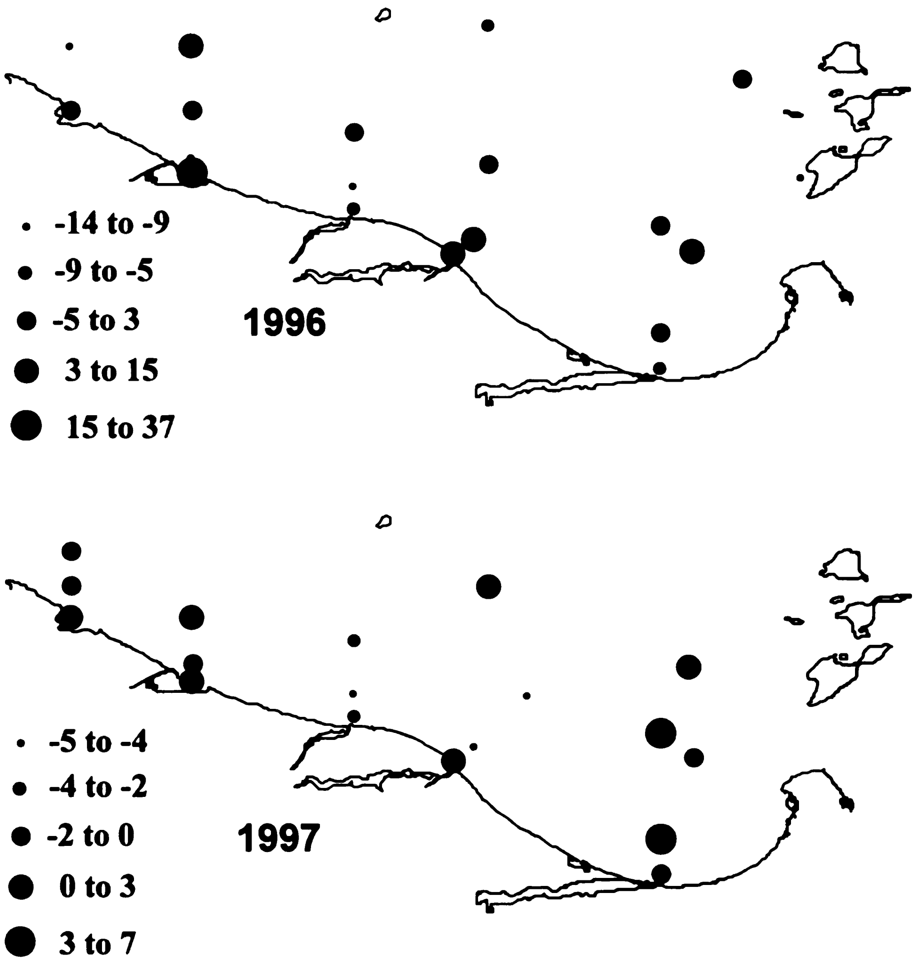


Figure 25. Deviations from mean annual values for zooplankton at sampling sites in western Lake Erie in spring, 1996, and 1997.

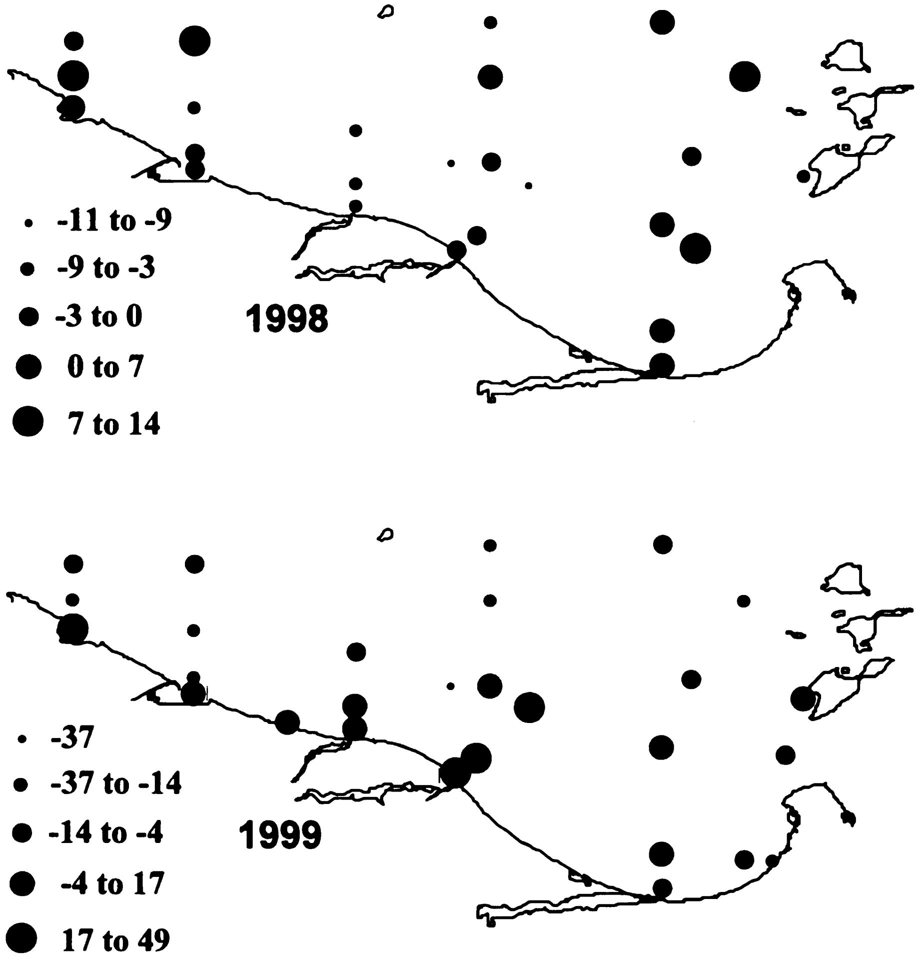


Figure 26. Deviations from mean annual values for zooplankton at sampling sites in western Lake Erie in spring, 1998, and 1999.

Ichthyoplankton Prey Abundance

Density of larval fish was over 1,500/1,000 m^3 in early June 1994, then decreased to under 500/1,000 m^3 by the third week of the month before increasing again to over 2,500/1,000 m^3 at the end of June. Density of larval fish prey was lowest in 1995 with only 11/1,000 m^3 in early June and showed an increase throughout the month to almost 500/1,000 m^3 by the end of June. In 1996, larval fish prey density was about 50/1,000 m^3 and increased steadily throughout the month to 987/1,000 m^3 by the end of June. Larval fish prey density was about 50/1,000 m^3 in early June 1997 and increased steadily to 987/1,000 m^3 by the end of June. Larval fish density was highest throughout June of 1998, beginning at over 1,200/1,000 m^3 in early June and increasing to almost 2,000/m^3 by the end of the month. Larval fish density increased from about 60/1,000 m^3 in early June, 1999 to over 1,100/1,000 m^3 at the end of the month (Figure 27). Similar to the distributions of walleye larvae and zooplankton, densities of ichthyoplankton were generally higher at shallow nearshore sites (Figures 28 and 29).

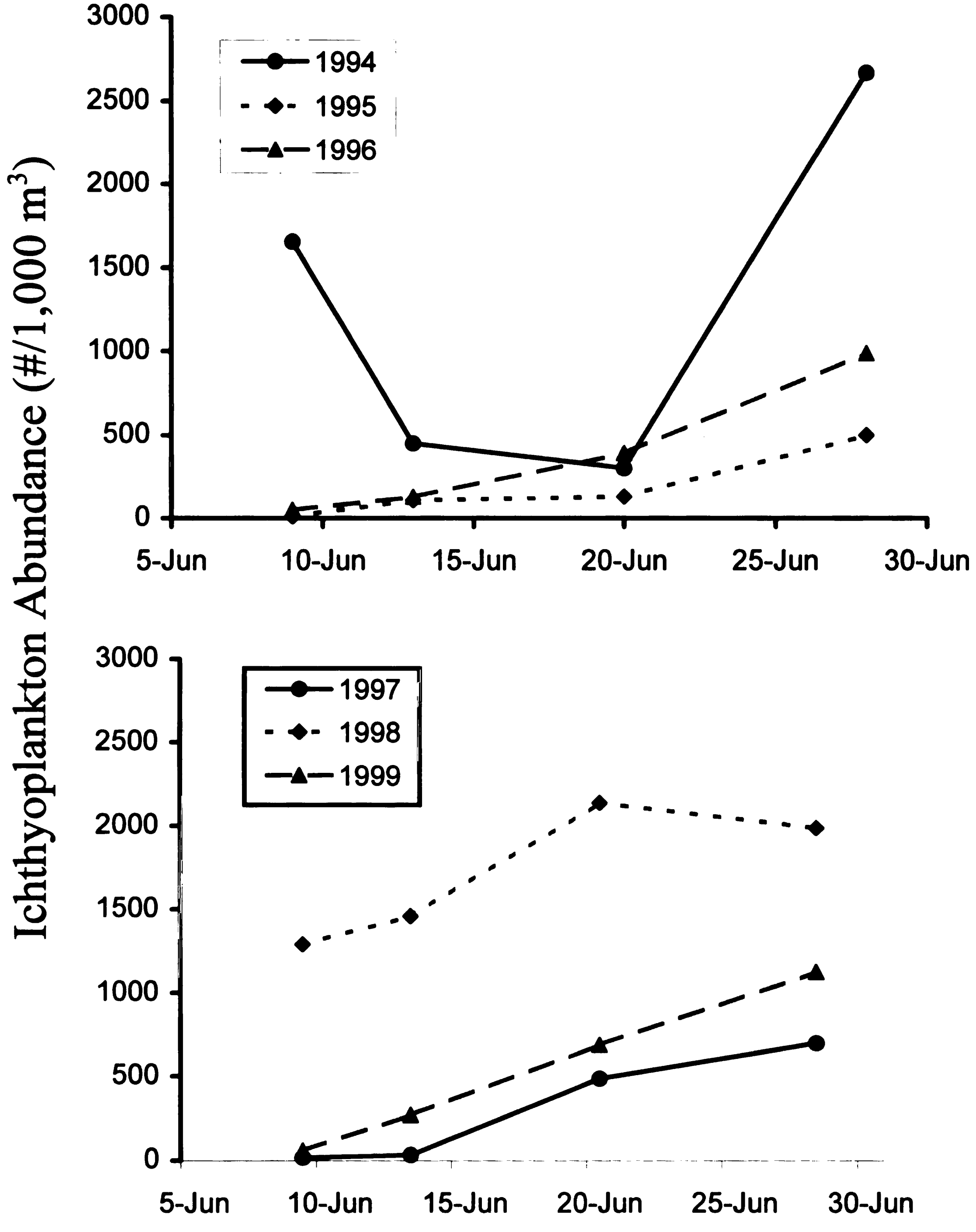


Figure 27. Abundance of ichthyoplankton prey at nearshore sites in western Lake Erie during the period 10 June – 30 June, 1994 – 1999.

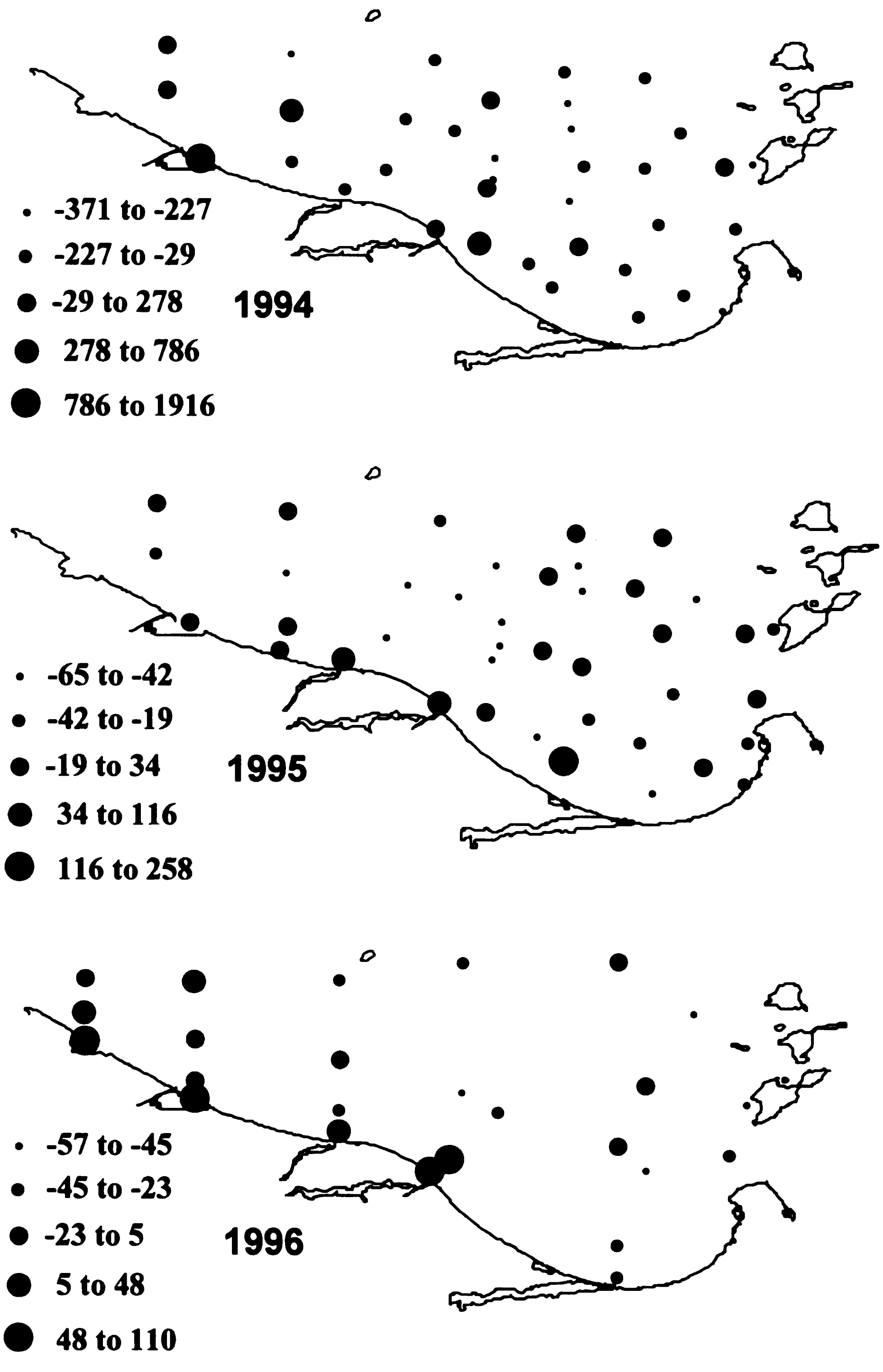


Figure 28. Deviations from mean annual values for non-walleye ichthyoplankton prey species at sampling sites in western Lake Erie in spring, 1994, 1995, and 1996.

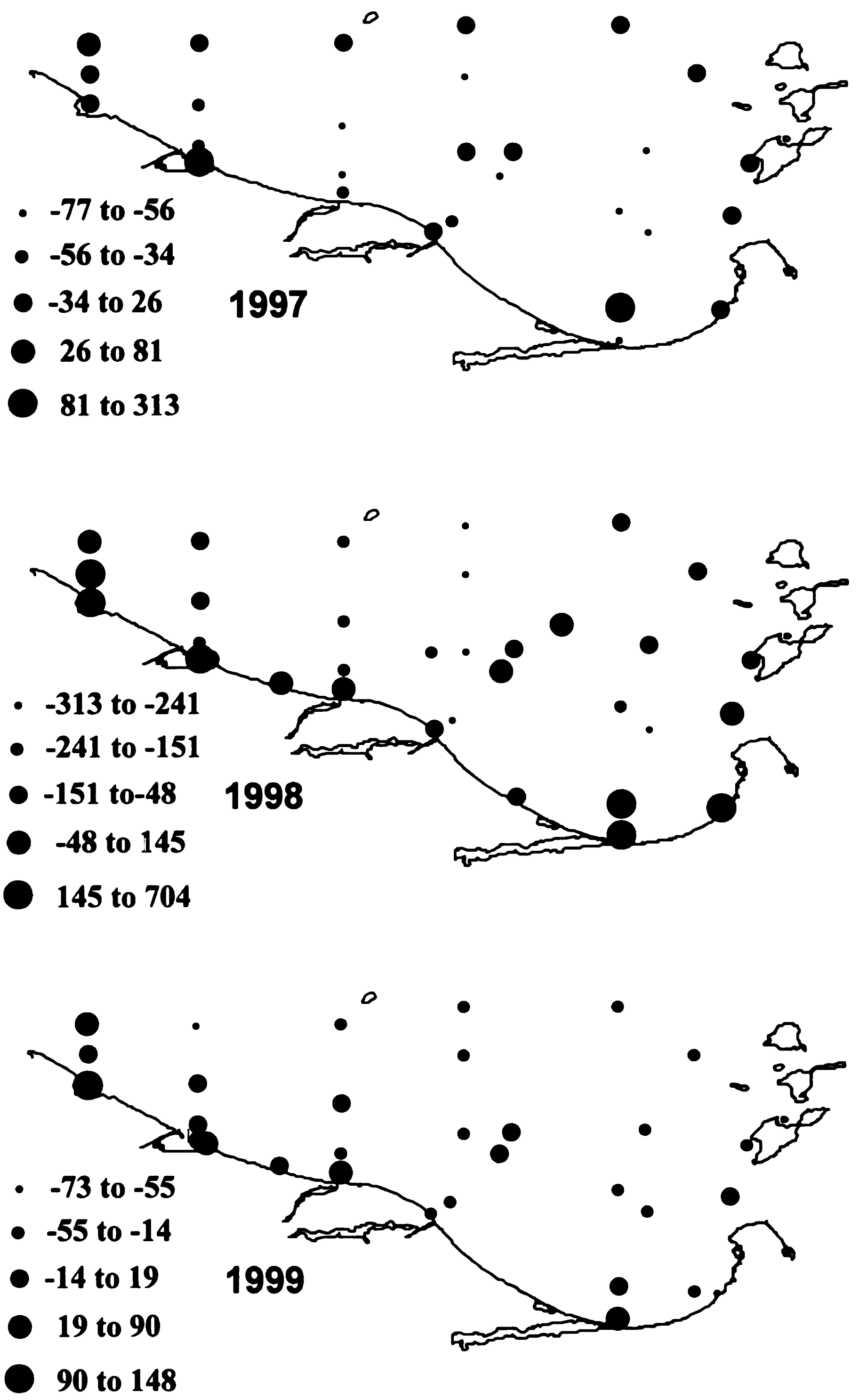


Figure 29. Deviations from mean annual values for non-walleye ichthyoplankton prey species at sampling sites in western Lake Erie in spring, 1997, 1998, and 1999.

Growth of Age-0 Walleye

Newly hatched sac-fry walleye averaged between 6.0 and 7.2 mm TL in all years of the study. Age-0 walleye grew to a length of 46 mm TL by the end of June 1994, 25 mm TL by the end of June 1995, over 30 mm TL by the end of June 1996, over 34 mm TL by the end of June 1997, greater than 35 mm TL by the middle of June 1998, and over 44 mm TL by the end of June 1999 (Figures 30, 31, and 32). Specific growth rates of zooplanktivorous walleye were greatest in 1994 and 1999 with rates of 0.53 and 0.45 mm/day respectively. Specific growth rate was lowest during the zooplanktivorous larval period in 1996 at a rate of only 0.19 mm/day (Table 5). Specific growth rates during the piscivorous age-0 period were highest in 1998 and 1999 with rates of 1.39 and 1.32 mm/day respectively. Specific growth rate was lowest during the piscivorous period in 1995 with a rate of only 0.29 mm/day (Table 5).

Table 5. Specific growth rates of age-0 walleye during periods of zooplanktivory, piscivory, and for entire period May - June in western Lake Erie from 1994 – 1999.

Year	Zooplantivorous Period	Piscivorous Period	May - June
1994	0.53	1.18	0.70
1995	0.32	0.29	0.31
1996	0.19	0.82	0.34
1997	0.31	1.00	0.53
1998	0.36	1.39	0.49
1999	0.45	1.32	0.73

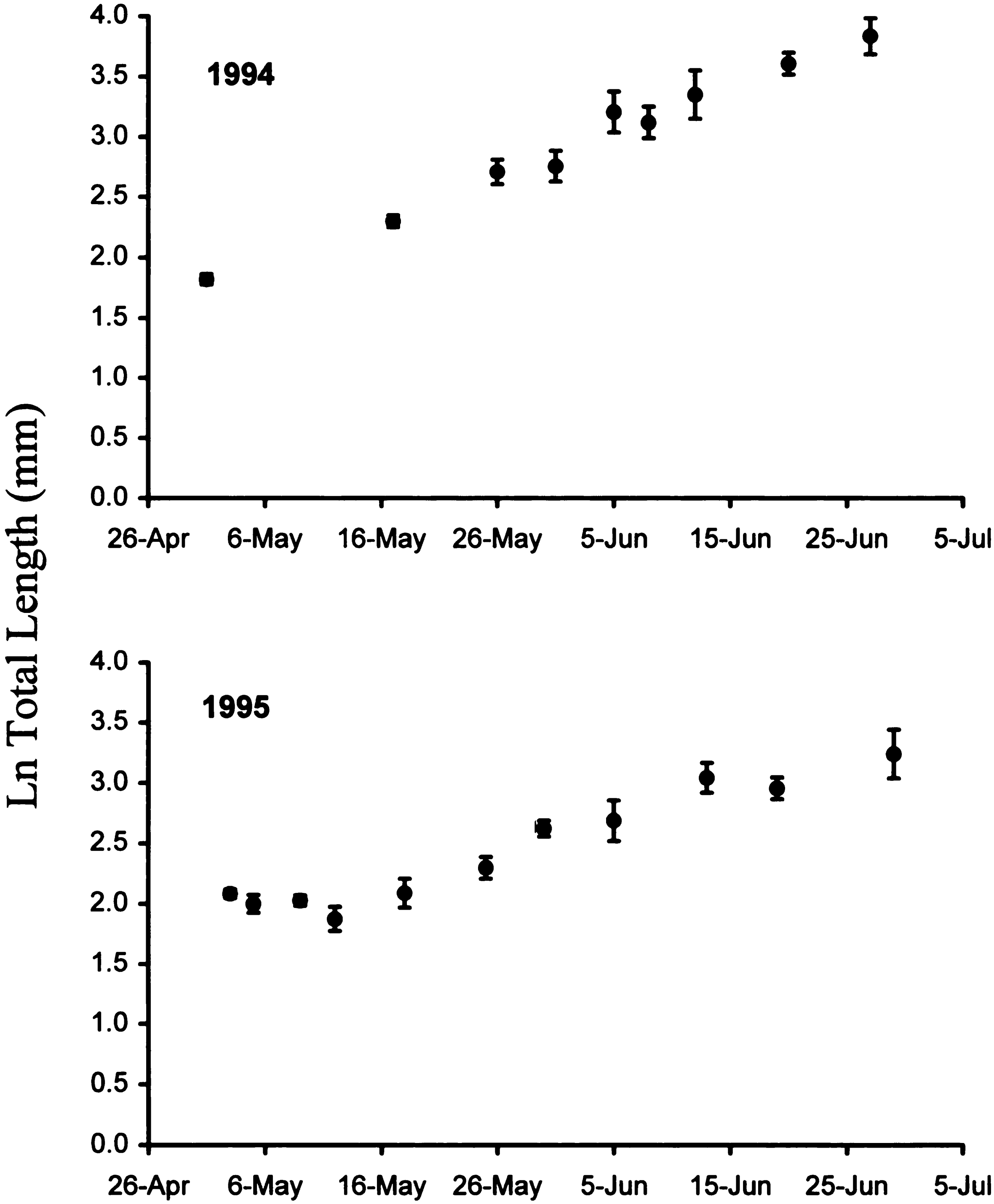


Figure 30. Log-transformed (Ln) total lengths (mm) of age-0 walleye collected in western Lake Erie, 1994 and 1995.

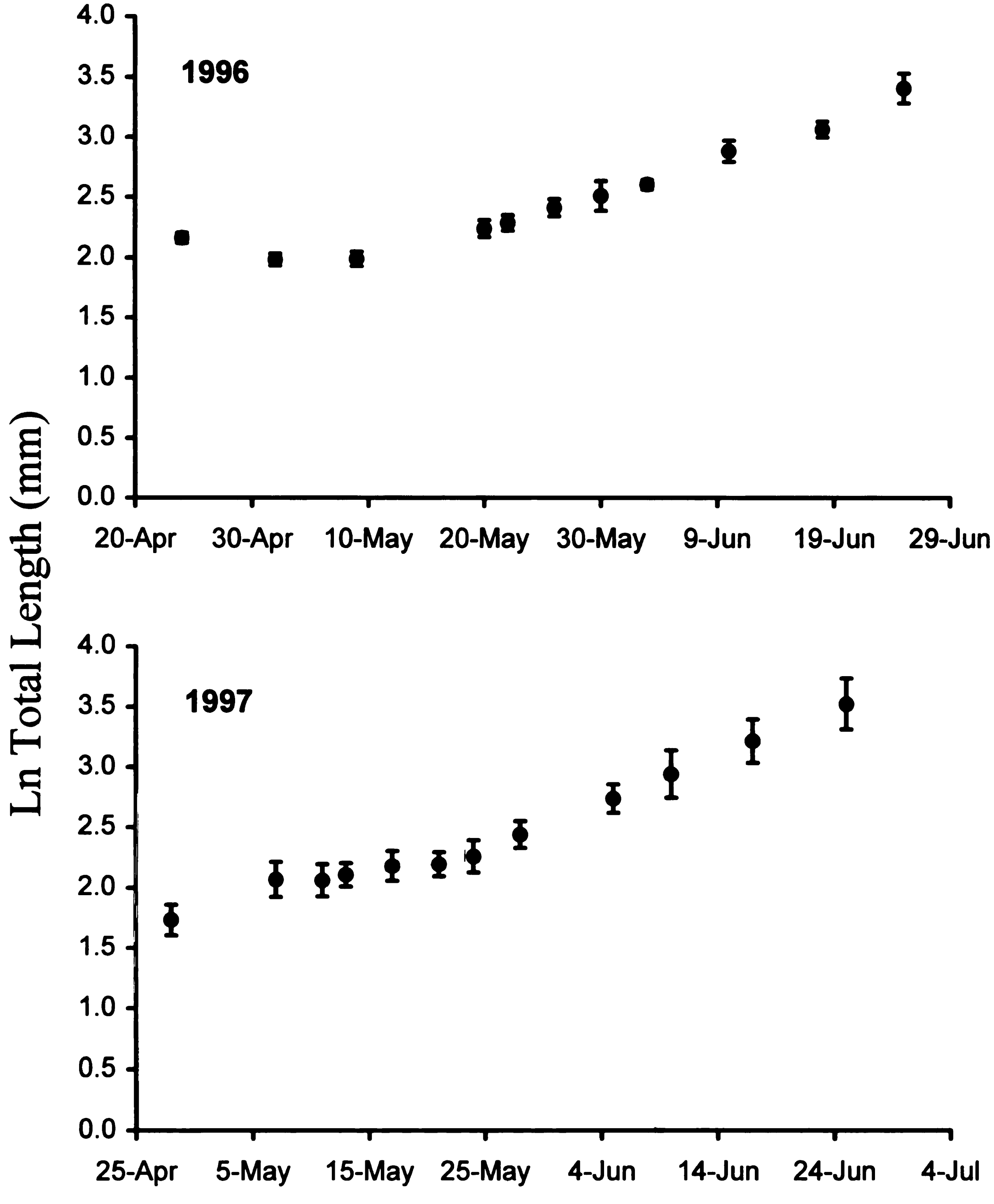


Figure 31. Log-transformed (Ln) total lengths (mm) of age-0 walleye collected in western Lake Erie, 1996 and 1997.

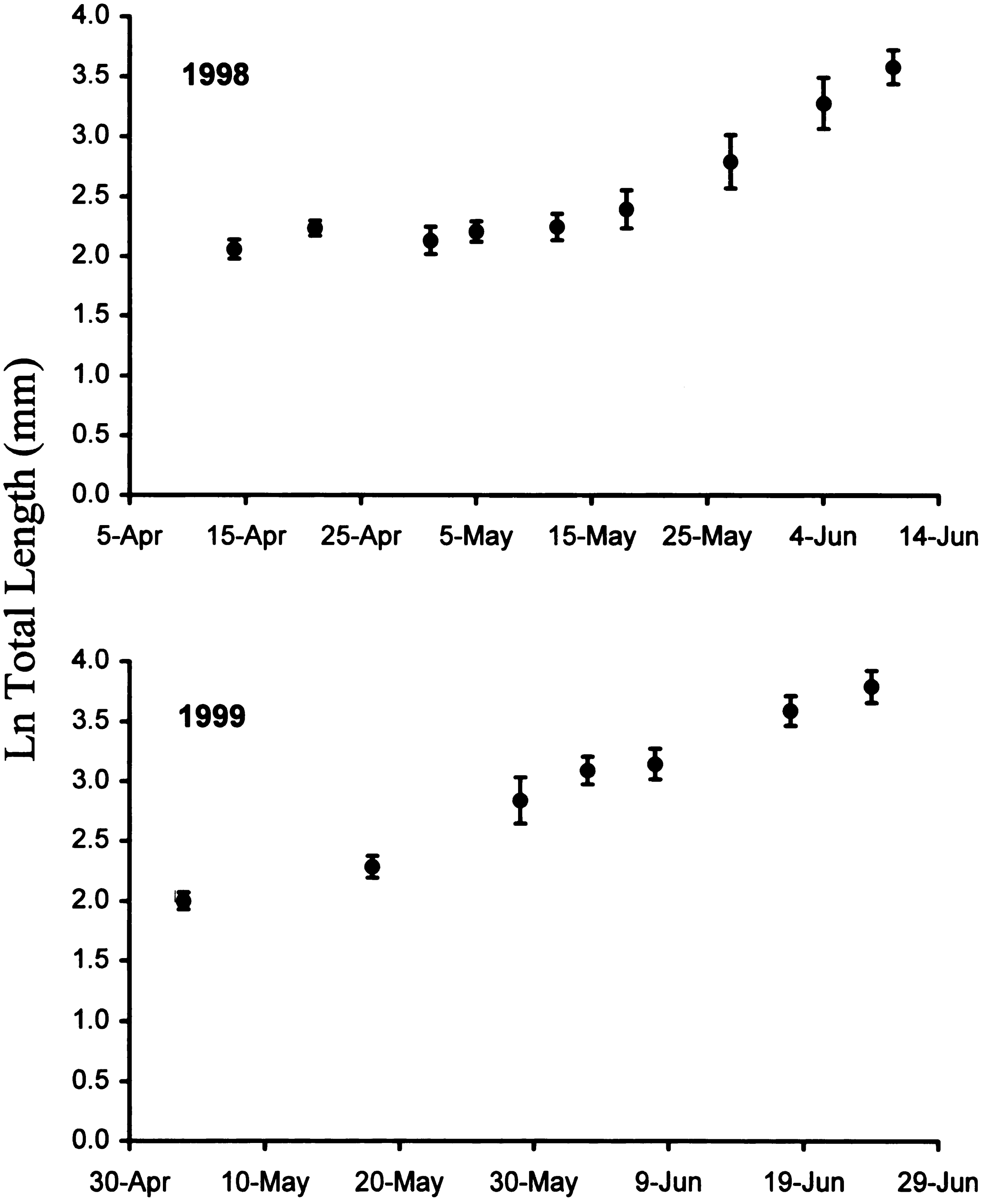


Figure 32. Log-transformed (Ln) total lengths (mm) of age-0 walleye collected in western Lake Erie, 1998 and 1999.

Specific growth rates of pelagic larval walleye during the period May 1 through June 10, when the fish were zooplanktivorous, were positively associated with zooplankton densities during the same time period in each year (sample correlation coefficient $r = 0.66$, $p = 0.16$, $n = 6$; Figure 33). A regression equation using an exponential function fit to these data showed that zooplankton density explained about 26% of the variability in specific growth of zooplanktivorous walleye larvae from 1994 – 1999 (the linear regression equation explained 43%). Conversely, the relationship between specific growth rate of larval zooplanktivorous walleye and water warming rate during the same time period was less pronounced (sample correlation coefficient $r = 0.155$, $p = 0.769$, $n = 6$; Figure 33). I found similar results when I examined the relationship between specific growth rate of age-0 walleye after June 10 when the fish are primarily piscivorous. Specific growth rate was positively associated with abundance of ichthyoplankton prey (sample correlation coefficient $r = 0.694$, $p = 0.126$, $n = 6$; Figure 34) and the logistic regression fit to these data showed that ichthyoplankton prey density accounted for over 67% of the variability in specific growth rate during this time period during the six years of my study. Similar to the relationship between specific growth rate of zooplanktivorous walleye and water warming rate, the growth of piscivorous walleye demonstrated no discernable association with water warming rate (sample correlation coefficient $r = -0.152$, $p = 0.720$, $n = 6$; Figure 34).

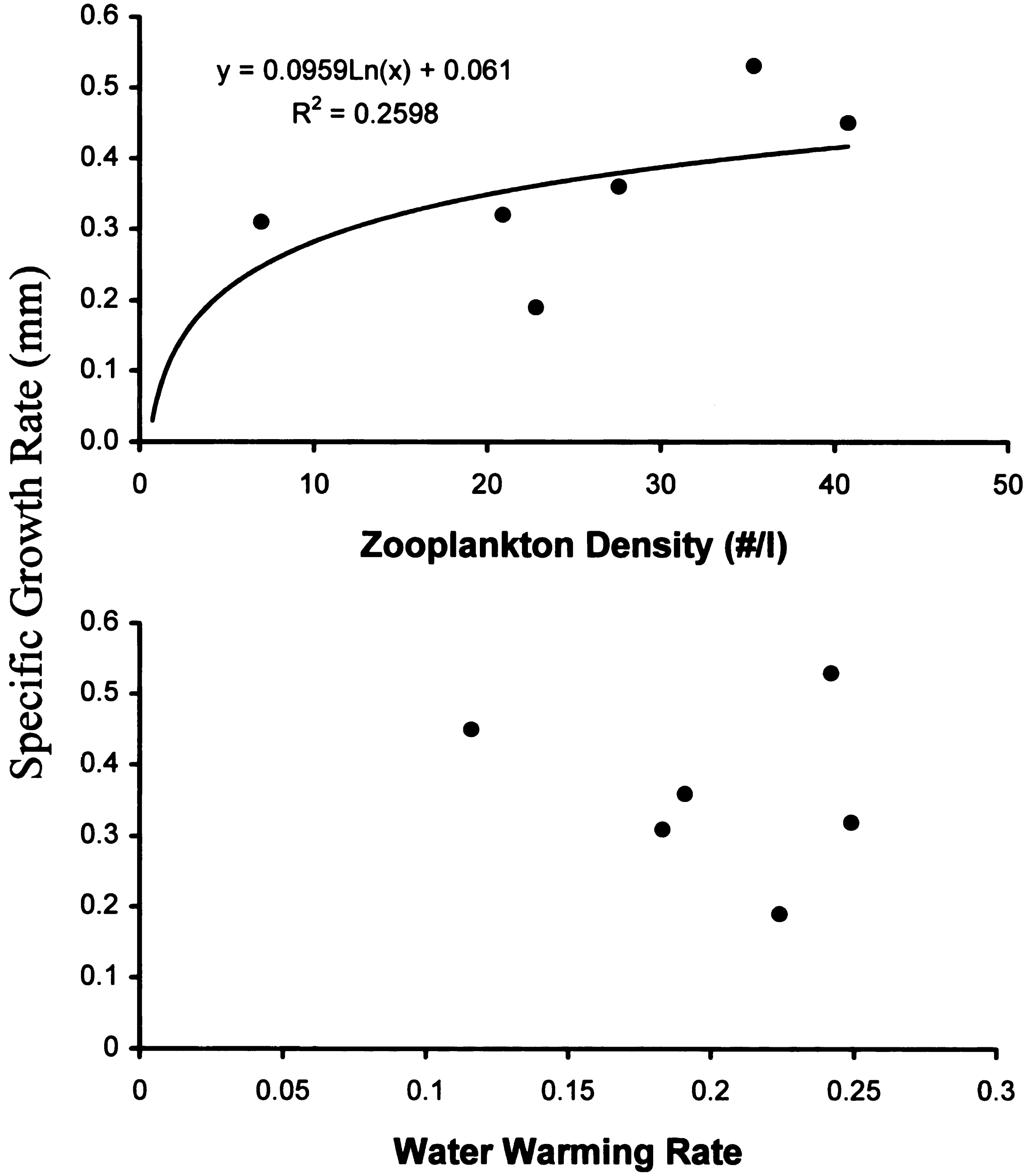


Figure 33. Relationship between specific growth rate of zooplanktivorous pelagic walleye larvae and zooplankton abundance (top panel) and pelagic walleye larvae and water warming rate (bottom panel) for the period May 1 - June 10, 1994-99.

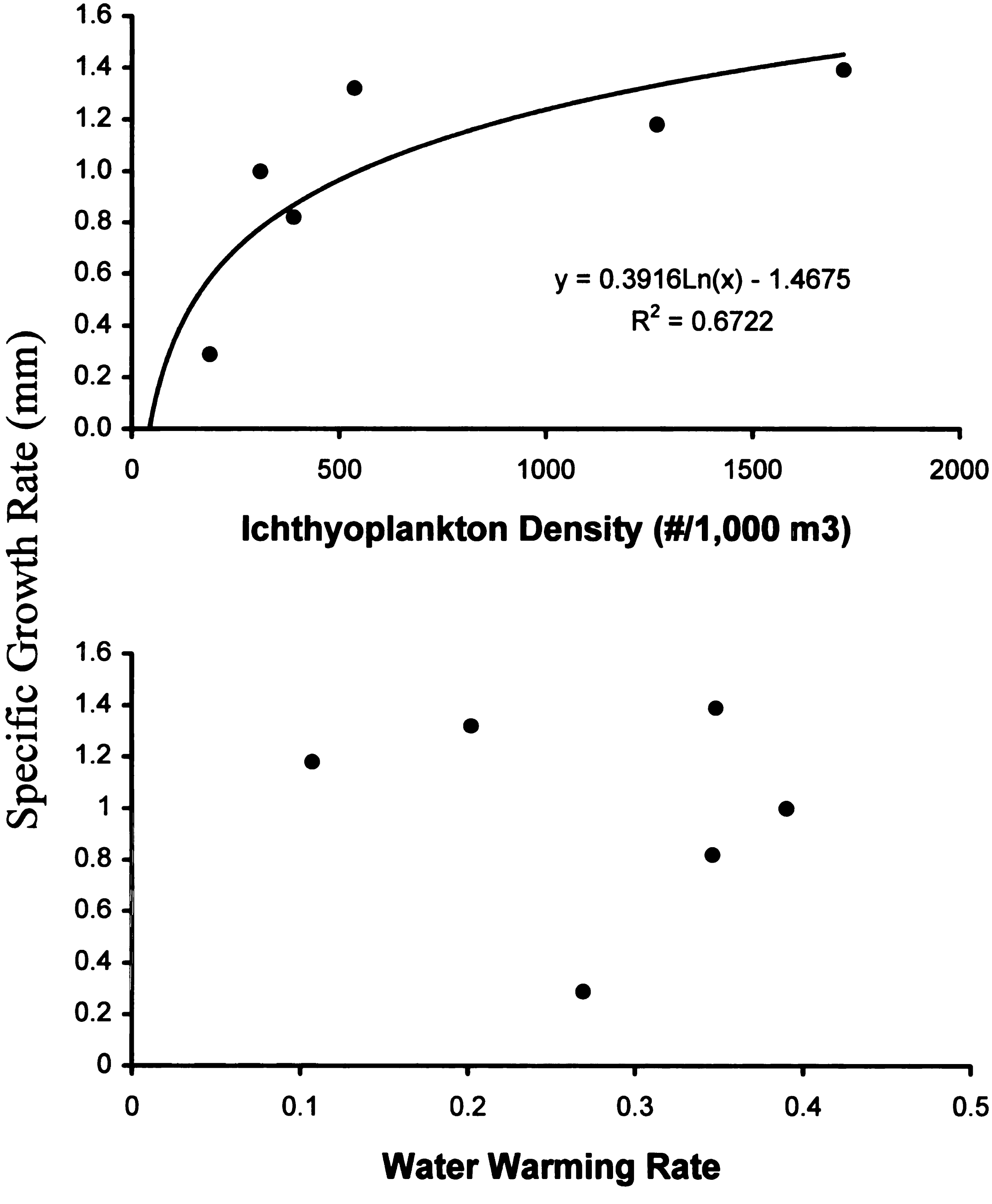


Figure 34. Relationship between specific growth rate of piscivorous pelagic walleye larvae and ichthyoplankton abundance (top panel) and pelagic walleye larvae and water warming rate (bottom panel) for the period June 10 – June 30, 1994 - 99.

Larval Walleye Survival

I estimated the daily instantaneous mortality rate in 1994 using catch data from May 19 – June 6 (Figure 21) for fish ranging in size from 9.9 mm on May 19 to 25 mm on June 6 (Figure 30). In 1995 I used catch data from May 25 – June 13 (Figure 21) when fish size ranged from 9.9 mm on May 25 to 21 mm on June 13 (Figure 30). In 1996 I used catch data from May 26 – June 10 (Figure 22) when fish ranged in size from 11.1 mm on May 26 to 17.8 mm on June 10 (Figure 31). I estimated the mortality rate in 1997 using catch data from May 17 – June 20 (Figure 22) when pelagic walleye larvae ranged in size from 8.9 mm on May 17 to 22.1 mm on June 20 (Figure 31). In 1998 I estimated the mortality rate using catch data from May 4 - June 3 (Figure 23) when pelagic walleye larvae ranged in size from 8.4 mm on April 30 to 24.7 mm on June 10 (Figure 32). In 1999 I estimated the mortality rate using catch data from June 3 – 7 (Figure 23) when pelagic walleye larvae were 21.5 and 23.5 mm TL, respectively (Figure 32). These time periods defined the descending limb of the catch curves for pelagic walleye larvae.

The instantaneous mortality rates, their 95% confidence limits, and translations into total mortality rates are listed in Table 6. The regression lines used to estimate the mortality rates for 1995, 1998, and 1999 were significantly different from zero. The instantaneous mortality estimate for 1996 was the lowest at 0.022/day while the rate estimated for 1994 was the highest at 0.078/day. Total mortality was lowest in 1996 with an estimate of 28.1% and highest in 1998 at 83.8% (Table 6).

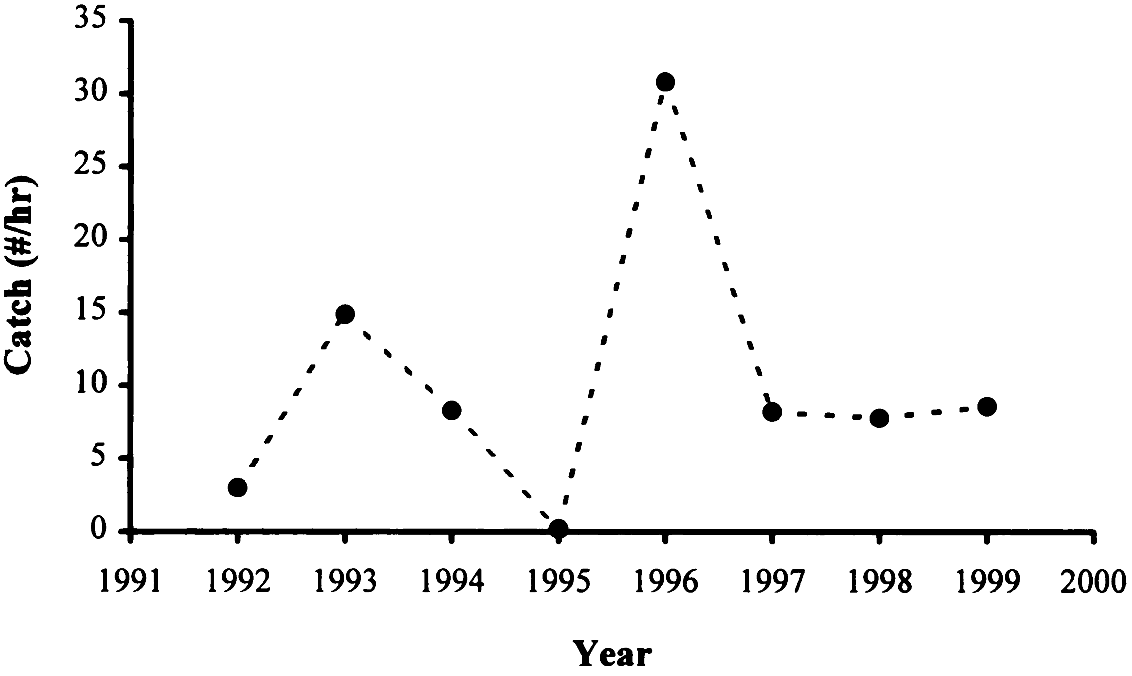
Table 6. Daily instantaneous mortality rates (Z), 95% confidence limits, total mortality rates (A), and p-values for regressions used to calculate instantaneous mortality rates for pelagic larval walleye collected in western Lake Erie, 1994 – 19998.

	Z	95% Confidence Limit	A (%)	p-value
1994	0.078	$0.191 \geq Z \geq -0.035$	75.4	0.094
1995	0.053	$0.098 \geq Z \geq 0.009$	63.5	0.017
1996	0.022	$0.075 \geq Z \geq -0.031$	28.1	0.069
1997	0.030	$0.114 \geq Z \geq -0.054$	63.9	0.241
1998	0.065	$0.125 \geq Z \geq 0.005$	83.8	0.039
1999	0.118	$0.145 \geq Z \geq 0.013$	37.6	0.021

Fall Age-0 Walleye Abundance Index

Demersal age-0 walleye abundance in Ohio Division of Wildlife October bottom trawl surveys ranged from a low of 0.2/hr of trawling in 1995 to a high of 30.8/hr of trawling in 1996. The low value in 1995 indicates that this was the weakest walleye year-class to form during the six years of my study while the high value in 1996 indicates that this was the strongest year-class formed. Index values in 1994, 1997, 1998, and 1999 were 8.3, 8.2, 7.8, and 8.6 fish/hr of trawling respectively (Figure 35, Table 7).

To assess the relationship between water warming rate during the walleye egg incubation period and the fall year-class strength index, I plotted the index of fall walleye abundance against spring water warming rate for years from 1960 to 1997. Historic data were obtained from the Ohio Division of Wildlife and Busch et al. (1975). The index of fall walleye abundance never exceeded 5 fish per hour of trawling when waters warmed at rates less than 0.2 degrees C/day but greatly exceeded that number at higher warming rates (Figure 35) indicating that 0.2 degrees C/day may be a critical minimum threshold warming rate for walleye egg survival in western Lake Erie.



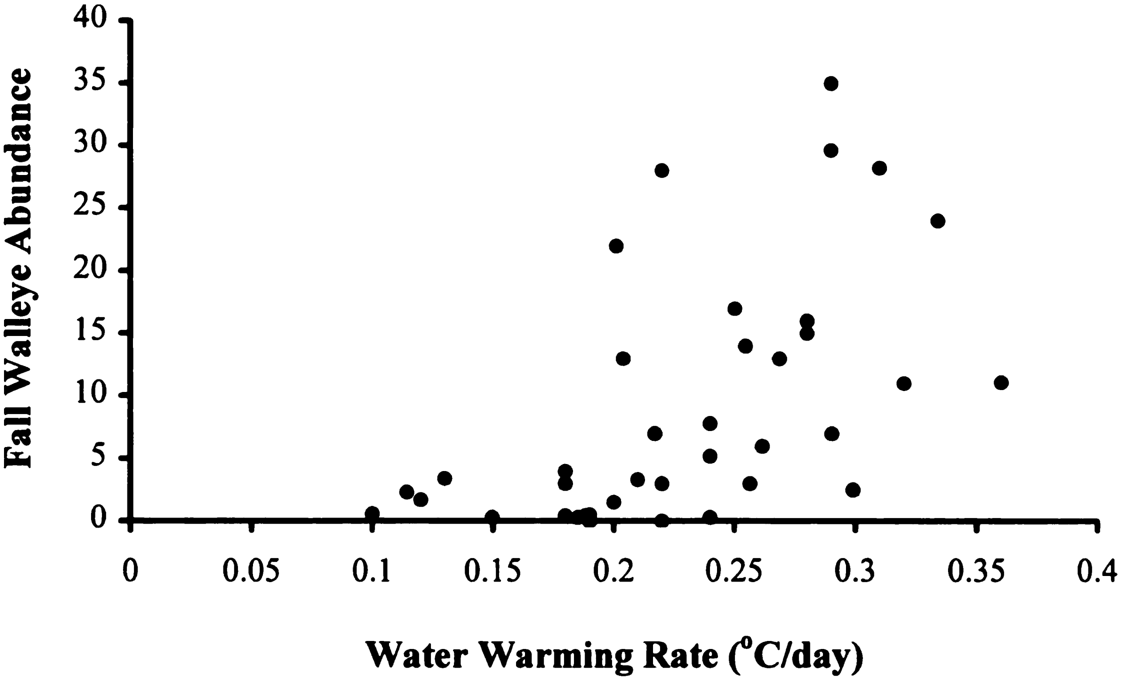


Figure 35. Catch of age-0 walleye in Ohio Division of Wildlife October bottom trawl surveys, 1992 – 1999 (Top). Relationship between spring water warming rate and abundance of age-0 walleye collected in Ohio Division of Wildlife bottom trawls. Data from Busch et al. 1975, Roseman 1997, Ohio Division of Wildlife 2000.

Discussion

Based on the catch of demersal age-0 walleye in Ohio Division of Wildlife October bottom trawl surveys, my research was able to document the events that occurred during the early life history stages of reef-spawned walleye that led to the formation of a broad range of year-class strengths. In 1995 I observed processes contributing to the development of one of the weakest year-classes in the past 15 years. In contrast, I documented the events that led to the formation of one of the strongest walleye year-classes in 1996. While fall indices of year-class strength were quite similar for years 1994, 1997, 1998, and 1999, the events that occurred during the ontogeny of these year-classes were dramatically different. Using data presented above and summarized in Table 7, I will compare and contrast the events that led to the formation of these six year-classes.

The 1995 walleye year-class is one of the weakest year-classes formed in the past 2 decades (Lake Erie Walleye Task Group 1999). The walleye egg incubation period in 1995 was one of the least favorable for egg survival that I observed. Water warming rate in 1995 was the lowest in all 6 years of my study and strong wind events were frequent during the egg incubation period. Because slow water warming rates increase egg incubation time (Smith and Koenst 1975), eggs experienced prolonged exposure to the effects of wind and wave action that displaced eggs from favorable incubation areas on reefs. The prolonged incubation period also increased the risk of predation and disease (Johnson 1961, Hurley 1972). I observed that egg viability decreased on reefs through April and early May in 1995 when I noticed a large amount of fungus on the eggs. Mean egg survival estimates in 1995 were lowest of any of the six years of my study. Egg

Table 7. Water warming rate during walleye egg incubation periods, number of days between April 1 and May 15 with winds 25-50 km/h originating from between 260° and 110°, number of days between April 1 and May 15 with winds exceeding 50 km/h originating from between 260° and 110°, mean walleye egg relative abundance on reefs, mean walleye egg survival (%), index of larval walleye abundance (#/1,000 m^3), pelagic larval walleye survival (%), specific growth rate (mm/d) of age-0 walleye from May through June, and October bottom trawl index values for demersal age-0 walleye in western Lake Erie, 1994 – 1998. * - 2 of the 14 wind days in 1998 exceeded 50 km/h.

Year	Warming Rate (C/day)	Wind Days > 25 km/h	Eggs (#/tow)	Egg Survival (%)	Larvae (#/1,000 m^3)	Larval Survival (%)	Growth Rate (mm/d)	Fall Index[2] (#/ h trawling)
1994	0.22	15	11,300	[1]0.350	20.7	24.6	0.70	8.3
1995	0.16	21	3,610	[1]0.105	3.5	36.5	0.31	0.2
1996	0.22	15	7,230	0.211	8.1	71.9	0.34	30.8
1997	0.19	17	5,450	0.225	13.1	36.1	0.53	8.2
1998	0.24	14*	695	0.210	16.8	14.2	0.49	7.8
1999	0.18	17	-----	-----	3.8	62.4	0.73	8.6

1) From Roseman et al. 1996.
2) Ohio Division of Wildlife 2000.

viability generally increased during incubation periods in other years of my study.

Congruent with low egg densities and survival on reefs, pelagic larval walleye were also rare in samples in 1995 with a larval walleye density index value of only 3.5/1,000 m^3. Average growth rate of age-0 walleye through June was the lowest of all six years of my study. Even though water temperatures warmed quickly in late April and May when walleye feed primarily on zooplankton, the abundance of zooplankton remained below 20/liter through May, limiting walleye growth during this period. Water temperature rose slowly during June in 1995 and the abundance of edible ichthyoplankton prey was also very low. Survival of pelagic larvae was 36.5% and, coupled with low larval abundance, led to the lowest fall abundance index observed during my study of 0.2 fish/ h of trawling. Numerous laboratory and field studies have demonstrated that growth of larval walleye is limited by low water temperatures and low prey abundance (Kelso 1972, Spykerman 1974, Li and Mathias 1982, Serns 1982, Fox 1989, Johnston 1999) and can lead to low survival rates, consistent with my conclusions for factors controlling walleye year-class formation in western Lake Erie in 1995 .

In contrast to the extremely weak year-class formed in 1995, the 1996 year-class was exceptionally strong, with a fall abundance index of 30.8 fish/h of trawling. I observed relatively high egg abundance on reefs and good egg survival in 1996. Waters warmed quickly in 1996 at 0.22 °C/day and the frequency of wind events was low (15) providing favorable conditions for egg incubation, resulting in high egg survival rate (0.211) and moderate abundance of pelagic larvae (8.1/1,000 m^3). The factor that contributed most to the high fall abundance of age-0 walleye in 1996 was the exceptionally high larval survival rate of 71.9%. While mean zooplankton abundance was low in May and early June, with mean densities similar to those observed in 1995, zooplankton abundance was higher at inshore sites where larval walleye were concentrated. The abundance of edible ichthyoplankton was also higher in 1996 and waters warmed quickly during June contributing to good growth rates and the high survival of pelagic larvae.

While October bottom trawl index values were similar in 1994, 1997, 1998, and 1999 at about 8 age-0 walleye/h of trawling, the combination and magnitude of factors contributing to year-class formation varied between years. I observed the highest egg abundance in 1994 accompanied by fast water warming during incubation and few strong wind events leading to high egg survival and the highest larval walleye densities observed during my study. Zooplankton were very abundant and waters warmed quickly during the zooplanktivorous feeding period. Zooplanktivorous walleye larvae responded to the good conditions exhibiting high specific growth during this time period. Ichthyoplankton prey abundance was high in June but water warming rate during the piscivorous period in June was slow in 1996. Piscivorous walleye still exhibited good growth rates. Despite the high abundance and good growth of larval walleye, survival was only 24.6% leading to the moderate fall abundance index value of 8.3 fish/h of trawling (Table 7).

In 1997, water warming rate during the egg incubation period was somewhat low at 0.19 °C/day, the frequency of wind events was low and egg abundance and survival were moderate. Abundance of pelagic larval walleye was moderate at 13.1/1,000 m^3 but zooplankton abundance was low, averaging less than 10/l throughout May and early June.

Water warming rate during the zooplanktivorous period was also somewhat low at 0.18 °C/day and zooplankton numbers were also low. Specific growth rate during the zooplanktivorous period was moderate at only 0.31 mm/day. Water warming rate was quite high during the piscivorous period in June and edible ichthyoplankton prey were plentiful. Consequently, walleye specific growth rate was higher in June at 1.00 mm/day. Survival of pelagic walleye larvae was moderate in 1997 at 36.1% leading to a moderate catch rate of demersal walleye during the fall bottom trawl survey of 8.2/h of trawling (Table 7).

Walleye began spawning on reefs in mid-March of 1998, about a week earlier than in other years of my study, and egg numbers were quite high when the catastrophic storm hit on April 8. While water warming rate was high during the egg incubation period in 1998 (0.24 °C/day) and the total number of days with strong wind events was low (14). However, the egg incubation period experienced the effects of 2 days worth of gale-force winds. On average, over 80% of the eggs spawned prior to the storm event were removed by the strong wind-generated wave and current action created by the storm. Consequently, mean egg abundance on reefs was quite low in 1998 and egg survival was moderate. Larval abundance was moderately high at 16.8/1,000 m^3, despite the loss of eggs from reefs. Zooplankton abundance was above average during May and early June and water warming rate was moderate at 0.19 °C/day. These factors translated into a moderate specific growth rate for zooplanktivorous pelagic walleye of 0.36 mm/day. Edible ichthyoplankton abundance was exceptionally high in June and water warming rate was high at 0.35 C/day during the piscivorous period in June.

Corresponding to these favorable growth conditions, specific growth rate of piscivorous walleye was the highest observed during my study at 1.39 mm/day. Larval survival was 14.2%, the lowest observed in this study, producing a fall abundance index estimate of 7.8/h of trawling (Table 7).

Water warming during the egg incubation period of 1999 was somewhat low at only 0.18 C/day and 17 strong wind events occurred. Egg abundance on reefs in 1999 appeared to be comparable with those of 1996 and 1997, although data from the peak abundance period are missing. Egg survival was probably low in 1999 based on the low water warming rate during egg incubation and subsequent low abundance of pelagic larvae. Water warming rate was slow during May and early June but zooplankton abundance was quite high. Specific growth rate of zooplanktivorous larvae was high at 0.45 mm/day. Edible ichthyoplankton were plentiful in 1999 and water warming rate was moderate at 0.20 C/day. Specific growth rate of piscivorous walleye was quite high at 1.32 mm/day. The relatively favorable conditions experienced during the piscivorous larval period allowed fast growth rates which were transmitted to high larval survival (62.4%). Despite low larval abundance, the high survival of the larvae was reflected in the moderate fall year-class strength index of 8.6/h of trawling (Table 7).

In summary, the best walleye year-classes are formed in years with fast water warming rates throughout egg incubation and pelagic larval periods, storm events are rare during the egg incubation period, and prey abundance is high in May and June. These favorable conditions promote high egg abundance and survival on reefs and fast growth rates and high survival rates of larvae. Because having this combination of factors occur all in the same year is rare, the ability of a walleye cohort to compensate for poor survival at an early life history stage by increasing survival later in life is important in order to produce strong year-classes. My data provide some evidence that age-0 walleye demonstrate such compensatory responses. For example, egg abundance and survival on reefs was probably low in 1999 and produced a low number of larvae in the western basin. The cohort was able to compensate for low egg survival and low larval abundance by taking advantage of favorable conditions and responding with high growth and survival rates during zooplanktivorous and piscivorous feeding stages resulting in a moderate fall year-class strength (Table 7).

While evidence of compensatory responses in walleye growth and survival are common for older fish, few studies have documented such responses for age-0 walleye. Through a population modeling exercise, Jensen (1993) concluded that compensation during the larval life stage was not necessary for regulation of populations size. Other studies have focused on size selective mortality of walleye, specifically cannibalism during the winter period (Chevalier 1973, Forney 1976, 1980, Madenjian et al. 1991, Madenjian et al. 1996). These studies concluded that if first year growth was slow, then age-0 walleye were exposed to predation by older walleye for longer periods. However, cannibalism is rare among walleye in Lake Erie (Knight et al. 1984, Francis and Vondracek 1990, Hartman and Margraf 1992, Madenjian et al. 1996) and recruitment of age-2 fish to the stock was unrelated to first year growth (Madenjian et al. 1996).

I observed important patterns in physical and biological processes that occurred repeatedly during the six years of my study. First, I found that egg abundance was greatest on shallow points of reefs early in walleye spawning and egg incubation periods but gradually decreased as eggs were washed to deeper sites on the reefs. This pattern indicates that walleye actively spawn on the shallowest sites on the reefs and rely on water currents to transport the eggs to favorable incubations sites. Previous work on Lake Erie reefs found the shallow areas of reefs to be smoother with less complexity (less porous, low variety of particle sizes) than deeper sites (Herdendorf and Braidech 1970, Roseman 1997). Wave energy models developed by physical limnologists indicate that shear stress, the amount of energy necessary to move bottom particles, decreases with depth (Miller et al. 1977). Eggs remaining on shallow exposed sections of reefs would be more vulnerable to removal by wave and current action caused by storm events than those incubating at deeper sites. My data show this to be true as egg abundance at deep sites (like Cone reef) did not decline as sharply during the April 8-10, 1998 storm.

I also found a definite pattern in egg viability and survival. The proportion of viable eggs in samples was generally higher later in the egg incubation period, with 1995 being the exception, as I explained above. Also, egg survival estimates were generally higher for periods later in the egg incubation period. These results suggest that egg mortality rates are higher early in the incubation period which is supported by laboratory studies conducted by other scientists. Latif et al. (1999) and Heidinger et al. (1997) observed the majority of egg mortality to occur during the first 100 hours after fertilization. Latif et al. (1997) considered the first 100 hours as a critical period for egg development and added that any environmental stress on eggs during this period would increase mortality. As I mentioned earlier, Allbaugh and Manz (1964) observed that egg viability increased as incubation periods progressed because dead walleye eggs became buoyant and were washed from incubation sites.

The third important pattern I observed was the accumulation of walleye larvae at shallow nearshore areas along the coast of the western basin. These areas proved to be more conducive to good growth and survival of age-0 walleye by having increased water temperature, darker waters, and higher prey densities than offshore sites. Growth rate and development of walleye sac-fry is temperature dependent as temperature determines the rate of yolk absorption while growth of post sac-fry is a function of food consumption and metabolism, both of which are temperature regulated (McElman and Balon 1979, Johnston and Mathias 1994). As described earlier, much evidence exists to demonstrate the relationship between warmer water temperatures and larval walleye growth and survival (Trometer and Busch 1999, Rieger and Summerfelt 1999) and this advantage was evident in my data. Also, walleye are known to perform better in darker waters, showing increased growth and survival in laboratory experiments (Bristow et al. 1996, Regier and Summerfelt 1997), also evident in my data. Finally, the literature abounds with evidence defining the positive relationship between prey abundance and walleye growth and survival (Carlander and Payne 1977, Kelso 1972, Kempinger and Churchill 1972, Mills and Forney 1988, Fox 1989) that is also supported by my observations (Figures 33 and 34). Ultimately, my research underscores the importance of these coastal areas for age-0 walleye growth and survival and emphasizes the need to understand coastal processes and their significance to walleye ecology.

One repeatable process that I did not measure but was still evidently critical to walleye year-class strength formation is the role of lake currents in dispersing fish from reefs and transporting them to the shallow coastal nursery areas. Because I observed age-0 walleye to become concentrated in the same locations year after year during my research (Figures 3 – 9), lake currents must function in similar manners during at least portions of every spring when walleye larvae are dispersing from egg incubation areas. These currents provide the physical linkage between egg incubation areas and the warmer, more productive coastal zone nursery areas. The lack of information on water current patterns and their role in larval walleye dispersal and distribution represents a void in our knowledge about walleye ecology in western Lake Erie.

Conclusion

My results emphasize the important role of physical processes in structuring the year-class strength of walleye in western Lake Erie. My results are unique in that few studies have shown the direct cause and effect relationships between physical processes and fish population dynamics in freshwater systems. My results revealed that both episodic events (weather-related events) and subtle variability (temperature dependent development) in early life history vital rates can significantly effect the year-class development of walleye in western Lake Erie. While we can modify the physical habitat in which fish populations exist, we do not have the capabilities to manage or manipulate most physical processes. For example, we can construct artificial reefs with deep crevices to shelter eggs from strong wave and current action, but we cannot alter the actual wave and current action to any appreciable degree that would benefit egg survival. Instead, we must rely on developing a sound understanding of the linkages between physical processes and the ecological processes that regulate fish production and recruitment. By doing so, we will be able to better predict the response of fish populations to variability in their habitat and respond with appropriate management strategies.

Chapter 2

PREDATION ON WALLEYE EGGS BY FISH ON REEFS IN WESTERN LAKE ERIE

Abstract

Predation on fish eggs can negatively impact the recruitment of some fishes. To assess the potential impact of egg predation on walleye year-class development, I examined the diets of fishes from gillnet and egg pump collections on reefs in western Lake Erie during walleye egg incubation periods from 1994 – 1999. I collected no potential egg predators in samples taken in 1994 but from 1995 – 1999 I caught up to 11 different species of fish on reefs in addition to spawning walleye. Catch per effort of potential egg predators in gillnets generally increased as egg incubation periods progressed. Catch per unit effort of white perch was highest in all years except 1998 when catches of trout perch and yellow perch were higher. On average, white perch stomachs contained more eggs than other egg predators in all years except 1998 when yellow perch were observed to eat more eggs. I also found low numbers of walleye eggs in the stomachs of logperch, trout perch, sculpin, spottail shiner, rock bass, and round goby. My results indicate that prolonged incubation periods may increase the potential for egg loss due to predation.

Introduction

Dense patches of fish eggs produced by mass spawning offer exceptional feeding opportunities to predators (Wolfert et al. 1975, Frank and Leggett 1984, Schaefer and Margraf 1987). At a more general level, prey aggregations are widely known to attract large numbers of predators, and aggregated prey can suffer high mortality under these circumstances (Kerfoot and Sih 1984). While egg predation has been observed by avian predators (Botton 1984) and invertebrates (caddis larvae, Fox 1978; planarians, Newburg 1974; amphipods, DeBlois and Leggett 1991; crayfish, Horns and Magnuson 1981), fish are considered the most important predators of fish eggs in many aquatic communities. Mortality estimates ranging from 1.6 to 70% of the annual egg production have been reported in studies examining benthic egg predation by fish (Bailey and Houde 1989).

In Lake Erie, walleye deposit their eggs on reefs and in riffle areas of tributaries in early spring and provide no parental care (Ney 1978). This leaves dense aggregations of eggs vulnerable to a host of potential mortality factors including removal by water currents, siltation, and predation. Wolfert et al. (1975) found yellow perch to be the most important predator of walleye eggs on Kelly's Island Shoal in western Lake Erie in 1969-71. During a study in western Lake Erie tributaries from 1981-83, exotic white perch were found to consume large quantities of walleye and white bass eggs (Schaefer and Margraf 1987). These studies concluded that prolonged egg incubation periods increase the vulnerability of eggs to predation and increase the impact that predation might have on year-class development. Further, the recent invasion of Lake Erie reefs by round gobies (*Neogobius melanostomus*, Jude et al. 1992) has created increased concern about walleye recruitment variability as these invasive fish may become major predators on fish eggs.

Predation of incubating walleye eggs on reefs in western Lake Erie could have a serious detrimental effect on walleye year-class strength when incubation periods are prolonged and egg predators become abundant on reefs. Further, the observed high density of round gobies on reefs in the summer of 1998 and 1999 (> $20/m^2$) (personal communication, Dr. Ken Baker, Heidelberg College, Tiffin, OH) raises questions about the impact that these fish will have on the abundance and survival of reef-spawned walleye eggs. In this chapter I document the extent of predation by fish on incubating walleye eggs on reefs in western Lake Erie. My specific objectives are to determine the timing of appearance and relative abundance of potential egg predators and the extent that they feed on walleye eggs.

Methods

Variable mesh gillnets were fished overnight on reefs during peak spawning periods in April and early May 1994 - 1999 to collect potential walleye egg predators. Two 40 m gillnets were fished simultaneously. 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 to 4.2 m of water on either Toussaint or Locust Pt. reef. Table 8 lists sampling sites and dates for each year. I selected Toussaint and Locust Pt. reefs as sampling sites for egg predators because I observed high walleye egg densities on these reefs and for logistical considerations.

Upon capture, potential egg predators were anesthetized in tricaine methanesulfonate, 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 common sucker (*Catastomus commersonii*), quillback sucker (*Carpiodes cyprinus*), and 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 (Table 9). These fish were preserved whole in 10% formalin and dissected later. I calculated the average number of eggs per stomach and percent frequency of occurrence of eggs in stomachs for each egg predator (Bowen 1996). I also calculated the catch-per-unit-effort (CPUE) for all species collected in gillnets by dividing the total catch of each species by the total number of hours gillnets were fished for each sampling date and for the entire sampling period.

Results

No fish other than spawning walleye were collected in gillnets fished overnight on April 20 and 26, 1994. In 1995 I collected a total of 49 fish in 3 nights of gillnetting totaling 30 hours of effort (Table 8). I collected an additional 7 fish with the egg pump (Table 9). Following walleye (1.20/hour), white perch had the highest CPUE (1.12/hour) while spottail shiner had the lowest (0.11/hour; Table 10). Few fish were captured in gillnets set on 13 April 1995 (n = 11) but CPUE increased on subsequent nights (Figure 36), especially of white perch, the most common species collected. The stomachs of trout perch *Percopsis omiscomaycus*, yellow perch, logperch *Percina caprodes*, johnny darter *Etheostoma nigrum*, white perch, and an unidentified sculpin (Cottidae) contained walleye eggs in 1995. The stomachs of walleye, rock bass *Ambloplites rupestris* and greater redhorse sucker did not contain walleye eggs. Walleye eggs appeared in 86% of white perch stomachs with an average of 349 walleye eggs per stomach (Table 10).

In 1996 I collected 58 fish in 3 nights of gillnetting totaling 35 hours of fishing effort (Table 8). I collected one logperch with the egg pump (Table 9). CPUE of all potential egg predators increased throughout the sampling period from a low of 0.75 on April 13 to over 1.46 on May 3 (Figure 36). CPUE was highest for white perch (Table 11). I found walleye eggs in the stomachs of log perch, spottail shiner, trout perch, white perch, and yellow perch in 1996. White perch were observed to consume the largest numbers of walleye eggs averaging 372 eggs/stomach and walleye eggs were in 90% of stomachs examined. Walleye eggs also appeared in stomachs of logperch, spottail shiner, troutperch, and yellow perch in 1996 (Table 11).

In 1997 I collected 210 fish in 3 nights of gillnetting with a combined effort of 38 hours. I collected a single logperch with the egg pump (Table 9). Catch per unit effort was highest for white perch and troutperch at 2.10 and 2.03/hour respectively (Table 12). CPUE of all potential egg predators increased from a low of 1.16 on April 19 to 8.92 on May 2 (Figure 36). Walleye eggs appeared in stomachs of logperch, silver chub (*Hybopsis storeriana*) spottail shiner, troutperch, white perch, and yellow perch in 1997. White perch were again observed to consume the most walleye eggs at an average of 131 per stomach. Frequency of occurrence of walleye eggs in white perch stomachs was 43% while 50% of yellow perch stomachs had eggs. Stomachs of alewife (*Alosa* *pseudoharengus*), brown bullhead (*Ictalurus nebulosus*), common sucker, smallmouth bass (*Micropterus dolomieu*), walleye, and white bass did not contain walleye eggs (Table 12).

I collected 142 fish in gillnets in 1998. I also collected 4 logperch with the egg pump in 1998 (Table 9). Troutperch appeared most frequently in collections with a catch per unit effort of 1.39/hour. Yellow perch were the next most common followed by white perch (Table 13). Catches of potential egg predators increased throughout April. CPUE increased from 0.50 to 6.75 between April 6 and April 23 (Figure 36). Round gobies appeared in my samples for the first time in 1998, I collected 21 in gillnets and 14 with the egg pump. Eggs were found in the stomachs of logperch, rock bass, round goby, spottail shiner, trout perch, white perch, and yellow perch. Eggs appeared in higher numbers in the stomach of yellow perch (385/stomach) than any other fish. Stomach of white perch averaged 208 eggs while round gobies averaged only 2 (Table 13). Stomachs of common sucker, freshwater drum (*Aplodinotus grunniens*), and walleye did not contain eggs (Table 13).

Table 8. Dates, times and locations where gillnets were fished in western Lake Erie in 1994 through 1999. Effort was constant across all sample periods (2 – 40 m variable mesh gillnets).

Date	Location	Time Fished
April 13, 1994	Toussaint	1800 – 0700
April 17, 1994	Toussaint	1800 – 0700
April 18, 1994	Toussaint	1100 – 1500
Total effort (hrs)		30
April 13, 1995	Toussaint	2000 - 0700
April 17, 1995	Toussaint	1900 - 0700
April 24, 1995	Toussaint	1900 - 0700
Total effort (hrs)		35
April 13, 1996	Toussaint	1900 - 0700
April 21, 1996	Locust Pt.	1900 - 0700
May 3, 1996	Locust Pt.	1900 - 0800
Total effort (hrs)		37
April 19, 1997	Toussaint	1900 - 0800
April 26, 1997	Toussaint	1900 - 0700
May, 2, 1997	Toussaint	1900 - 0800
Total effort (hrs)		38
April 6, 1998	Locust Pt.	1900 - 0700
April 15, 1998	Locust Pt.	1900 - 0700
April 18, 1998	Locust Pt.	1900 - 0800
April 23, 1998	Locust Pt.	1900 - 0700
Total effort (hrs)		49
April 7, 1999	Locust Pt.	1900 – 0700
April 11, 1999	Locust Pt.	1900 - 0700
April 30, 1999	Locust Pt.	1900 – 0700
Total effort (hrs)		36

Table 9. Date, location, species, and number (in parentheses) of fish collected incidentally during egg sampling on reefs in western Lake Erie. 1995 – 1999.

Date	Location	Species (number)
April 13, 1995	Niagara Reef	Logperch (2)
April 17, 1995	Toussaint Reef	Sculpin (1)
April 24, 1995	Niagara Reef	Johnny Darter (1)
		Logperch (1)
April 13, 1996	Cone Reef	Logperch (1)
April 19, 1997	Toussaint Reef	Logperch (1)
April 10, 1998	Crib Reef	Round Goby (2)
	Locust Pt. Reef	Round Goby (3)
	Niagara Reef	Logperch (1)
April 15, 1998	Crib Reef	Logperch (1)
	Niagara Reef	Logperch (2)
	Round Reef	Round Goby (3)
	Toussaint Reef	Round Goby (3)
April 18, 1998	Crib Reef	Round Goby (2)
	Niagara Reef	Round Goby (1)
	Toussaint Reef	Round Goby (2)
April 23, 1998	Cone Reef	Round Goby (1)
	Crib Reef	Round Goby (1)
	Toussaint Reef	Round Goby (1)
April 28, 1998	Niagara Reef	Round Goby (1)
	Toussaint Reef	Round Goby (1)
March 31, 1999	Locust Pt. Reef	Round Goby (1)
April 8, 1999	Cone Reef	Round Goby (6)
	Crib Reef	Round Goby (9)
	Locust Pt. Reef	Round Goby (5)
	Niagara Reef	Round Goby (5)
	Locust Pt. Reef	Round Goby (7)
	Niagara Reef	Round Goby (2)
	Round Reef	Round Goby (10)
	Toussaint Reef	Round Goby (8)
May 5, 1999	Cone Reef	Round Goby (3)
	Crib Reef	Round Goby (5)
	Locust Pt. Reef	Round Goby (7)
	Niagara Reef	Round Goby (2)
	Round Reef	Round Goby (1)
	Toussaint Reef	Round Goby (1)

I collected a total of 157 fish in gillnets fished for a total of 36 hours on reefs in 1999. I collected more round gobies in 1999 than in 1998, especially with the egg pump. I collected 9 round gobies in gillnets (Table 14) and an additional 72 with the pump (Table 9). White perch were the most frequently encountered species with a catch per unit effort of 3.25/hour (Table 14). The increasing trend in CPUE over time was again evident in 1999. CPUE for all fish combined increased from 1.25 on April 7 to 9.42 on April 30 (Figure 36). Eggs were prevalent among the stomach contents of white perch and yellow perch with an average of 397 and 387 eggs per stomach respectively. Round gobies consumed eggs in relatively low numbers averaging less than 2 per fish. Eggs were also found in the stomachs of quillback sucker, spottail shiner, troutperch, and white sucker (Table 14).

Fish on reefs also consumed prey items other than walleye eggs. White perch and yellow perch were observed to have amphipods, zooplankton, and fish in their stomachs. Walleye diets were composed mainly of fish although some stomachs contained amphipods. Troutperch, logperch, and spottail shiners all consumed amphipods. Round goby diets consisted primarily of small dreissenid mussels (<5 mm) and amphipods.

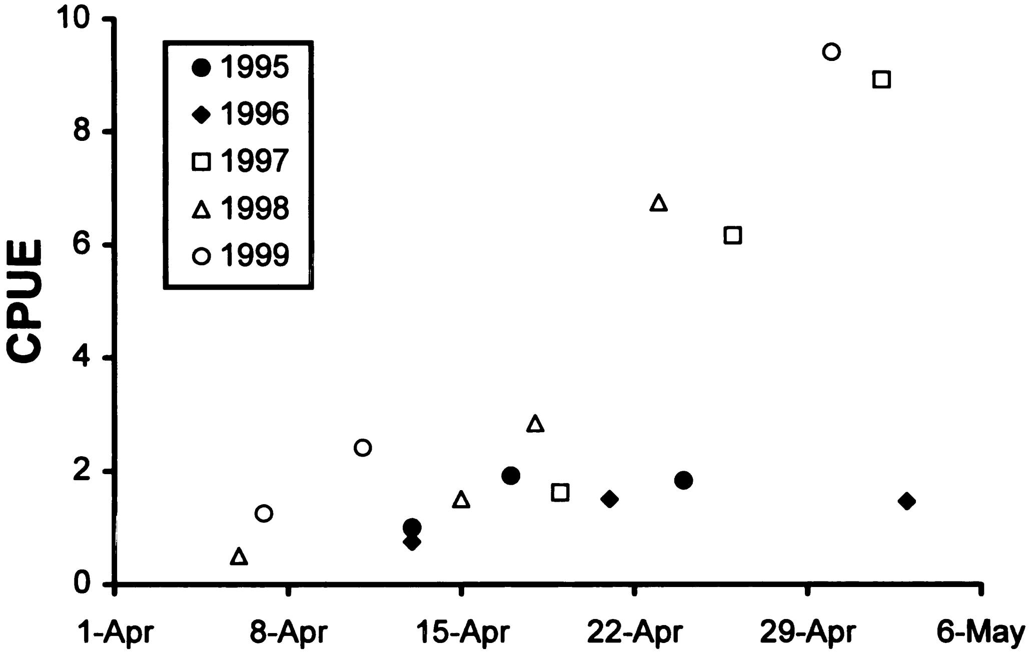


Figure 36. Catch-per-unit-effort (CPUE) of potential egg predators (excluding walleye) in gillnets fished on reefs in western Lake Erie 1995 – 1999.

Table 10. Catch per net-hour (CPUE), total number of fish collected, mean length (TL) of fish collected, number of empty stomachs, average number of walleye eggs per stomach, and frequency of occurrence of walleye eggs in stomachs for fish collected from reefs in western Lake Erie in the spring of 1995. n/a in CPUE column indicates fish not collected in gillnets.

Species	CPUE (#/hour)	# Fish Collected	Mean TL (mm)	# Empty Stomachs	Average # Walleye Eggs	Frequency of Occurrence (%)
Grtr. Redhorse	0.03	1	225	1	0	0
Johnny Darter	n/a	1	44	0	2	100
Logperch	n/a	3	68	1	10	66
Rock Bass	0.03	1	195	1	0	0
Sculpin	n/a	1	76	0	21	100
Trout Perch	0.37	13	107	6	4	38
Walleye	1.20	42	452	10	0	0
White Perch	1.12	35	225	6	349	86
Yellow Perch	0.03	1	81	0	5	100

Table 11. Catch per net-hour (CPUE), total number of fish collected, mean length (TL) of fish collected, number of empty stomachs, average number of walleye eggs per stomach, and frequency of occurrence of walleye eggs in stomachs for fish collected from reefs in western Lake Erie in the spring of 1996. n/a in CPUE column indicates fish not collected in gillnets.

Species	CPUE (#/hour)	# Fish Collected	Mean TL (mm)	# Empty Stomachs	Average # Walleye Eggs	Frequency of Occurrence (%)
Logperch	n/a	1	66	0	8	100
Spottail Shiner	0.11	4	75	0	19	100
Trout Perch	0.24	9	84	2	24	78
Walleye	0.32	12	452	10	0	0
White Perch	0.81	30	240	3	372	90
Yellow Perch	0.05	2	79	0	51	100

Table 12. Catch per net-hour (CPUE), total number of fish collected, mean length (TL) of fish collected, number of empty stomachs, average number of walleye eggs per stomach, and frequency of occurrence of walleye eggs in stomachs for fish collected from reefs in western Lake Erie in the spring of 1997. n/a in CPUE column indicates fish not collected in gillnets.

Species	CPUE (#/hour)	# Fish Collected	Mean TL (mm)	# Empty Stomachs	Average # Walleye Eggs	Frequency of Occurrence (%)
Alewife	0.03	1	165	1	0	0
Brown Bullhead	0.03	1	187	1	0	0
Common Sucker	0.03	1	503	1	0	0
Logperch	n/a	1	107	1	10	66
Silver Chub	0.03	1	224	0	3	100
Smallmouth Bass	0.03	1	375	1	0	0
Spottail Shiner	0.45	17	113	8	8	53
Trout Perch	2.03	77	106	65	2	16
Walleye	0.97	37	462	35	0	0
White Bass	0.39	15	288	15	0	0
White Perch	2.10	80	207	46	131	43
Yellow Perch	0.42	16	210	8	31	50

Table 13. Catch per net-hour (CPUE), total number of fish collected, mean length (TL) of fish collected, number of empty stomachs, average number of walleye eggs per stomach, and frequency of occurrence of walleye eggs in stomachs for fish collected from reefs in western Lake Erie in the spring of 1998. n/a in CPUE column indicates fish not collected in gillnets.

Species	CPUE (#/hour)	# Fish Collected	Mean TL (mm)	# Empty Stomachs	Average # Walleye Eggs	Frequency of Occurrence (%)
Common Sucker	0.02	1	333	1	0	0
Freshwater Drum	0.02	1	382	0	0	0
Log Perch	n/a	4	66	0	22	100
Rock Bass	0.02	1	1.6	0	3	100
Round Goby	0.29*	35	51	6	2	6
Spottail Shiner	0.10	5	111	0	12	60
Trout Perch	1.39	68	110	27	46	21
Walleye	0.63	31	430	29	0	0
White Perch	0.31	15	243	3	208	73
Yellow Perch	0.53	26	221	2	385	85

* 14 of the 35 round gobies collected in gill nets

Table 14. Catch per net-hour (CPUE), total number of fish collected, mean length (TL) of fish collected, number of empty stomachs, average number of walleye eggs per stomach, and frequency of occurrence of walleye eggs in stomachs for fish collected from reefs in western Lake Erie in the spring of 1999. n/a in CPUE column indicates fish not collected in gillnets.

Species	CPUE (#/hour)	# Fish Collected	Mean TL (mm)	# Empty Stomachs	Average # Walleye Eggs	Frequency of Occurrence (%)
Gizzard Shad	0.03	1	304	1	0	0
Quillback Sucker	0.11	4	366	1	184	75
Round Goby	0.25*	81	69	14	1.7	4.9
Smallmouth Bass	0.03	1	372	0	0	0
Spottail Shiner	0.11	4	117	0	18	100
Trout Perch	0.31	11	111	3	34	73
Walleye	0.42	15	452	10	0	0
White Perch	3.25	117	221	24	397	79
White Sucker	0.03	1	379	0	86	100
Yellow Perch	0.11	4	207	0	387	100

* 9 of the 81 round gobies collected in gillnet

Discussion

I collected no egg predators in gillnets in 1994 suggesting that egg predation was not a major source of egg mortality in that year. In the following years, I documented that several species of fish inhabited reefs during walleye egg incubation periods and did indeed consume eggs. While species composition and relative abundance of fish was different between years, I found it difficult to identify a deleterious effect that egg predation might have had on egg abundance or survival. In most years, egg predators did not become abundant on reefs until late in the egg incubation period, after eggs had started to hatch and after the effects of wind and water currents had taken place. Therefore, it is difficult to notice any appreciable decline in egg abundance or survival due specifically to predation by examining trends in egg abundance.

Based on CPUE, the relative abundance of egg predators was noticeably different between years. CPUE was highest in late April and early May of 1997, 1998, and 1999 suggesting the potential for egg predation was also higher in those years. However, egg abundance, egg survival, and larval abundance were moderately high in 1997 (Table 7) showing no discernable impact from predation. In 1998, the effects of the storm in early April outweighed any other source of egg mortality in that year. In 1999, I did not have sufficient egg sampling data to determine trends in egg abundance and survival, but larval abundance was very low suggesting low egg abundance and/or increased egg mortality during that spring (Table 7). Relative abundance and CPUE of egg predators was higher in 1999 than any other year allowing me to conclude that egg predation likely was a larger source of egg mortality in 1999 than in other years.

Survival rates of viable walleye eggs ranged from about 10% to 50% during incubation periods across the six years of this study. Egg survival is generally much higher for species that exhibit parental guarding of eggs through hatching. Bain and Helfrich (1983) observed over 65% of bluegill (*Lepomis macrochirus*) eggs to emerge from nests guarded by adult bluegill but only 14% of eggs hatched in unguarded nests. In contrast, eggs that are spawned in fall and totally abandoned by their parents can suffer high mortality from predation. Burbot (*Lota lota*) and deepwater sculpin (*Myoxocephalus thompsoni*) are known to eat large numbers of lake trout (*Salvelinus namaycush*) and whitefish (*Coregonus clupeaformis*) eggs in lakes Michigan and Superior (Bailey 1972, Wojcik et al. 1986). In some European lakes, ruffe (*Gymnocephalus cernuus*) feed extensively on coregonine eggs and may suppress coregonine populations. Ruffe consumed 80 - 90% of vendace (*Coregonus albula*) eggs in Lake Syamozera, Russia and egg predation by ruffe is also considered a major factor in the decline of European whitefish (*Coregonus lavaretus*) in the same lake (Pokrovskii 1961 cited in DeSorcie and Edsall 1995). The egg survival rates I estimated for walleye on western Lake Erie reefs appear intermediate of those reported in these other studies; higher than species that afford no parental care yet lower than species providing total parental care. I hypothesize that, because walleye remain on the reefs during much of the egg incubation period, many predators are deterred from the reefs by the presence of a congregation of large piscivores. My CPUE estimates indicate that abundance of fish other than walleye begins to increase only after peak walleye spawning has occurred and walleye abundance decreases on reefs.

White perch appeared to be the most important consumers of walleye eggs on reefs during this study. White perch were also considered important predators of fish eggs in other systems. Schaefer and Margraf (1987) found fish eggs (including walleye eggs) in white perch stomachs collected from the Sandusky River, OH in the spring of 1982 and 83. White perch are also thought to be important predators of striped bass *Morone saxatilis* eggs and larvae in Chesapeake Bay (Setzler et al. 1980; Monteleone and Houde 1992). Yellow perch are also considered important predators on fish eggs in some systems. Similar to my results, Wolfert et al. (1975) found yellow perch to consume substantial numbers of walleye eggs on Kelly's Island Shoal in western Lake Erie in the late 1960s. Yellow perch were observed to consume lake trout eggs from spawning shoals in large quantities in Keuka Lake, NY, hindering efforts to establish self-sustaining lake trout stocks in the lake (Fitzsimons 1990).

Round gobies appeared in my egg predator collection in 1998 and became quite abundant in 1999, especially as incidental catch in egg pump samples. Ohio Division of Wildlife scientists also observed large numbers of age-0 round gobies in bottom trawls in 1998 (ODW 2000). The size of the round gobies I collected from reefs in 1998 and 1999 is below that reported by other researchers. Several large (>150 mm TL) round gobies were observed during SCUBA surveys on reefs in July and August of 1998 and 1999 (personal communication, Dr. Ken Baker, Heidelberg College, Tiffin, OH). Round gobies were observed to exceed 200 mm TL in the St. Clair and Detroit rivers (Jude et al. 1995). The fish I collected in egg pump samples and gillnets were considerably smaller, averaging only 51 mm in 1998 (Table 12) and 69 mm in 1999 (Table 13) and were probably not representative of the round gobies population on reefs in those years.

Round gobies did not consume eggs in any appreciable numbers. Mean number of walleye eggs in round goby stomachs was about 2 in both years when I collected round gobies on reefs (Tables 12 and 13). The low numbers of eggs consumed by round gobies may be a function of their size. Chotkowski and Marsden (1999) found that round gobies smaller than 50 mm TL did not consume lake trout eggs in laboratory studies. They also found that mottled sculpin consumed more lake trout eggs than round gobies of similar sizes. Even though walleye eggs are about half the diameter of lake trout eggs (2 mm vs. 5 mm; Auer 1982), round gobies still did not consume them in appreciable numbers on western Lake Erie reefs. Still, the potential for round gobies to become important predators on walleye eggs remains.

I observed that egg predator relative abundance and CPUE increased during April and May in all years of the study (Figure 36). Wolfert et al (1975) also observed a successive increase in the abundance of fish on Kelly's Island Shoal after peak walleye egg abundance occurred in 1969-71. This trend of increasing predator abundance is important, especially in years when waters warm slowly, prolonging incubation periods. The longer the incubation period, the more opportunity there is for predation and the greater the potential for deleterious effects on walleye reproductive success.

Dissertation Synthesis

LINKING EVENTS DURING WALLEYE EARLY LIFE HISTORY TO YEAR-CLASS DEVELOPMENT

Physical processes structure the environmental setting in which many biological processes take place. In the previous chapter I identified specific factors and mechanisms that influence the vital rates of egg and larval stages of walleye providing insight to the ecological functions mediated by physical processes. I was able to relate physical processes (such as storm events and water warming rate) and physical habitat characteristics (depth, clarity) to the distribution, abundance, growth, and survival of walleye early life history stages. My field research has provided the opportunity to examine walleye year-class strength development across a broad range of environmental extremes in terms of physical and biological habitat characteristics which led to large interannual differences in walleye year-class strength. My data reveal important repeatable patterns that occur during walleye early life history ontogeny that play important roles in structuring walleye year-class strength. In this dissertation synthesis, I will describe these repeatable patterns and discuss the linkages between physical and biological processes that influence walleye early life history vital rates in western Lake Erie and how these events structure walleye year-class strength.

Lake Erie supports the world's largest naturally reproducing population of walleye. Spawning stock size fluctuated between 46.8 (1994) and 70.8 (1998) million fish during the course of my study. The 17-year long-term average stock size is about 65.6 million fish (Lake Erie Walleye Task Group 1999). Early studies on Lake Erie walleye found a weak relationship between walleye stock size and year-class strength but concluded that spring water warming rate was positively correlated to recruitment (Busch et al. 1975). More recent population modeling work revealed a stronger stock-recruitment relationship by including prey abundance in fall prior to spawning (especially age-0 gizzard shad abundance) and spring water warming rate into the stock recruitment model (Madenjian et al. 1996). Madenjian et al. (1996) were able to explain 92% of the variation in recruitment of age-2 walleye between 1981 and 1993 with their model. Their results support the hypothesis proposed by Henderson and Nepszy (1994) that mature females needed adequate lipid reserves during the winter to spawn the following spring. While these studies were able to relate spawner characteristics and condition to recruitment on a lake-wide basis, they provide little insight about the dynamics of year-class formation of specific spawning stocks in the lake.

The Lake Erie walleye population is composed of many discrete spawning stocks (Stepien 1995), some of which spawn in different rivers and reefs in the east, central, and western basins of the lake (Regier et al. 1969, Hatch et al. 1987). Due to the large geographic expanse of Lake Erie, different spawning areas can be exposed to different environmental conditions within a given year which affect year-class development of the different stocks. While exact proportions are unknown, there is consensus among researchers and fisheries managers that the majority of walleye spawning occurs in the western basin of the lake, either in tributary rivers or on midlake reefs (Hatch et al. 1987, Knight 1998). Research conducted by scientists at Ohio State University and Ohio DNR in the Maumee and Sandusky rivers concurrent with the first 2 years of my study revealed a significant negative relationship between river discharge and indices of fall walleye year-class strength in western Lake Erie (Mion et al. 19998). Years with high levels of precipitation resulted in high river discharge and low larval walleye abundance and survival rates. Further, Mion et al. found a strong positive relationship between peak larval walleye abundance in rivers and indices of walleye year-class strength in fall with the highest values occurring in 1994 and the lowest in 1995, similar to what I observed for reef-spawned fish in those same years.

Walleye typically spawn earlier in the Maumee and Sandusky rivers than on reefs in western Lake Erie. The peak larval walleye out-migration period in the rivers occurs between mid-April and early May (Mion et al. 1998) usually coinciding with the peak spawning and egg incubation period on reefs. Therefore, because walleye life history stages most vulnerable to physical processes associated with storms overlap in time (larvae in rivers, eggs on reefs), spring storms occurring over the western basin can limit survival in both river and reef habitats simultaneously. The same spring storms that produce high winds creating strong wave and current action on the reefs also typically deposit precipitation in the surrounding watershed increasing discharge in tributaries.

This was indeed the case in 1995, when storms were prevalent and precipitation was high in April and early May (> 13 cm; NCDC 2000), larval abundance was low in rivers (Mion et al. 1998), larval abundance was low throughout the western basin, and the fall index of walleye year-class strength was low. In contrast, the April 1998 storm occurred at a time in the month when spawning activity on reefs was high but before hatching and out-migration of larvae in rivers likely had peaked. Therefore, the April 1998 storm likely had no effect on larval survival in the Maumee River. I observed a moderately high mean larval abundance in the western basin in 1998 and the fall index of year-class strength was also above average despite the loss of eggs from the reefs due to the April storm. Based on my observations of larval abundance and distribution in western Lake Erie, I postulate that years like 1998 that experienced poor recruitment from one source (reefs) may be buffered by good recruitment from the other source (tributaries) and 1998 appears to be one of those types of years. In support of this argument, catches of walleye larvae were consistently higher at sites near Maumee Bay in 1998; over 90% of all walleye larvae collected in 1998 were captured at 6 sites adjacent to Maumee Bay. My hypothesis relies on the assumption that reef spawned larvae were not transported via lake currents to these sites near Maumee Bay. Unfortunately, information on water currents with resolution adequate to estimate larval drift patterns in spring is not presently available.

Eggs on reefs are vulnerable to storms. In years like 1995, when many storm events occurred, there was a cumulative effect of egg loss from the reefs reducing egg abundance and survival. In 1998, however, the reefs experienced few storm events but the timing and magnitude of the storms was critical. Walleye began spawning on reefs earlier than usual in 1998 due to early ice-out and warm temperatures during March. I collected the first eggs on March 23, 1998 and by the first week of April egg numbers were comparable to those observed in mid-April in previous years. Because a large portion of the total spawning stock had already spawned on the reefs by this time, the catastrophic storm event that occurred between April 8 and 10 removed a large portion of reef-spawned eggs limiting the production of walleye from reef habitats in 1998.

Early in the spawning season I observed the highest numbers of eggs on shallow sites on reefs. As incubation progressed, egg numbers declined at shallow sites and were generally more abundant at deep sites. For example, in 1998 over 80% of the eggs were collected from shallow sites on the reefs before the storm while only 19% of the eggs were collected from shallow sites after the storm. The substrate at the shallow summits of reefs is typically smoother with less complexion than deeper sites, especially for the shallowest of reefs (Herdendorf and Braidech 1972) allowing eggs to be removed by currents more easily than from deep sites. Wave energy models developed by physical limnologists indicate that shear stress, the amount of energy necessary to move bottom particles, decreases with depth (Miller et al. 1977). Thus, we would expect egg removal to be inversely related to depth.

Years with a high frequency of spring storms also typically have low water warming rates. My results support those of Allbaugh and Manz (1964) and Busch et al. (1975) who observed slower water warming rates in years when spring storms were prevalent. In my study, the highest frequency of spring storms occurred in 1995 and this year also had the lowest water warming rate. Conversely, spring storms were infrequent in 1994 and 1998, years when waters warmed quickly. The index of fall walleye abundance never exceeded 5 fish per hour of trawling when waters warmed at a rate less than 0.2 °C/day but greatly exceeded that number at higher warming rates indicating that 0.2 °C/day may be a critical minimum threshold warming rate for walleye egg survival in western Lake Erie. As I explained in greater detail in the previous chapter, faster water warming rates promote egg and larval survival by decreasing the period of time these life history stages are vulnerable to mortality caused by storms, disease, and predation.

Slow water warming rates during egg incubation and pelagic larval periods prolong the duration that these life history stages are exposed to predation. While predation can have substantial effects on the year-class development of some fishes (Bailey and Houde 1989), it is difficult to determine the magnitude of predation on walleye eggs and larvae in western Lake Erie. While my study and that of previous researchers on western Lake Erie reefs documented that fish consumed walleye eggs (Wolfert et al. 1975), these studies were unable to determine the magnitude of egg predation as a source of mortality due to a lack of information concerning the abundance of egg predators. Both studies were able to identify what fishes were present on the reefs during walleye egg incubation periods and how many eggs these fishes consumed. Both studies documented an increase in predator abundance over the course of the egg incubation period. These studies concluded that the longer the eggs incubated on the reefs, the greater the potential for predation. Fast water warming rates reduce incubation periods and shorten the time that eggs are vulnerable to mortality agents such as predation.

Water temperature also has significant consequences for walleye during the pelagic larval period. Studies have shown that walleye larvae have higher gas bladder inflation rates, higher prey consumption and assimilation rates, faster swimming speeds, faster growth rates, and higher survival rates in warmer waters than in cold waters (Clapp et al. 1997, Regier and Summerfelt 1999, Trometer and Busch 1999). My results show that walleye larvae become concentrated in shallow nearshore areas of western Lake Erie after hatching in each year of my study. These nearshore areas have different limnological characteristics than offshore areas. My data indicate that nearshore waters are generally warmer and darker (more turbid) than offshore waters and thereby provide better nursery habitat for developing age-0 walleye. Because growth of fish is temperature-dependant, warmer nearshore areas are conducive to faster growth rates for larval walleye than cooler offshore waters. Unfortunately, I collected few walleye larvae at offshore sites and catches were inconsistent providing me with no means to estimate growth rates for fish at offshore areas of my study area. My data from nearshore sites does provide a comparison of growth rates between years and shows that walleye grow faster in years with warmer waters. Faster growth of age-0 walleye moves fish through the size-specific predatory gauntlet faster, thereby reducing the potential for predation and other mortality agents that can occur during vulnerable early life history stages.

Productivity of prey resources is also generally higher in warmer waters than cooler waters (Wetzel 1975) providing fish with an additional growth advantage by inhabiting areas with warmer waters. My data indicate that zooplankton usually had higher densities were generally higher at nearshore sites during late April and May when walleye are zooplanktivorous (Roseman 1997). Ichthyoplankton prey were also generally more abundant in nearshore areas in June when age-0 walleye switch from eating zooplankton to fish (Roseman 1997). Coinciding with the switch in diet from zooplankton to fish, I observed age-0 walleye to become demersal between 25 and 30 mm TL, typically occurring by mid-June in each year of my study. Once walleye become demersal, the young fish disperse throughout the western basin and follow schools of baitfish into deeper waters of the central and eastern basin of the lake in the fall (Regier et al. 1969, Knight and Vondracek 1993). Walleye generally return to natal spawning sites in the western basin as mature adults at age-3 (Muth and Ickes 1993).

Nearshore waters were also generally more turbid than offshore waters in all years of my study. As I discussed in greater detail in Chapter 1, larval and juvenile walleye are known to perform better in darker waters. Laboratory studies have shown that larval walleye had faster swimming speeds, faster growth, improved gas bladder inflation, and higher survival rates in darker waters (Bristow et al. 1996, Regier and Summerfelt 1997). In western Lake Erie, nearshore waters are darker due to the mixing action of lake waters against the shoreline and the input of suspended sediments from tributaries (Burns 1985).

Management Implications

Water levels in western Lake Erie show natural fluctuations during spring due to seiche activity associated with storms (Gedney and Lick 1972, Burns 1985). Further, a declining trend in lake water levels has been observed over the past three years (Army Corps of Engineers 2000). Lower water levels increase the amount of reef surface area exposed to high-energy wave and current action. My research indicates that wave and current action can displace eggs from favorable incubation areas decreasing egg abundance and increasing mortality. While natural fluctuations in lake water levels will occur due to variable precipitation and evaporation rates in the Great Lakes basin, resource managers need to consider the implications of low water levels in regard to fish habitat before initiating plans that would further reduce water levels in Lake Erie (large scale withdrawals, dams, canals).

Additionally, my research on egg distribution on reefs provides important information useful in creating new spawning shoals. Walleye eggs were observed in high abundance on the tops of reefs suggesting that the majority of spawning takes place over the shallowest points on the reefs, typically < 5 m. Eggs were subsequently washed off the tops off the reefs and deposited at deeper sites on reefs or in surrounding areas, depending on the severity of the wave and current energy that removed them. Artificial reef construction should consider this fact and possibly construct reefs with wide peripheral margins of porous substrate (such as cobble) at deeper depths surrounding the summit to catch eggs that wash off the peak of the reefs. Further, reefs should be positioned to avoid strong wind and wave activity associated with storms that could remove eggs from incubation sites. Lastly, the reef should be located in an areas where lake currents will transport emerging larvae to favorable nursery areas.

My research identified that nearshore coastal areas in western Lake Erie are important as nursery habitat for fish and emphasizes the need to restore and protect these areas. Specifically, areas such as Potters Pond (larval sampling site 4, Appendix 1) and Metzger Marsh in 1994 (see Roseman 1997) that are/were embayments from the main portion of the basin proved to be exceptionally important nursery areas for larval fish. I consistently observed the highest densities of larval fish at these areas and sites adjacent to them. Metzger Marsh was dyked off from the main lake basin between fall of 1994 and the spring of 1995. I continued to sample outside of the dyke and still collected large numbers of larvae, but the quantity of the habitat was greatly reduced and the natural coastal processes (currents, sediment movements, thermal regime; Bowden 1983) were modified. Much of the shoreline in western Lake Erie has been reinforced with hard materials to prevent erosion and act as flood control. This armoring of the shoreline removes the natural land/water interface and interferes with lacustrine processes responsible for structuring the limnological characteristics of nearshore waters important as nursery habitat for walleye and other fishes. Coastal zone planners should consider the biological value of these coastal areas and their associated natural processes. Efforts should be devoted to reconstructing natural hydrologic patterns to facilitate the continued restoration of Lake Erie and its fisheries.

History has shown that management decisions for one species can have reverberating effects throughout aquatic ecosystems, as we have seen with the walleye population and fish community in Lake Erie (Knight and Vondracek 1993, Koonce et al. 1999, Nicholls 1999). The continued rehabilitation and future sustainability of our fishery resources depends on the application of new information, such as I have presented in this dissertation, towards a holistic ecosystem management approach (Ferreri et al. 1999). My work has provided a detailed account of factors contributing to the development of six walleye year-classes, emphasizing the role of physical processes in mediating walleye early life history vital rates that added to the instability of the population. While I do not propose that physical processes are more important than biological processes in determining the vital rates of walleye eggs and larvae or structuring year-class strength, I do contend that physical processes create the environment in which biological processes occur. Further, I agree with Walters and Collie (1988) that research efforts should not focus solely on examining physical processes but rather should involve multidisciplinary approaches that examine the ecological linkages through which environmental variability influences the vital rates of fish populations, as I have attempted to do here.

APPENDICES

Appendix 1. Coordinates (decimal degrees) of western Lake Erie reef sampling sites for 1996 – 1999.

Reef	**Longitude**	**Latitude**
Cone	83.046333	41.666817
Crib	83.008833	41.646400
Locust	83.065467	41.645867
Niagara	82.975050	41.664533
Round	82.987383	41.618550
Toussaint	83.016667	41.631667

Appendix 2. Coordinates (decimal degree) for larval sampling sites in western Lake Erie, 1996 – 1999.

Site	Long	Lat
1	83.40000	41.72500
2	83.35000	41.70000
3	83.33333	41.73333
4	83.30000	41.68000
5	83.30000	41.70000
6	83.30000	41.72167
7	83.22500	41.64167
8	83.22500	41.65167
9	83.22500	41.68000
10	83.22500	41.72167
11	83.12500	41.53333
12	83.12500	41.55000
13	83.12500	41.66667
14	83.12500	41.72167
15	83.06333	41.59167
16	83.05000	41.60000
17	83.01667	41.63167
18	83.00833	41.64667
19	83.04167	41.64667
20	83.04167	41.70000
21	83.04167	41.73333
22	82.93500	41.52000
23	82.93500	41.54167
24	82.93500	41.60833
25	82.91667	41.65000
26	82.91500	41.59333
27	82.93500	41.73333
28	82.88333	41.70000
29	82.84667	41.63833
30	82.8583	41.603
31	82.86667	41.53833
32	82.88333	41.53833

Appendix 3. Use of a geographic information system in identifying patterns during walleye early life history stages in western Lake Erie.

Geographic information systems (GIS) are quickly becoming a popular tool to analyze fisheries data. The most common fisheries-related uses of GIS include mapping and modeling fish distributions and aquatic habitats and evaluating the effects of watershed land use on aquatic communities and habitat (Stanbury and Starr 1999, Fisher and Toepfer 1998). The use of GIS in my analysis, while initially a large undertaking to organize and format the data for the software, yielded a faster and more easily interpretable product than the visual analysis methods I employed in my thesis (Roseman 1997). GIS is a useful tool to examine fish population demographics in relation to habitat features that affect their life histories. I found it easier to summarize my large dataset and view trends in attributes across the large spatial expanse of my sampling area as well as across temporal scales within and between years.

While I treated all of the data in my GIS as discrete point samples in my analysis, statistical kriging routines do exist that allow the interpolation of point data into continuous contoured surfaces (Little et al. 1997). Most kriging routines assume that there is a continuous rate of change in attribute values between points and some software platforms allow the user to input their own statistical algorithm. These methods construct statistically optimal predictions for data at unobserved locations using a relatively small spatially explicit sample with low resolution (Oliver and Webster 1990, Little et al. 1997). Data that I collected on water temperature and water clarity most likely conform to this assumption because they usually change at a gradual rate from one sampling site to the next. Biological data such as fish and zooplankton densities do not typically conform to these assumptions. Fish and zooplankton typically have patchy distributions with discrete areas of high and low density (this study, Patalas and Salki 1992). These types of distributions would have abrupt changes in their values between sampling points which would violate the assumption of a smooth or continuous rate of change between sites.

An interesting field study would be to sample ichthyoplankton and zooplankton at small spatial intervals throughout a grid to assess the degree of change in their density through space. The spatial interval between sampling points would determine the resolution of the data (10 m, 100 m, 1,000 m, etc.). Such fine-scale distribution information would be useful in developing a kriging algorithm based on known rates of change between points. Implementing this type of sampling design in areas with consistent densities should not be necessary, such as the offshore regions of my study area where walleye densities were consistently low. A more useful application of this design would be to begin the sampling in a nearshore zone where we know densities are high and extend the sampling grid towards offshore points.

Spatial modeling and data management using GIS will become increasingly important as fisheries management principles move from single-species scenarios to ecosystem and watershed paradigms. GIS is rapidly becoming a standard method in solving fisheries management problems. The fisheries management agencies responsible for managing the Lake Erie fish community are presently incorporating the ArcView system as one of their analysis tools. The GIS I developed using my larval fish and habitat data will serve as a uniform data model for the development of the Lake Erie fish community GIS. This GIS will include all historic fisheries assessment and habitat data concerning the Lake Erie fish community (Personal communication, R. Knight, Ohio DNR, Sandusky Fisheries Unit, Sandusky, OH) and be useful in developing management plans that facilitate the rehabilitation and sustainability of Lake Erie fishery resources. Additionally, my data will be in a format that will make it possible for other researchers to directly incorporate into their work for comparative analysis and further field sampling, highlighting the value of GIS in providing a level of coordination and continuity important for cooperative multidisciplinary research.

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