RIVER DISCHARGE DRIVES DIFFERENTIAL SURVIVAL OF LARVAL WALLEYE

A Thesis

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By

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ABSTRACT

Walleye (*Stizostedion vitreum vitreum*) in Lake Erie have historically experienced large fluctuations in recruitment success, which has important implications for walleye population dynamics as well as food web interactions in Lake Erie. Because walleye year-class strength is likely set during the larval life stage, we explored factors underlying larval survival during outmigration in the Maumee and Sandusky rivers, Ohio’s primary walleye spawning tributaries. We estimated daily larval production and used otoliths to estimate hatch-dates of larvae surviving outmigration. Comparing production and survival distributions demonstrated strong temporal patterns of larval survival that were unrelated to walleye production patterns. Daily survival varied greatly during the larval hatch (~ 4 wk), with short, discrete periods of high survival (4 - 7 d) accounting for 75 - 84 % of total survivors. Larval survival was inversely related to river discharge, likely due to direct effects of suspended sediments; this ran counter to our original hypothesis that survival of larval walleye would be positively related to discharge. Interactions between temperature and zooplankton density also influence larval survival. Post-outmigration densities of larval walleye in Maumee and Sandusky bays were strongly correlated (Maumee Bay: $r^2 = 0.99$, Sandusky Bay: $r^2 = 0.94$) with Ohio Division of Wildlife (ODW) estimates of late-
summer juvenile abundance (i.e., year-class strength) of Lake Erie walleye. Climatic events during the larval hatch likely drives recruitment success of walleye, thus influencing food web and community dynamics in Lake Erie. Because walleye year-class strength fluctuations appear weather-related, large-scale climatic perturbations, such as global warming, may operate to increase variability of walleye year-class strength. These effects may be mitigated by reduced exploitation of spawning walleye coupled with watershed management to lower discharge and suspended sediments.
Dedicated to the memory of John and Kathryn Mion
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INTRODUCTION

Survival of juveniles (or seedlings in plants) of most species tends to be low and variable as compared to other life stages (O'Donoghue 1994). Inteannual variability in their survival strongly affects population dynamics of species across a wide range of taxonomic groups, including plants (Sacchi and Price 1992, Ostfeld and Canham 1993), marine invertebrates (Roughgarden et al. 1984), insects (Fischer and Moore 1993), fish (Houde 1989), birds (DeSante 1990), and mammals (Kruule et al. 1991, O'Donoghue 1994). Quantifying mechanisms underlying this variability is necessary for a holistic understanding of population and, ultimately, community dynamics.

Understanding mechanisms governing year-class strength of fishes has long been a primary problem in aquatic ecology as variable year-class strength produces equivalent variability in adult population size (Gulland 1982, Sissenwine 1984). Numerous hypotheses have been proposed to explain interannual variability of year-class strength of fishes, most of which have been concerned with early-life mortality resulting from interactions of abiotic and biotic factors with size and ontogeny of larval fishes (Miller et al. 1988, Sale 1990, Houde 1994, Leggett and DeBlois 1994). A broad suite of hypotheses continues to persist because few have been explicitly proven or disproven with
any generality, largely due to the complexity and subtlety of processes driving recruitment coupled with the often conflicting data presented by researchers pursuing single-factor causes of year-class strength variability (Houde 1987, Leggett and DeBlois 1994). Recently, however, the utility of considering finer scales of variability among larval fish and environmental factors has been effectively demonstrated. Rather than considering survival of annual cohorts of larval fishes as a whole, examining characteristics and survival of individual larvae or small aggregations of larvae (grouped temporally or spatially) appears to lend greater insight into mechanisms driving year-class strength (Methot 1983, Crecco and Savoy 1985, Crowder et al. 1992, Rice et al. 1993). As such, intra-annual patterns of larval survival may elucidate mechanisms underlying inter-annual variability of year-class strength, a perspective we pursue with river-spawning walleye (Stizostedion vitreum vitreum) populations in Lake Erie.

As the terminal predator and valued sport and commercial fish, walleye are quite important both ecologically and economically in Lake Erie and historically have exhibited large variations in year-class strength (Hatch et al. 1987). Previous studies have attributed this variability to abiotic factors (e.g., temperature and storm events, Busch et al. 1975) and biotic factors (e.g., competition and predation, Hartman 1972) as well as overfishing, ecosystem alterations such as excessive nutrient input, invasions of exotic species, and degradation of traditional (riverine) spawning areas (Leach and Nepsy 1976, Schneider and Leach 1977). With a long history of these perturbations (Regier and Hartman 1973, Schneider and Leach 1977), Lake Erie is a difficult and
uncertain environment for fisheries managers. Mechanistically understanding variations in walleye year-class strength would improve the ability of managers to predict broad-scale trends in the Lake Erie fish community in response to continually changing conditions and to more precisely target management efforts.

For many marine and freshwater fishes, including river-spawning walleye, early life stages rely on physical transport mechanisms such as oceanic currents or upwellings, wind-driven surface currents, or river discharges to carry them to distant nursery areas (Norcross and Shaw 1984). Both deterioration of these currents (Nelson et al. 1977, Shelton and Hutchings 1982) and anomalous hydrographic events (Baily 1981) can be related to poor survival and hence low year-class strength. Clearly, success of larvae in reaching nursery areas, coupled with coincident environmental conditions, likely has profound implications for recruitment variability of fishes.

Herein we quantify mechanisms underlying year-class strength of Lake Erie walleye, specifically those which spawn in the Maumee and Sandusky rivers, Ohio, concentrating on river outmigration of larval walleye to nursery areas in the bays. That a high degree of environmental variability within food-poor rivers coincides with critical stages of walleye otogeny made establishment of year-class strength during outmigration quite plausible. Given that prolonged river residence time may reduce larval survival (Priegel 1970), we tested the hypothesis that strong larval survival was positively related to rapid outmigration from rivers, resulting from high discharge, to bays, by quantifying daily
production and survival of larval walleye in the Maumee and Sandusky rivers during 1993-95. Specifically, we compared larval survival to daily variation in discharge. By understanding field patterns of survival of larval walleye, we can gain important insights into walleye population dynamics, ultimately improving our ability to predict fish community structure within a changing ecosystem.
METHODS

Study Area

As Ohio's two largest tributaries to western Lake Erie, the Maumee and Sandusky rivers (Figure 1) drain largely agricultural and urban areas (16,395 and 3,240 km², respectively), thus carrying high suspended sediment and nutrient loads (USGS 1992). Mean daily discharges were about 120 m³/s and 28 m³/s in the Maumee and Sandusky rivers, respectively, during 1924 through 1992 (USGS 1992). Low gradients and the strong intrusive effect of Lake Erie generate low current velocities (typically < 10 cm/s, this study), making flow reversals common in both rivers (Bedford 1992). Gravel riffles, used by spawning walleye, began about 25 km upstream of the mouths in each river. In the Sandusky River, upstream movement of walleye was limited by the Ballville Dam in Fremont, OH, whereas no such impediments existed in the Maumee River. Each river empties into a large bay (Maumee Bay: 5,441 ha, Sandusky Bay: 14,692 ha), with depths typically ranging between 2-3 m.

Field Data Collection

We sampled the Maumee and Sandusky rivers and bays each spring during 1993-95. Three sample sites were established in each river: 1) an
upstream site immediately below walleye spawning riffles, 2) a midstream site about midway between spawning areas and the river mouth, and 3) a downstream site near the river mouth (Figure 1). All sites were sampled twice weekly in 1993 and three times weekly in 1994-95 during late March through early June, a period encompassing hatching and river residence of larval walleye. Our river sampling was designed to quantify spatial and temporal trends in larval walleye density, movement, and survival, as well as environmental conditions, during outmigration. We also sampled weekly in the bays to quantify densities of larval walleye surviving outmigration. In 1993, we sampled three bay sites twice each week. Bays were sampled on a finer spatial scale (six sites weekly) in 1994-95 to gain greater resolution in larval walleye dispersal and densities in the bays.

We collected biotic and abiotic environmental data at each sample site. Zooplankton were sampled using 31-cm diameter, 153-micron mesh nets lowered to the bottom and vertically hauled to the surface to provide a sample of the entire water column. For counting, samples were rinsed onto a small, circular counting dish divided into 16 sectors. Under a dissecting scope, individuals of each taxon in 1/8 of the dish were counted; these numbers were then used with the following formula to project the total number of individuals in the entire sample:

$$[\frac{\# \text{ counted}}{1/\text{fraction of dish counted}} \times \frac{1}{\text{fraction of sample in dish}}]$$

If the projected number of individuals of a taxon was < 25, we stopped counting that taxon. If the projected number was > 25, then > 50 individuals of that taxon
were counted. After completing the section in which the 50th individual was counted, we stopped counting that taxon, and again projected the total number of individuals in the sample. Lengths of the first 22 individuals of each taxon encountered were measured (total body length, excluding spines, helmets, and caudal rami) using a digitizing pad and microcomputer. Zooplankton lengths were converted to biomass using taxon-specific length - dry weight regressions (G.G. Mittlebach, Kellogg Biological Station, Michigan State University, East Lansing, MI, unpublished data).

Surface water temperatures were taken at 1 m depth on each sampling date. Daily discharge data were obtained from United States Geological Survey gauges on both rivers (USGS 1995).

To collect walleye larvae in the rivers and bays, we towed 1 X 2 m (mouth size), metered neuston nets of various net sizes (500-, 1000-, 1800-micron meshes, with successively larger meshes used as average larval walleye size increased) through the top meter of the water column at about 1 - 1.5 m/s for 3-5 min during daylight. We completed two tows at each site on each sampling date (one upstream and a second downstream in the rivers). Because ichthyoplankton are often unevenly distributed within rivers (Corbett and Powles 1986, Harvey 1991), nets were towed diagonally to integrate samples across the width of the river. Upon collection, all ichthyoplankton were preserved immediately in 95% ethanol. In the laboratory, we identified (Auer 1992) and counted walleye larvae. For each sample date, we weighed (0.1 mg wet weight) and measured (0.1 mm TL) up to 20 walleye larvae from each site.
We analyzed larval walleye collected at all river sample sites to quantify diets and determine when larval fish became prey for walleye. We examined the entire digestive tract as guts from walleye larvae were essentially undifferentiated tubes and digestion rates were likely similar throughout the gut. All gut and stomach contents were identified and measured per methods described above; prey biomass was estimated using length-dry biomass regressions (G.G. Mittlebach, Kellogg Biological Station, Michigan State University, East Lansing, MI, unpublished data).

*Larval Production Model*

To quantify survival of larval walleye, we combined mean density and variability of larvae at upstream sample sites into a model estimating daily and annual production of larval walleye in each river. In developing this model, we assumed that (1) larval densities at upstream sites were composed solely of newly-hatched larvae (larval walleye swim up from the substrate and begin drifting immediately upon hatching, Corbett and Powles 1986), (2) dates of first and final occurrence of walleye larvae in our upstream samples suggested true hatch duration (river sampling began before larvae appeared and ended after they disappeared), (3) all larvae drifted in the top 1 m of the water column, (4) samples taken at upstream sites each date were independent (i.e., larvae were transitory, thus we did not resample the same population of larvae on different sample dates at the upstream sites), and (5) larval densities were uniform within the upstream area sampled and through time across sample dates. We first
estimated total volume of the section of river characterized by our upstream
tows (river sample volume \( V \): 86,450 and 22,144 m\(^3\) for the Maumee and
Sandusky rivers, respectively) from surface area measures on topographic
maps of the section. To estimate daily numbers of newly-hatched walleye
drifting downstream, we combined estimates of walleye densities from our
samples with estimates of flush rates of these sample sites. To calculate how
many times river sample volumes were completely flushed each day of the
larval hatch \( F \) (flushes per day), we divided daily river discharge by the river
sample volume:

\[
F = \frac{\text{daily river discharge (m}^3/\text{d)}}{V}.
\]

Daily river discharge was calculated for each day as river discharge rate (m\(^3\)/s,
from USGS gauging stations on each river) divided by 86,400 (s/d). We then
estimated daily production of larval walleye \( (P_d) \) (walleye larvae produced per
day) as:

\[
P_d = (WF) \left( \frac{V}{100} \right)
\]

where \( W \) = larval walleye density in our samples (larvae \( \times 100 \) m\(^3\)). For non-
sampled dates, we could not calculate a mean and variance for each daily larval
production estimate. Rather, we assumed that larval walleye densities
estimated for each sample date did not change until the next sample date. We
calculated total larval production \( (P_T) \) as the sum of daily larval production over
all dates (both sampled and non-sampled).

Because we wanted to assign some measure of confidence to this
estimate of total production, we needed an estimate of variance. We derived

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this estimate of variance through the following steps. 1) Within-day variance of walleye density \( (s_w^2) \) was calculated for each sample date from the two replicate neuston net tows. 2) Within-day variance of daily walleye production estimate \( (s_p^2) \) was calculated by assuming a normal distribution of larval walleye densities. Given that daily larval production values were calculated as walleye densities transformed by a factor of \((FV/100)\) (see equation 1), variance of this estimate can be calculated as:

\[
s_p^2 = s_w^2 (FV/100)^2.
\]

3) If we assume that sample dates are independent and that within-day variance on a given sample date also describes variance on subsequent non-sampled dates, then we can calculate variance of the sum of daily larval production (i.e., \( s_T^2 \), variance of total larval production) as the sum of the variances of daily production:

\[
s_T^2 = \Sigma s_p^2.
\]

The assumption of independence among sample dates may be extreme; thus, this variance may more accurately be thought of as a maximum variance. The 95% confidence interval around \( P_T \) was then:

\[
P_T \pm (SE \ P_T) (1.96).
\]

**Otolith Analysis**

To quantify spatial and temporal trends in larval survival during outmigration, we used otolith analysis to estimate daily age and hatch dates of
larval walleye caught at mid- and downstream sites in both rivers. Further, though these analyses would not tell us how quickly individuals migrated through the river, we would gain insight into river residence time for larvae and how it changed at each sample site during the hatch. For every sample date on which larval walleye were collected, we removed sagittal otoliths from up to 10 randomly chosen larvae from both sites. Otoliths were mounted whole and cleared on glass slides using a polyester resin, then were aged by a single reader using a transmitted-light microscope at 400X magnification. To avoid biasing counts, otoliths were read blindly; the reader did not know either date of capture or size of larva. The reader randomly chose whether to read the left or right sagitta; ring deposition patterns did not differ between sides. Otoliths were read twice; if readings were within 10%, larval age was taken as the mean of the two readings. If a second reading was not within 10%, otoliths were read a third time; if any reading was not within 10% of the mean, the otolith was discarded. Hatch date for each larva was calculated as date of collection minus estimated age in days.

Knowing age at first increment deposition and periodicity of increment deposition is critical to accurate otolith analyses (Jones 1986). To address these issues, we, working with Edward Roseman (Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI), conducted a marking experiment with larval walleye in 1994. Roseman gillnetted spawning adults on Lake Erie reefs to collect gametes that were used to culture larvae for this experiment. One day after hatching, about 800 - 1,000 larval walleye were
marked in a solution of alizarin complexone for 2 h. Alizarin complexone is absorbed into calcareous structures such as otoliths, leaving a red band that indicates the day of marking. Following marking, about half the larvae were placed in each of two enclosures in a ~ 0.25 ha pond. The enclosures allowed the fish to be exposed to in-situ light and temperature regimes, both of which may influence patterns of otolith increment deposition (Jones 1986), and allow these results to be applied to wild-caught walleye larvae. Larvae and zooplankton were sampled at weekly intervals while temperatures were recorded with a thermograph. Otoliths were processed and analyzed as described above.

**Survival Estimates**

We sought to determine the proportion of larvae surviving to mid- and downstream sample sites attributable to individual hatch dates within a year. We first compared the distribution of hatch dates of larvae from mid- and downstream sites to the full distribution of hatch dates to determine if mid- and downstream survivors were drawn randomly from all hatch dates. For each sample date at each site, we estimated the hatch-date distribution from the otoliths of larvae sampled on that date. To estimate the hatch-date distribution for all fish surviving to mid- and downstream sites over the season, we weighted each daily hatch-date proportion by an estimate of relative density of fish at the sample site that day, before summing over all dates. Relative density was measured as number of larvae captured per 100 m$^3$, assuming that larvae
collected on a given day at the upstream site represented larvae that had hatched that day. Thus, the full hatch-date distribution was estimated from a distribution of daily larval densities at the upstream site. This distribution of daily production (upstream site) was then compared to distributions of hatch dates of survivors from mid- and downstream sites using a chi-squared test.

To evaluate spatial and temporal trends in larval survival during outmigration each year, we generated a daily index of survival (IS) for the mid- and downstream sites in both rivers. IS was calculated by dividing the total downstream density of larvae attributable to each hatch date by the estimated number of larvae produced that day. Thus, we had an IS value for each day of the larval hatch, which, in turn allowed us to assess fine-scale variability in overall survival of larval walleye. With IS values, variability of river discharge was compared with variability of survival of larval walleye.

Because bays integrate all larvae surviving river outmigration, we used annual peak densities of larval walleye in each bay as an index of cumulative survival of larvae spawned in the rivers. We also compared peak bay larval densities to Ohio Division of Wildlife (ODW) estimates of juvenile walleye catch-per-unit-effort (CPUE) in Lake Erie during August (ODW 1996). This late-summer index of juvenile abundance has been strongly correlated with walleye year-class strength (R. Knight, ODW, Sandusky, OH, pers. comm.); hence, this allowed us to examine the relationship between bay larval abundance and relative measures of walleye year-class strength in Lake Erie.
RESULTS

Larval Hatch

Larval walleye typically were produced during mid-April through mid- to late-May in the Maumee and Sandusky rivers (Table 1). Mean hatch durations were $28 \pm 2.2$ d (mean $\pm$ SE) in the Maumee River and $29 \pm 4.0$ d in the Sandusky River. Hatch duration did not differ between rivers across years (paired t test, $P = 0.58$).

River Discharge, Water Temperature, Zooplankton Density, and Diets

Intra-annual patterns of river discharge during the larval hatch were similar in both rivers across years. While the magnitude of discharge was greater in the Maumee River than in the Sandusky River (owing to the former's much larger main channel), a visual comparison of their patterns of discharge revealed their similarity. River discharge varied greatly during the larval hatch, with peak discharges in all years occurring early in the hatch (usually mid-April). Discharge trends during larval walleye residence varied among years. In 1993 and 1994, discharge was low and stable in both rivers. Conversely, discharge was higher and more variable during 1995, with several high discharge events occurring in both rivers.
As with discharge, annual patterns of water warming were similar across rivers. Trends in rate of water temperature increase did not differ between rivers, but did differ across years (ANCOVA, heterogeneity of slopes: river effect, $P = 0.685$; year effect, $P < 0.0001$; river*year interaction effect, $P = 0.97$). Rate of warming was greater during 1995 than in either 1993 or 1994, which did not differ (Tukey's multiple comparisons, $P < 0.05$). Overall temperature ranges were similar across rivers and years.

Larval walleye feeding success in the rivers was compromised by low zooplankton densities. Appreciable feeding only occurred at the downstream sites, and even there feeding rates were low. In the Maumee River, percentage of larvae from the downstream site having empty guts was 93.3, 81.4, and 98.3 % in 1993, 1994, and 1995; in the Sandusky River, these percentages were 76.9, 34.8, and 82.5 %. Note that feeding success was particularly great in the Sandusky River during 1994, when zooplankton densities were unusually high.

Zooplankton densities were extremely low at all sample sites in both rivers, typically < 1 individual/L, during larval walleye residence (Figure 2). In all years, zooplankton densities did not increase until late-May, when larval walleye already had passed through the rivers. The one exception was at the downstream site in Sandusky river during 1994 when densities increased in late-April, becoming moderately abundant during walleye residence through May.
Larval Production

Estimated annual production of larval walleye differed markedly between rivers and within rivers across years. More larvae were produced by the Maumee River each year (paired t test, \( P = 0.04 \)), ranging 4.5 - 33 times higher than in the Sandusky River (Table 1). In the Maumee River, production differed among all years (non-overlapping 95\% CI’s, Table 1). The Sandusky River produced similar numbers of walleye larvae during 1993 and 1994 (overlapping 95\% CI’s, Table 1), with both years exceeding 1995 production (non-overlapping 95\% CI’s, Table 1).

Number of larvae produced per day ranged over several orders of magnitude within any 1 year. Because river discharge transports newly-hatched larvae downstream, we examined the influence of river discharge on daily production by regressing daily production on daily discharge in each river. Although daily discharge was nearly positively related to daily production in each river, it explained only a small proportion of the variation in daily production (Maumee River, all years pooled; \( r^2 = 0.04; P = 0.06 \); Sandusky River, all years pooled; \( r^2 = 0.04; P = 0.06 \)).

Otolith Analyses

We collected 15 walleye larvae from the pond enclosures for analysis at the end of the first week of the marking experiment. Unfortunately, all walleye larvae in both enclosures died during the second week. All of the 15 known age (8 d) larvae collected from the first week aged to 8 d by their otoliths. Thus, we
concluded that first ring deposition occurred the day of hatch and that ring deposition in larval walleye was daily.

We used otoliths (N=920) from larval walleye to estimate the ages and hatch dates of larvae surviving to both mid- and downstream sites. We refer to a larva’s age at collection as its river residence time (RT). To assess trends in larval walleye movement within the rivers, we examined how larval RT varied across years and sites within each river. Mean RT differed between sites and between years in the Maumee River (2-way ANOVA: \( F=14.86; \ df=5, 509; \) year effect, \( P<0.0001; \) site effect, \( P=0.01; \) year*site interaction effect, \( P=0.15 \)). Mean RT was greater in 1994 than either 1993 or 1995, which did not differ (Tukey’s multiple comparisons, \( P<0.05 \)); as expected, downstream RT’s were greater than midstream (Tukey’s multiple comparisons, \( P<0.05 \)). Conversely, a significant interaction between year and site effects on RT in the Sandusky River (2-way ANOVA: \( F=9.41; \ df=5, 404; \) year effect, \( P=0.09; \) site effect, \( P=0.0001; \) year*site interaction effect, \( P=0.004 \)) make interpretation of year and site effects difficult. However, downstream RT’s were greater than midstream (Tukey’s multiple comparisons, \( P<0.05 \)), which is probably a true response given the strength of the site effect in the ANOVA model.

Because larval drift is likely passive (Corbett and Powles 1986), larval RT would likely be related to river discharge. We assessed this relationship by regressing mean larval RT on every sample date at the downstream sites on the mean daily discharge over the 5 d previous to each sample date. For both rivers, we pooled data across years and \( \log_{10}(x+1) \) transformed both discharge
and RT to stabilize the variance. Larval RT was related inversely to river discharge in Maumee ($r^2 = 0.10; P = 0.016$) and Sandusky rivers ($r^2 = 0.28; P<0.0001$).

*Larval Survival in Rivers*

Larval survival varied greatly during the hatching period for walleye larvae in both rivers. To evaluate the influence of daily production on the hatch-date distribution of survivors, we regressed daily percent of total survivors at mid- and downstream sites on daily percent annual production. For these tests, proportions were arcsine square root transformed. Regressing a percentage on another percentage effectively restricts the possible slopes to values between -1 and 1, because the set of x-values and the set of y-values must each sum to 100. Thus, this analysis restricts the likelihood of getting significant results as the slope is restricted to the half of all possibilities that are most like zero (the null hypothesis). Despite this limitation, we still found daily production and survival to be correlated at the midstream ($r^2=0.09, P=0.006$) and downstream ($r^2=0.10, P=0.005$) sites in Maumee River, though these relationships explained only 10 % of the total variation. These two variables were unrelated at the Sandusky River midstream ($r^2=0.01, P=0.509$) and downstream ($r^2=0.03, P=0.131$) sites.

We used information from otoliths to help explain this low correlation between larval production and survival to downstream sites. We first compared temporal distributions of larval production at upstream sites to hatch-date
distributions of survivors to midstream sites (determined by otoliths) and next compared hatch-date distributions of survivors to midstream sites with hatch-date distributions of survivors to downstream sites.

Hatch-date distributions of larvae surviving to midstream sites were very different from daily production distributions (Figure 3, $\chi^2$ test: $P<0.05$ both rivers, all years). Hatch-date distributions of survivors to downstream sites differed somewhat from hatch-date distributions of survivors to midstream sites (Figure 4, $\chi^2$ test: $P<0.05$ both rivers, all years except Sandusky River during 1995: $P=0.264$), but these differences were not nearly as pronounced as differences with larval production-date distributions.

Patterns of hatch-date distributions of survivors to mid- and downstream sites likely were driven by river discharge. Visual comparison of hatch-date distributions of survivors to both mid- and downstream sites with discharge (Figures 3 and 4) revealed that dates having relatively high survival typically occurred only during periods of low discharge. Conversely, survival of larvae was low during high-discharge events.

Days characterized by high larval survival were not evenly distributed across the hatch duration, but rather were focused into short discrete periods. This phenomenon occurred at both mid- and downstream sites in each river across all years. Though hatches usually continued for about 4 wk, most survivors derived from only 4 - 7 d each year (Table 2). Although these hatch periods accounted for 75 - 83 % of the survivors to downstream sites, these
dates accounted for only 5 - 52 % of total larval production upstream. High-
survival timing was markedly consistent across years, always occurring during
April 27 - May 7 in the Maumee River and April 23 - May 4 in the Sandusky river.

For each day larvae hatched, we calculated an IS (Index of Survival, see
Methods) value for larvae collected at mid- and downstream sites in each river.
Comparing daily mid- and downstream IS values to river discharge revealed a
dramatic inverse relationship between larval survival and discharge (Figure 5).
This emphasized that days of high survival only occurred during very low
discharge; even moderate discharge increases resulted in uniformly low
survival. Survival of larval walleye was extremely variable at low discharges
suggesting that low discharge was a necessary, but not sufficient, condition for
high survival.

Larval Recruitment

Densities of walleye larvae in bays were strongly related to late-summer
abundance of juvenile walleye in Lake Erie (Figure 6). Annual ODW estimates
of inshore and offshore juvenile walleye CPUE were correlated strongly with our
estimates of peak bay density. These ODW data revealed that 1994 was a
strong walleye year-class, 1993 was moderate, and 1995 was an extremely
weak year class. Further, because river discharge strongly influenced larval
survival in rivers, which, in turn, was well correlated with juvenile abundance, we
examined the historical relationship between river discharge and juvenile
walleye abundance. Because Lake Erie has historically been subject to great

20
temporal variability in biotic and abiotic conditions, we chose data from 1986-92 (in addition to our study years), as conditions (walleye population size, fish community structure, nutrient status, etc.) were most like our study period. Juvenile walleye CPUE was negatively correlated with river discharge during May 1986-95, when the majority of larval walleye river residence occurred, based on 1993-95 data (Figure 7). These relationships reflect patterns similar to those for IS and discharge in that high juvenile abundance only occurred during low river discharge years, whereas high river discharge resulted in much lower juvenile abundance.
DISCUSSION

Walleye Recruitment Success

Typically, variability of year-class strength in fishes derives from high and variable mortality during early life history stages. Some disagreement exists, however, concerning whether processes regulating year-class strength primarily operate during larval (Crecco and Savoy 1985, Myers and Cadigan 1993) or post-larval (Forney 1976, Sissenwine 1984, Peterman et al. 1988) stages. Houde (1994) contends that control of year-class strength for freshwater fishes having large larvae (like walleye) likely occurs through density-dependent mechanisms during the juvenile stage. In contrast, we believe that year-class strength of river-spawned walleye is determined by density-independent factors operating early in the larval stage. Similar findings have emerged from other studies of river-spawning walleye populations (Priegel 1970, Johnston et al. 1995) and reef-spawning walleye in Lake Erie (Busch et al. 1975). Spawning in areas prone to unpredictable, extreme variations in abiotic conditions driven by climatic (storm) events (Hynes 1970, Busch et al. 1975), walleye vary dramatically in year-class strength. Thus, episodic storm events appear to regulate survival of larvae, in turn driving walleye year-class strength.
River discharge strongly regulated larval walleye survival in the Maumee and Sandusky rivers across 3 years. Early- and late-hatching larvae survived poorly, whereas larvae hatching during mid-period survived well and likely contributed to walleye year-class strength. Our findings are consistent with other studies employing otolith-based hatch-date analyses to examine survival variability of larval fishes (Methot 1983, Crecco and Savoy 1985, 1987, Rice et al. 1987b). In all, larval fishes, hatching at different times over a protracted period, experience high and variable survival soon after hatching and exhibit intra-annual patterns of survival that were consistent across years. Year-class strength was established during periods of high larval mortality and was driven by a relatively small subset of total larval production. Moreover, survival of larvae was not related to adult or egg density, but rather direct and indirect effects of abiotic factors. These similarities occurred in spite of the range of species (4 species represented), hatch sizes (2.9 - 9.5 mm), and systems (rivers, freshwater lakes, oceans). Using current hypotheses regarding size-, ontogeny-, or system-based characteristics (Sissenwine 1984, Miller et al. 1988, Houde 1994) would have led us to vastly divergent predictions of critical mechanisms regulating year-class strength for our and the aforementioned studies. Obviously, though, some generality underlies mechanisms influencing larval survival of these species. These studies underscore the importance of individual-based data in generating and testing general hypotheses regarding fish recruitment (Miller et al. 1988, Pepin and Miller 1993).
Year-class strength in fishes is a product of interactions between production and survival; neither one alone determines success. Although larval walleye densities in the bays were unrelated to annual production of larvae in the rivers, the magnitude of larval production during periods of high survival likely substantially influences walleye year-class strength. For example, total larval production in the Maumee River during 1995 (our weakest year-class) was about twice as much as in 1994 (our strongest year-class). However, production during high survival was almost 4.5 times greater in 1994 than in 1995, suggesting that a fine-scale match/mismatch (sensu Cushing 1975) between larval production and environmental influences walleye year-class strength. Clearly, however, high survival periods were based on relative daily percentages of larvae surviving river outmigration, rather than an absolute measure of numbers surviving. Identifying hatch dates with "high survival" only has meaning relative to other hatch dates within a year. Larval production during the high survival periods was similar in 1993 and 1994; yet total survival was greater in 1994. Apparently, conditions, even during high survival, were less conducive to strong larval survival in 1993 than 1994.

Mechanisms Underlying Larval Walleye Survival

In the following section, we outline and discuss those factors likely most important in regulating survival of larval walleye in rivers: discharge, water temperature, zooplankton density, and predation.
**River Discharge.** We originally hypothesized that survival of larval walleye would be positively related to river discharge as higher discharge would reduce larval RT. Conversely, however, survival of larval walleye was *strongly and negatively* related to discharge. Other studies of river-spawned larval fishes have documented similar patterns, noting both direct (Harvey 1987) and indirect (Crecco and Savoy 1985) effects of discharge on larval survival. In our case, discharge directly affected survival of walleye larvae as we found a strongly negative relationship between discharge and daily survival of walleye larvae. Further, hatch-date distributions of survivors to mid- and downstream sites were fairly similar, whereas both differed from upstream production distributions, suggesting that survival was determined early in outmigration. Direct discharge-related mortality likely derives from increased suspended sediment which typically occur during high, turbulent discharge (Waters 1995). Whereas high concentrations of suspended sediments can cause gill damage and suffocation in larval fishes (Cordone and Kelley 1961), suspended particles also could create strong scouring action that could damage fragile, newly-hatched larval fishes (Lloyd 1987). Also, as egg incubation areas for walleye in the Maumee and Sandusky rivers are shallow gravel-cobble riffles, turbulent flow could potentially kill emerging walleye larvae by driving them against the substrate. Damaged larvae were common in our upstream samples, especially during the early portion of the hatch. Thus, interactive effects of discharge and suspended sediments experienced by newly-hatched walleye larvae likely creating a substantial bottleneck to walleye recruitment immediately upon hatching.
As a transport medium for larval walleye in the Maumee and Sandusky rivers, discharge also may indirectly affect survival of larval walleye by mediating larval RT. Low gradients coupled with lake influxes make still water and flow reversals common in the lower reaches of the rivers (Bedford 1992). Indeed, frequent flow reversals occurred during our sampling. Prolonged larval RT likely creates a setting where survival of larval walleye is determined by complex interactions among a suite of factors (see below). Thus, passage through the hydrographically uncertain downstream areas of the rivers may be another critical point during outmigration of larval walleye.

Water Temperature and Zooplankton Density. Walleye success while in the rivers may actually derive from a complex set of interactions among discharge, water temperature, and zooplankton density, with the influence of water temperature and zooplankton mediated by discharge. At high discharge, survival was low, irrespective of temperature or food availability. Further, those larvae that survive hatching at high discharge likely would to have short river residence, thus bypassing temperature and zooplankton effects related to extended river residence. However, at low discharge, coupled with rapid warming, low prey, and greater yolk metabolism, may greatly reduce larval condition and survival. As larval walleye typically occur in these rivers during rapid warming, zooplankton density may be critical to larval survival during low-discharge years (sensu Crecco and Savoy 1985, 1987). Indeed, atypically high zooplankton density at the downstream site in the Sandusky River during 1994 was associated with feeding success and high survival of larval walleye.
**Predation.** Predation can influence recruitment success of larval fishes (Hunter 1981); it also may drive the consistent intra-annual patterns of larval walleye survival documented in both rivers. Their high densities coupled with shallow river depths make larval walleye especially susceptible to predators. In walleye spawning tributaries to Oneida Lake, NY, predators congregate and feed on larval walleye as they swim up from the substrate (Regier et al. 1969). Conceivably, late-hatching larvae in the Maumee and Sandusky rivers could have encountered severe predatory mortality because they experienced uniformly low survival, despite typically low discharges. Many piscivorous fishes migrate up the Maumee and Sandusky rivers during early- to mid-May to spawn in the same habitats used by walleye (Schaeffer and Margraf 1987), including white perch (*Morone americana*), white bass (*Morone chrysops*), yellow perch (*Perca flavescens*) which eat larval walleye (Colby et al. 1979). Thus, late-hatching larval walleye may face a substantial predatory gauntlet immediately upon hatching.

**Synthesis of Mechanisms.** Regularity of temporal patterns of larval walleye survival evident in the Maumee and Sandusky rivers may derive from a spatio-temporal progression of abiotic and biotic factors important to determining larval survival (Figure 8). Strong effects of discharge and predation act early in outmigration to largely shape temporal distributions of surviving larvae. Upon hatching, discharge was the primary determinant of larval survival. Because discharge was typically highest during mid- to late-April (after which it declined greatly, except during 1995), early-hatched larvae experienced high
discharge-related mortality. Mid- and late-hatched larvae were less likely to experience high discharges, though storm-related high discharges also could occur during these periods. Predation effects are most likely concentrated on late-hatching larvae. Thus, mid-hatching larvae typically enjoy reduced discharges and little predation, resulting in consistent high survival to the midstream site relative to earlier and later periods of the hatch.

Though most larval mortality likely occurs between up- and midstream sites, mechanisms operating between mid- and downstream sites may further refine temporal distributions of survivors ultimately occurring at downstream sites. The few early-hatching larvae surviving initial high discharges likely survive well through the lower portions of the rivers as low temperatures reduce yolk metabolism, ensuring energetic reserves in the face of low food availability. Similarly, mid-hatching larvae, experiencing moderate temperatures and variable food availability (e.g. zooplankton may sometimes occur in relatively high densities, as in the Sandusky River during 1994), likely survive well through the lower rivers. Late-hatching larvae, however, require high zooplankton abundance as they typically face high, energetically-expensive temperatures that probably result in high mortality. As in the upper rivers, mid-hatching larvae are most likely to experience conditions conducive to high survival through the lower rivers. Ultimately, though, interactions among the timing of the above factors likely regulates the formation and persistence of high survival periods.

Though size-dependent mortality is of general importance in explaining recruitment variability in fishes (Miller et al. 1988), our results suggest that these
processes may be less important for river-spawned walleye. Direct effects of river discharge upon larval walleye are not likely size-selective across the size range of newly-hatched larvae. Similarly, if predation is important, it too would not likely operate in a size-dependent manner. Weak swimming ability of larval walleye (Houde 1969), coupled with the large size difference between predators (mature white perch, white bass, and yellow perch) and prey, ensures a high capture probability for predators (Miller et al. 1988). In our view, variability among individual walleye larvae is much less important than time of hatching in driving survival probabilities in these systems.

Abiotic factors can have powerful, albeit usually indirect (via biotic interactions such as food production, predation, etc.) effects on population and community dynamics (Dunson and Travis 1991). Large-scale climatic events structure fish recruitment variability, acting to regulate proximate factors (Smith and Eppley 1982, Legendre and Demers 1984). Our results are unique, however, in that regular (as opposed to intermittent or catastrophic) *direct* influences of an abiotic factor, river discharge, on larval fish survival occurred over 3 years. Given the direct link with larval survival, climatic conditions during the hatch may be accurate qualitative predictors of walleye year-class.

Our results are consistent with earlier observations of synchrony of fish year-class strengths over large geographic areas in freshwater (Koonce et al. 1977) and marine (Koslow 1984) systems as generated by large-scale climatic processes. The Maumee and Sandusky rivers appeared to be tightly linked in terms of intra- and inter-annual variability of abiotic factors as regional climatic
processes driving discharge and temperature variability seem to affect both river systems similarly. Thus, if abiotic factors are of primary importance in establishing year-class strengths of some fish species, then the climatic forces driving these factors should affect all systems within a region similarly. The result, then, being similar annual trends in year-class strength across many disparate rivers and lakes. Given the synchrony of walleye hatching periods between both rivers and the closely coupled response of the rivers to climatic events, we would expect that magnitude of larval survival also would be closely coupled between rivers each year; high discharge events during the larval hatch, survival would be equally poor in both rivers.

That both bay densities of larval walleye and mean May river discharge are strongly related to August abundance of juvenile walleye in Lake Erie suggests that either 1) river-spawned walleye regulate the Lake Erie walleye population or 2) that mechanisms regulating survival of reef-spawned larval walleye are similar to those mechanisms operating on river-spawned larvae. The first possibility is unlikely as most Lake Erie walleye spawn on open-lake reefs (R. Knight, pers. comm.). In our view, the second possibility, however, is quite plausible. Survival of eggs and newly-hatched larvae on the reefs is negatively related to storms and high wind events, owing to the abrasive action of waves damaging eggs and larvae as well as washing eggs from protective reef substrate (Busch et al. 1975). High discharge (and, presumably, low survival of larval walleye) from rivers also is driven by storms (Coghlan 1984). Further, walleye spawn in rivers several weeks before reefs as rivers warm more
rapidly in spring than the lake (Parrish et al. 1989). Because walleye life stages most vulnerable to storm effects (yolk-sac larvae in the rivers, eggs on the reefs) overlap in time, survival likely will be similar between rivers and reefs as storms ultimately operate along different causal pathways to drive larval survival in both habitats. As such, no compensatory mechanisms appear to influence survival of river- or reef-spawned walleye, suggesting that climatic events alone shape walleye year classes. Given the linkage in survival between rivers and reefs, annual recruitment to the walleye population in Lake Erie will be more variable than if river and reef survival were not linked, likely explaining the historical variability of walleye year-class strength.

Management Implications

As the terminal predator, walleye play a pivotal role in the Lake Erie fish community. As such, large annual variations in its year-class strength translate to strong community-wide effects. Through predation, walleye largely drives species composition and variation in the Lake Erie fish community, an influence that varies with walleye abundance (Knight and Vondracek 1993, M. Kershner, Aquatic Ecology Laboratory, The Ohio State University, Columbus, OH, pers. comm.). By regulating prey, walleye effects cascade through multiple trophic levels (sensu Carpenter et al. 1985). Thus, understanding mechanisms regulating walleye abundance in Lake Erie provides considerable insight into community structure and function. This understanding is critical to managers striving to maintain walleye populations at levels sufficient to achieve desired
community structure while satisfying demands of consumptive user groups. Managing to stabilize walleye year-class strength at high levels is essential to realization of these goals.

Maximizing the temporal breadth of larval production in the rivers likely would contribute towards stabilizing variability of walleye year-class strength. Spawning walleye are subject to intense angling pressure in the Maumee and Sandusky rivers. Because high larval survival can arise even from periods of low production, we feel regulations limiting angling pressure on spawners may increase walleye production. Specifically, early and late periods of walleye spawning should be protected from angling (even though these are relatively low-survival periods for larvae). Numbers of spawners are likely to be low during these periods; yet, they may produce high numbers of larvae. Given the episodic nature of factors regulating larval survival, maximizing larval production over the longest possible interval would increase the total number of surviving larvae. Small numbers of spawners could be severely influenced by high angling pressure, potentially contracting the temporal breadth of production. Angling might be limited to a 1 - 2 wk period during which spawner densities are highest, thus eliminating pressure when densities are low.

Lake Erie continues to be beset by lake-wide perturbations, such as changing nutrient status and invasions of exotic species. Further, even larger-scale perturbations, such as global warming, likely will influence formation of walleye year-classes by altering patterns of precipitation and stream flow. Precipitation events likely will increase in frequency and intensity during late-
winter and early-spring, resulting in greater and more variable stream flows (Nemec and Schaake 1982, Gleick 1987) during the critical larval stage. Thus, managers could expect a general decline in walleye year-class strength and, subsequently, population size in response to global warming, with strong year-classes becoming increasingly rare. However, these effects may be mitigated somewhat through watershed management. Improving land-use practices to reduce overland flow and sediment inputs would improve conditions for survival of larval walleye by reducing periods of extremely high discharges and turbidity. Holistic management policies, coupling watershed management with efforts to lengthen periods of larval production, may maintain consistent walleye year-class strength in spite of increasing climatic and ecosystem variability.

In our research, we employed a problem-solving approach (Parrish et al. 1995) toward management of Lake Erie fishes, where the “problem” is predicting year-class strength of a key species (walleye) and fish community structure in the face of a rapidly changing ecosystem. The “solution” is had by developing an understanding of ecological mechanisms underlying fish recruitment, such that feedbacks from ecosystem-level variability to fish communities could be anticipated and mitigated appropriately. In this way, basic ecological research on population- and community-level processes also can provide knowledge to assist managers in designing dynamic, proactive management policies.
LITERATURE CITED


Ohio Division of Wildlife. 1996. Ohio's Lake Erie Fisheries, 1995. Ohio Department of Natural Resources, Division of Wildlife, Columbus, OH.


Table 1. Hatch period, estimated annual production, and peak bay density of larval walleye in the Maumee and Sandusky rivers, Ohio, during 1993-95. Larval production was estimated by a model combining river volume, variability of larval density, and river discharge. Peak bay densities were estimated only from inner bay sample sites (see Figure 1) as these likely provide the most accurate reflection of numbers of larvae entering the bay from the rivers.

<table>
<thead>
<tr>
<th>System</th>
<th>Year</th>
<th>Hatch Duration</th>
<th>Production of Larval Walleye</th>
<th>Peak Bay Density (#/100 m³ ± 1 SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maumee River</td>
<td>1993</td>
<td>April 23 - May 16</td>
<td>April 29</td>
<td>20.4 ± 2.0</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>April 22 - May 24</td>
<td>May 1</td>
<td>13.4 ± 1.2</td>
</tr>
<tr>
<td></td>
<td>1995</td>
<td>April 19 - May 18</td>
<td>May 12</td>
<td>24.8 ± 2.0</td>
</tr>
<tr>
<td>Sandusky River</td>
<td>1993</td>
<td>April 21 - May 13</td>
<td>April 27</td>
<td>3.2 ± 1.5</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>April 18 - May 24</td>
<td>May 9</td>
<td>3.0 ± 0.2</td>
</tr>
<tr>
<td></td>
<td>1995</td>
<td>April 17 - May 16</td>
<td>May 11</td>
<td>0.8 ± 0.1</td>
</tr>
</tbody>
</table>
Table 2. Comparison of percentage of larval production and survival occurring during discrete annual periods of high larval survival to downstream sample sites in the Maumee and Sandusky rivers, Ohio, 1993-95. Periods of high survival were calculated as the minimum number of days needed to account for at least 75% of total survivors. Actual percentages of survivors from this subset of days is given in the last column. Production (estimated by a model described in the methods) is presented as the percentage of annual production occurring during each period. Durations of total production periods are given in Table 1.

<table>
<thead>
<tr>
<th>System</th>
<th>Year</th>
<th>High Survival Hatch Dates</th>
<th>Production (%)</th>
<th>Survivors (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maumee River</td>
<td>1993</td>
<td>April 27, May 2 - 4</td>
<td>25.5</td>
<td>81.8</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>May 1 - 7</td>
<td>41.3</td>
<td>75.6</td>
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<tr>
<td></td>
<td>1995</td>
<td>May 4 - 7</td>
<td>5.1</td>
<td>76.9</td>
</tr>
<tr>
<td>Sandusky River</td>
<td>1993</td>
<td>April 23, 25, 26, 28, 29, May 1</td>
<td>52.1</td>
<td>77.7</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>April 27 - May 1, 4</td>
<td>22.1</td>
<td>80.0</td>
</tr>
<tr>
<td></td>
<td>1995</td>
<td>April 29 - May 3</td>
<td>17.3</td>
<td>83.6</td>
</tr>
</tbody>
</table>
Figure 1. Up-, mid-, and downstream sample sites (indicated by black boxes) in the Maumee and Sandusky rivers and bays, Ohio, with approximate distances to the river mouth. In the bays, the three sites closest to the river mouths constitute "inner" bay sites whereas the three farthest from the river mouth constitute "outer" bay sites.
Figure 2. Zooplankton densities from up-, mid-, and downstream sample sites in the Maumee River and Sandusky rivers, Ohio, during 1993-95. Note that the y-axis scale differs for upstream panels.
Figure 2

Maumee River
Upstream
- 1993
- 1994
- 1995

Sandusky River
Upstream
- 1993
- 1994
- 1995

Zooplankton Density (#/L)

Midstream

Downstream

423.2

April 15 April 30 May 15 May 30 April 15 April 30 May 15 May 30
Figure 3. Comparison between the distribution of larval walleye production from upstream sites (open bars) and hatch-date distributions of survivors to midstream sample sites (filled bars) during 1993-95 in the Maumee and Sandusky rivers, Ohio. In each pair of panels, bars represent daily percentages of either total larval production (bottom panel) or total larval density attributable to individual hatch dates (top panel) as determined by otolith aging. Note the abbreviated period of high survival evident at midstream sites relative to the total distribution of hatch dates. Only relative x-axis scales are provided for river discharge; scale of y-axes are the same across years for each river but large differences in cross-sectional area of each river channel prevented using the same y-axis scale for both rivers.
Figure 4. Comparison between hatch-date distributions of survivors to mid- (filled bars) and downstream sample sites (hatched bars) during 1993-95 in the Maumee and Sandusky rivers, Ohio. Midstream hatch-date distributions are duplicated from Figure 3 to allow direct visual comparison with downstream hatch date distributions. In each pair of panels, bars represent daily percentages of total larval density attributable to individual hatch dates as determined by otolith aging. Only relative x-axis scales are provided for river discharge; scale of y-axes are the same across years for each river but large differences in cross-sectional area of each river channel prevented using the same y-axis scale for both rivers.
Figure 4
Figure 5. Relationship between daily index of survival of walleye larvae at mid- and downstream sites and river discharge for the Maumee and Sandusky rivers, Ohio, during 1993-95. River discharge was the mean daily discharge for the 5 d following each date for which we calculated survival, which integrated discharge conditions over outmigration for larvae hatching each day. Discharge also was normalized to allow direct comparisons between rivers by dividing discharge by the cross-sectional area of each river channel (Maumee River: 450.0 m$^2$; Sandusky River: 145.1 m$^2$).
Figure 5

Panel A: Midstream
- MR 1995 (N=30)
- SR 1995 (N=28)
- MR 1994 (N=28)
- SR 1994 (N=32)
- MR 1993 (N=22)
- SR 1993 (N=23)

Panel B: Downstream
- MR 1995 (N=30)
- SR 1995 (N=28)
- MR 1994 (N=28)
- SR 1994 (N=32)
- MR 1993 (N=22)
- SR 1993 (N=23)
Figure 6. Relationship between juvenile walleye catch per unit effort (CPUE, CDW 1996) bottom trawling from Lake Erie in August with peak density of larval walleye in Maumee and Sandusky bays, Ohio, 1993-95. Inshore estimates reflect CPUE at trawling stations of 3 m depth; offshore reflects trawling stations of 9 m depth.
Figure 6

Maumee Bay - Inshore
$R^2 = 0.99$
1993
1994
1995

Sandusky Bay - Inshore
$R^2 = 0.93$
1993
1994

Maumee Bay - Offshore
$R^2 = 0.99$
1993
1994
1995

Sandusky Bay - Offshore
$R^2 = 0.94$
1993
1994
Figure 7. Relationship between juvenile walleye CPUE (ODW 1996) from Lake Erie in August and mean daily discharge from the Maumee and Sandusky rivers, Ohio, during May, 1986-95. The years of this study are noted as filled circles. Inshore estimates reflect CPUE at trawling stations of 3 m depth; offshore reflects trawling stations of 9 m depth.
Figure 8. Conceptual model of generalized trends in river discharge and water temperature during the larval walleye hatch coupled with the spatio-temporal influence of river discharge, predation, water temperature, and zooplankton density on survival of larval walleye during river outmigration. Interactions between time of hatching (early-, mid-, and late-hatching) and river location (up-, mid-, and downstream) largely determine which mechanisms are most important in determining larval survival. Arrows indicate movement between sites of larvae hatched during different periods; arrow thickness indicates relative probability of larval survival (increased thickness = increased survival probability). Factors influencing larval survival at that location are listed next to each arrow. See text for a complete discussion of this figure.
Figure 8

River Discharge

Water Temperature

April 15
(Early-hatching)

UPSTREAM (hatch)

High Discharge Risk
Low Predation Risk

MIDSTREAM

Low Temperature
Low Food Availability

DOWNSTREAM
Low Survival Probability

May 1
(Mid-hatching)

UPSTREAM (hatch)

Low Discharge Risk
Low Predation Risk

MIDSTREAM

Moderate Temperature
Variable Food Availability

DOWNSTREAM
High Survival Probability

May 15
(Late-hatching)

UPSTREAM (hatch)

Low Discharge Risk
High Predation Risk

MIDSTREAM

High Temperature Risk
Variable Food Availability

DOWNSTREAM
Low Survival Probability