ABSTRACT

FULFORD, RICHARD S. Food web interactions of larval yellow perch, *Perca flavescens*, in Lake Michigan: implications for recruitment. (Under the direction of James Rice)

Variability in annual recruitment for many fishes is correlated with survival during the larval phase. Yellow perch in Lake Michigan have experienced sustained recruitment failure since 1990 and this has been blamed on low larval survival. Direct examination of factors important to larval yellow perch survival in Lake Michigan is complicated by the large size of the lake (52,000 km²) and the short length of the pelagic larval period (30-40 days). Individual-based modeling is a valuable indirect method for assessing the importance of multiple factors to larval survival. I used an individual-based modeling approach combined with field data collection to test four hypotheses regarding factors limiting survival of larval yellow perch in Lake Michigan. I tested whether larval survival is limited by prey community composition, size-selective predation, advection of larvae into offshore habitat or an interaction of these factors. I sampled larval and zooplankton abundance in Lake Michigan along a transect from 1 – 32 km from shore in 2000 and 2001. I conducted laboratory experiments to quantify larval vulnerability to predation by three typical predators as a function of both predator and prey size. I also conducted laboratory experiments to quantify larval selectivity for different zooplankton prey as a function of larval size and prey community composition. I used the results of these experiments to develop an individual-based model specifically to describe growth and survival of larval yellow perch. Field data suggest that larval yellow perch are being transported from the nearshore to the offshore zone
of Lake Michigan, but the timing of this transport varies between years. Model simulations in which the offshore prey community and the timing of larval advection were both varied suggested that larval survival will be highest in years when advection occurs within two weeks of peak hatch, allowing larvae to exploit offshore prey resources early during ontogeny. The model predicts that larvae will make foraging decisions based on prey availability as well as innate preference and they will change their diet if they are exposed to different prey communities. Model simulations also demonstrated that predation currently may not be an important factor for survival of larval yellow perch in Lake Michigan. This result is because alewife is the only fish abundant in Lake Michigan known to eat larval yellow perch. Experimental results suggest that alewife feeding rate on larval yellow perch is a positive function of larval density; yellow perch densities are currently too low to induce significant predation by alewife. Predation appears to be more important in smaller systems where larval densities are higher and larvae are exposed to other predator species. Larval survival in Lake Michigan appears to be primarily limited by an interaction of prey community composition and the timing during the larval period of offshore advection. Both factors vary between years and a good year-class is predicted when the offshore prey community is rich in cyclopoid copepods and larvae are advected offshore early. Early access to cyclopoid copepods results in an earlier transition from feeding on rotifers to feeding on copepods, which is predicted to increase larval growth and decrease mortality. These results suggest that survival of larval yellow perch in Lake Michigan is affected more by density-independent factors such as physical transport and prey community composition; Lake Michigan more closely resembles a marine environment than a typical lake with respect to larval recruitment processes. The unique aspects of larval yellow perch dynamics in Lake
Michigan must be considered when applying lessons learned from analysis of larval yellow perch in other lakes to understanding survival of larval yellow perch in a large meso-oceanic system like Lake Michigan.
FOOD WEB INTERACTIONS OF LARVAL YELLOW PERCH, PERCA FLAVESCENS, IN LAKE MICHIGAN: IMPLICATIONS FOR RECRUITMENT

By
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A dissertation submitted to the Graduate Faculty of North Carolina State University in partial fulfillment of the requirements for the Degree of Doctor of Philosophy

ZOLOGY

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DEDICATION

This work is dedicated to several important people. First is my wife who has born the trials and labor of this work right along side me. She has been an inexhaustible source of love and support without which none of this would have been possible. Love truly endures all things. The second is my father and through him all hearing impaired persons who came before me. They suffered the inequities of life for those who cannot hear and the misperceptions of a society that often did not listen. They fought so I would not have to, and many did not reap the rewards that have benefited my professional life. I truly stand on the shoulders of giants. To all of you I dedicate all that follows both herein and in the future….Watch me work.
BIOGRAPHY

Richard was born in Tulsa, OK and attended Booker T. Washington High School. His interest in the natural world started under the tutelage of Peggy Hill who loved to take her students wandering about the Oklahoma prairie looking for animal specimens. He attended the University of Oklahoma where he came under the influence of a professor of aquaculture and spent several wonderful years learning to raise and identify fish. In 1991, he graduated cum laude with a Bachelors of Science degree in Zoology. Then adventure called and he was off to Fiji as a Peace Corps Volunteer. While living the island life, Rich helped many people start fish farms and many other people finish cases of beer. After two and a half years, Rich gained the dubious distinction of being the only person ever to spend that much time in the South Pacific and not get a tan. He moved to Norfolk, VA in 1994 to begin graduate work at Old Dominion University with Dr. Ray Birdsong. Tragically, Dr. Birdsong developed viral pneumonia and died before Rich had been there a year. This tragic event resulted in a move to Louisiana State University to continue graduate work. While in Louisiana, Rich finished a Masters of Science degree in wildlife and fisheries and more importantly he found a wife. About two minutes after the wedding ceremony, he and his blushing bride were off to Milwaukee for a summer of field sampling on Lake Michigan as a part of his doctoral program at North Carolina State University. Splendid is the crooked path that brought me to you; happy are the memories that always get me through.
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Lake Michigan is the second largest of the Laurentian Great Lakes (Figure 1.1) and has historically supported many productive sport and commercial fisheries for species such as lake trout *Salvelinus namaycush* (Wells and McLain 1973), deepwater ciscoes *Coregonus* spp. (Wells and McLain 1973), and yellow perch *Perca flavescens* (Francis et al. 1996). However, the fish community of Lake Michigan has undergone dramatic changes over the last thirty years (Madenjian et al. 2002). Nutrient enrichment (Johengen et al. 1994), point and non-point source pollution (Madenjian et al. 1998), and thermal habitat alteration by power plant effluent have degraded nearshore habitat (Madenjian et al. 1986). Increased connectivity between the Great Lakes, coastal and foreign waters by international shipping has led to numerous invasions by non-indigenous species such as alewife *Alosa pseudoharengus* and the zebra mussel *Dreissena polymorpha* (Hatch et al. 1981, Fleischer et al. 2001). Finally, commercial and recreational overfishing has been blamed for dramatic declines in native fish stocks such as the deep water ciscoes (Wells and McLain 1973).

Responses to these issues have followed a pattern of public awareness, initial study of the problem, hypothesis development, hypothesis testing, and in most cases, a reevaluation of management intended to maximize the probability of lake recovery.

Yellow perch is native to the Great Lakes and is widely distributed from Wisconsin to New England and from central Canada to as far south as South Carolina (Jenkins and Burkhead 1994). Adult and juvenile perch are primarily demersal and are found in waters less than 35 m deep. They are a schooling species that moves into shallow, rocky habitat in the late spring to spawn. Perch females are unique in that they have only a single ovary and each female produces one long strand of eggs (i.e., skeine) each year. Age at first maturity is between 2-4 years, but is thought to have declined closer to 2 years in Lake Michigan since
1991 (Wisconsin Department of Natural Resources *unpublished data*). Perch skeines naturally settle on hard substrate on the lake bottom. Incubation time is 14-21 days at the typical seasonal water temperature of 10-15°C (R. Fulford *unpublished data*). Newly hatched yellow perch take about 1-2 days to enter the pelagic environment and they remain pelagic for 30-40 days post hatch (dph). The larval period is characterized by movement into deeper waters away from shore (Kelso and Ward 1977, Whiteside et al. 1985, Post and McQueen 1988). In larger systems like Lake Michigan, little is known about the distribution of perch during the pelagic larval phase. Recent large-scale cooperative sampling for larval perch strongly indicates that they disappear rapidly after hatching from waters within 2 km of shore only to reappear in nearshore waters as juveniles after 40-50 days (Clapp and Makauskas 2002). The juvenile phase begins with movement back into littoral habitat and a transition from zooplanktivory to a diet dominated by benthic invertebrates (Hubbs and Lagler 1964).

Yellow perch is the most popular recreational sport and commercial fishery in Lake Michigan. At its peak between 1985 and 1993 the commercial fishery caught more than 2.5 million pounds (Great Lakes Fishery Commission *unpublished data*) of perch a year and yellow perch represented more than 85% of the total sport catch lakewide. By 1994 there was wide-spread concern among managers due to a lack of observable recruitment since 1989, and after a campaign to raise public awareness of an impending crash the commercial fishery was closed and the sports catch was reduced to twenty-five fish per day (Francis et al. 1996).

Management of yellow perch in Lake Michigan has been called a 'multijurisdictional challenge' (Francis et al. 1996). Four state management agencies and one Native American
tribal agency have authority over fisheries resources in Lake Michigan, each with its own priorities and approach. This managerial mélange was brought to the forefront of public awareness by the reported lakewide decline in the perch population in 1994. Initial public support within states for reductions in both the sport and commercial fishery quota was low, due largely to the perception that management action by a single state that affected only part of the lake would not solve the problem (Francis et al. 1996). The official response to this finding was the formation of the Yellow Perch Task Group (YPTG) by the Lake Michigan Technical Committee of the Great Lakes Fishery Commission. The YPTG was an effort in lakewide cooperation to investigate the perch problem and it had two charges: improve data sharing and communication between agencies, and assess the spatial discreteness of the stock.

One result of improved communication and data sharing among member agencies was an understanding of what we needed to know in order to clarify the causes of the observed recruitment failure for yellow perch. The YPTG outlined 17 primary hypotheses that they considered most important for identifying causes of yellow perch recruitment failure (Table 1.1). These hypotheses represented knowledge gaps in yellow perch population dynamics in Lake Michigan and ranged from biotic factors such as predation to abiotic factors such as temperature and damage from ultraviolet light penetration. However, members of the YPTG agreed on two things. First, the observed population decline was the result of sustained recruitment failure. Second, this recruitment failure was most likely due to a decrease in survival during the larval phase of life. This hypothesis was based on the observation that no strong year class had been produced since 1989 and that the egg and larval abundance in the spring did not shown signs of decline until 1996 (John Dettmers,
Illinois Natural History Survey *personal communication*). The egg and larval stage is also the life history period for which researchers had the least information (Clapp and Makauskas 2002). My research has been a part of the cooperative effort to address these 17 relevant hypotheses and possibly narrow the list to a set of key components important to larval perch survivorship and recruitment. Members of the YPTG devised a cooperative sampling plan to assess the lakewide distribution and abundance of larval yellow perch. This plan included seven sampling sites around Lake Michigan that have been sampled annually since 1998 (Figure 1.1). The research contained in this dissertation concerns sampling conducted at two sites: main body of Lake Michigan near Milwaukee, WI and Little Tail Point in southern Green Bay. Sampling at other sites was conducted by other agencies and while data from all sites were combined for separate analyses, no data from these other sites are included here.

It has been stated that the average fish is dead within a week (Sharp 1987). This seemingly innocuous statement holds great importance for fishes such as yellow perch that display high variability in annual recruitment. Mortality during the larval phase of life for fishes is frequently very high, so relatively small changes in larval survivorship can translate to large differences in year-class strength (Sissenwine 1984, Houde 1987). Many factors can be important to larval survival including predation (Cowan and Houde 1992), food density and quality (Cushing 1990, Sogard 1994), cannibalism (Brabrand 1995), temperature variability (Field and Butler 1994), and advection (Hare and Cowen 1996). However, finding the ‘smoking gun’ necessary to understand and reverse recruitment failure in specific fisheries, such as Lake Michigan yellow perch, can be complicated because factors that impact recruitment commonly interact in complex ways, with the importance of particular
factors changing over both temporal and spatial scales. An understanding of these interactions is necessary to make better use of recruitment data for management.

The analysis of larval population dynamics is further complicated by larval size, short larval stage and high mortality rates. The larvae of fish such as yellow perch are small (<6 mm at hatch) and easily dispersed from their initial hatching area by directional currents and simple Fickian diffusion (Smith and Stoner 1993, Ramzi et al. 2001). These conditions make detection of factors important to survival from field samples extremely difficult. Further, because of the short phase duration and high mortality of larvae the window of effective field sampling is small (<1 month). Finally, the complex nature of interacting factors during the pelagic larval phase makes comprehensive laboratory experiments prohibitive. Under these conditions, it has proven productive to take an indirect approach to understanding patterns in larval fish survival. In particular, it is useful to ask whether the relatively small numbers of survivors from the larval phase are a random sub-group of the original population, or do they possess particular characteristics that make them unique? This ‘Characteristics of Survivors’ approach has strong potential to provide results in cases like fish recruitment where the ‘average’ individual often does not survive (Rice et al. 1987b).

One methodology that has shown promise for our understanding of characteristics of larval survivors is individual-based modeling (IBM). Individual-based modeling differs from more traditional population modeling in that it tracks individual fate and then uses the characteristics of survivors to describe the recruited population (DeAngelis and Rose 1992). This approach has several advantages over a conventional modeling approach. First, it creates mechanistic links between extrinsic factors and larval survival. The IBM approach is based on understanding how factors like predation, foraging success, and temperature impact
larval growth and survival. These relationships can then be expressed explicitly in the model and used to predict how survivorship is affected by observed annual variability in these factors. The second advantage is that factors can be added to the model sequentially to allow for a layered examination of their relative effect on larval survivorship. As factors are added to the model, nested model results can be continually compared to field data to address whether a particular layer of complexity is important to population variability or is unimportant detail. Finally, IBM results are more likely than a population modeling approach to generate testable hypotheses regarding factors important to recruitment variability, because the IBM approach is based on mechanistic links between larval characteristics and survival.

The shortcomings of individual-based models are that they are complex, involve a high number of parameters, require larger amounts of data input and cannot be solved analytically (Murdoch et al. 1992). While the simplest answer is often the best, it is also important to address whether the flexibility of an IBM approach will generate more meaningful results for a particular problem (DeAngelis and Rose 1992). The most direct examination of the appropriateness of the IBM approach is to ask whether the IBM approach has been fruitful for similar fishery problems in the past. The IBM approach has been used successfully to investigate recruitment variability in many larval fishes including bloater, *Coregonus hoyi* (Rice et al. 1987b), Colorado squawfish *Ptychocheilus lucius* (Bestgen et al. 1997), bay anchovy *Engraulus mordax* (Cowan et al. 1996), American shad *Alosa sapidissima* (Crecco and Savoy 1985), and capelin *Mallotus villosus* (Pepin et al. 1992). Moreover, the individual-based modeling (IBM) approach focused on identifying important characteristics of survivors has been successful in disentangling the complex interactions of
multiple factors important to a general model of larval recruitment (Letcher et al. 1996, Rice et al. 1997, Paradis et al. 1999).

In the following chapters, I will use a combination of laboratory experiments, field data collection and an IBM approach to address four of the 17 hypotheses concerning survivorship of yellow perch during the pelagic larval phase. First, I will address the hypothesis that larval survivorship is limited by size-selective predation. Research in smaller systems has demonstrated that larval yellow perch can be a significant component of the diet of fish predators (Mason and Brandt 1996, Mayer et al. 2000). Predation on larval fishes is often described as being size selective in that vulnerability initially rises as larvae become larger and more active, reaches a maximum and then drops off as larvae become more capable of predator avoidance (Cowan and Houde 1992, Pepin et al. 1992).

Yet, little is known about predation vulnerability of larval yellow perch in a large, open system like Lake Michigan. A body of indirect evidence suggests that high densities of alewife can affect perch recruitment. Crowder (1980) found that the introduction of alewife into Lake Michigan was temporally correlated with a decline in the abundance of several native fishes, all of which had pelagic eggs or larvae that would be vulnerable to alewife predation. Moreover, in Indiana waters of Lake Michigan, high alewife abundance during the larval period for a yellow perch cohort can explain as much as 70% of the annual variation in abundance of that year class at age two (Shroyer and McComish 2000). Finally, high incidence of larval perch in alewife stomachs was observed in a small embayment of Lake Ontario when alewife presence coincided closely with high densities of 7-9 mm perch larvae (Mason and Brandt 1996). There is also growing anecdotal evidence that predation by other species such as white perch, *Morone americana*, may be important to larval yellow
perch survival in Green Bay, an embayment of Lake Michigan (Wisconsin Department of Natural Resources *unpublished data*).

These data suggest that predation may be an important factor controlling yellow perch survival during the larval stage in Lake Michigan. In chapter two I will use a series of laboratory experiments to explore the relationship between predator and prey relative size and larval yellow perch vulnerability to predation for a suite of predators common in the Lake Michigan system. I will use these data to build a predator-prey IBM to describe larval vulnerability to predation as a function of size and size variability. I will then use the model to ask if current conditions of larval and predator size and abundance in Lake Michigan support the predation hypothesis. In chapter four, I will expand this analysis to include natural variation in larval growth, and use the IBM to compare characteristics of survivors between adjacent year-classes of larval yellow perch in Green Bay. In this analysis I will ask two relevant questions: what factors appear most important to larval predation mortality in a particular year and is the IBM useful for identification of these factors in general?

The second hypothesis I will address is that larval survivorship is limited by the composition of the prey community. After predation, the most commonly cited form of mortality for larval fishes is starvation. The onset of first feeding occurs early for most freshwater fishes prior to the full recruitment of sensory systems or swimming ability (Blaxter 1986, Fuiman et al. 1998). Larval energetic reserves are usually quite low once the yolk-sac has been absorbed, which means that the window of opportunity for successful foraging and the avoidance of starvation can be small (Cushing 1990). Further, if foraging occurs but the prey community is deficient in optimal food resources, this may be manifested
as slow growth rates and an increased period of vulnerability to size-selective predation (Houde 1987, Rice et al. 1987a, Boisclair and Leggett 1989).

Prey resources can vary at many spatial scales from meters to kilometers. In chapter three I will use a series of foraging experiments to explore ontogenetic changes in prey selection based on both larval size and prey community composition. I will then use these relationships in build a larval foraging and growth IBM to predict how large-scale changes in foraging habitat may interact with ontogeny to affect larval growth.

The third hypothesis I will address is whether physical advection processes in Lake Michigan limit larval survivorship. Larval fishes are characterized as weak swimmers and highly intolerant to rapid changes in water temperature (Field and Butler 1994, Fuiman et al. 1999, Keller and Klein-MacPhee 2000). These observations suggest that early-stage larvae may be vulnerable to passive transport away from spawning grounds caused by episodic wind and current events, and may benefit from remaining in a water mass moving offshore if it exposes them to a more constant temperature regime. Further, larval yellow perch have been observed to actively leave the littoral zone during the larval stage (Post and McQueen 1988).

If larvae are readily advected out of nearshore habitat in Lake Michigan, than the relationship between advection and larval growth and survival needs to be better understood. Advection and migration are important to variation in survivorship for larvae of other species such as capelin Mallotus villiosus (Leggett et al. 1984), Atlantic cod Gadus morhua (Aadlandsvik and Sundby 1994), sole Solea solea (Ramzi et al. 2001), and walleye pollock Theragra chalcogramma (Kim and Kendall 1988). Advection can affect survival of larval fishes, but the impact of advection is dependent on whether or not larvae experience changes
in habitat quality because of advection. Advection has not been well addressed as a factor affecting survival of larval yellow perch, and it has potential to be important for larval yellow perch in Lake Michigan.

One reason larval advection has not received close attention for yellow perch is the small size of the pelagic habitat in most systems where yellow perch populations have been more thoroughly studied. Larval perch populations have been well studied in systems such as Oneida Lake, NY (Roseman et al. 1996) and the western basin of Lake Erie (Ludsin et al. 1999), as well as many smaller lakes throughout North American (Bulkley et al. 1976, Kelso and Ward 1977, Whiteside et al. 1985, Post and McQueen 1988). However, Lake Michigan is unique in being larger (52,000 km²), longer (494 km), deeper (mean depth 89 m) and generally more open than most other fresh-water systems containing yellow perch.

Several researchers have described the impact of episodic physical events such as upwelling on the movement of water around Lake Michigan (Mortimer 1971, Beletsky and Schwab 2001, Beletsky et al. 2003). Research has shown that variation in the periodicity and severity of upwelling in open marine systems can have a large impact on the transport fate of pelagic larval fishes (Heufelder et al. 1982, Bjorkstedt et al. 2002). If larval yellow perch are being transported out of the nearshore region of Lake Michigan, how does this transport impact the likelihood of survival for individual larvae?

In chapter five I will use a linked foraging/growth/predation IBM based on work from chapters two and three to address possible consequences of offshore advection for pelagic larval perch. I will examine how changes in prey community composition and water temperature between the nearshore and offshore zones of Lake Michigan interact with size-dependent vulnerability to predation to affect larval growth and survivorship. Is offshore
advection beneficial to larval perch survival, or are they truly ‘lost in the wilderness’ as some suggest (Clapp and Makauskas 2002)?

The final hypothesis I will address is the notion of a synergistic effect on larval survival of predation, foraging success and advection. In the final chapter, all of the data and conclusions generated in the preceding chapters will be brought together to address the question of how and when these factors interact to have a combined effect on larval perch survival. I will also address the question of which of the YPTG-generated hypotheses addressed here appear important to yellow perch larval survival based on the data, and can we narrow the list. If we can identify the hypotheses most important to larval recruitment, we can use these data to focus future research and develop management practices that maximize the likelihood of population recovery for yellow perch in Lake Michigan by improving the stability of larval survival. Ultimately these actions can improve the prospects for long-term sustainability of the fishery.

Literature Cited


Table 1.1. Major hypotheses for population decline of yellow perch after 1991 in southern Lake Michigan as compiled by the Lake Michigan Yellow Perch Task Group. Hypotheses in bold are addressed in this dissertation.

1) **Alewife predation on larval perch is limiting recruitment**
2) Zooplankton density limits recruitment of larval yellow perch
3) Water temperature affects early-life stage success
4) **Advection limits recruitment of juvenile yellow perch**
5) Inappropriate diet (nutrition) is limiting pre-demersal survival
6) **Zooplankton size and composition limit recruitment of larval yellow perch**
7) Increased water clarity increases alewife predation on larvae
8) Larval perch are starving to death
9) Reduced primary productivity affects larval foraging
10) Post yolk-sac fry survival is limited by a lack of swim bladder inflation
11) Embryonic mortality is limiting recruitment
12) Gamete quality is limiting recruitment
13) Stock-recruitment relationship is limiting recruitment
14) Disease is limiting pre-demersal survival
15) Contaminants are limiting survival of early-life stages
16) Weather is limiting pre-demersal survival
17) **Synergisms effectuate mortalities which limit recruitment**
Figure 1.1 Map of Lake Michigan showing regional orientation and the location of Yellow Perch Task Group (YPTG) sampling sites. Sites in black were sampled as a part of this study and sites in gray were sampled by other YPTG projects or agencies.

Yellow perch, *Perca flavescens*, in Lake Michigan have experienced sustained recruitment failure since 1990 due to increased mortality during the pelagic larval phase. Increased mortality of larval yellow perch has been tied indirectly to increased predation by alewife, but importance of predation to changes in larval recruitment must be better understood. I compared the relative importance of predation by alewife, *Alosa pseudoharengus*, white perch *Morone americana*, and adult yellow perch to larval survival in laboratory experiments and developed a multi-cohort individual-based predation model (IBM) optimized for examining patterns in size-dependent vulnerability to predation. Simulations exposing larval perch to predation by all three predators suggest that larval mortality due to alewife predation is more size dependent than predation mortality due to the other two predators and the range of sizes vulnerable to alewife is smaller. Predation by alewife may not be an important source of mortality for larval yellow perch in Lake Michigan at present due to the narrow range of vulnerable sizes and the low densities of larval perch in the open lake. Predation is more likely to be important in smaller, more productive systems where other predators species are also abundant. Modeling results also indicate that analysis of hatchdate distributions of surviving larvae in an individual-based model is a valuable tool for identifying factors most important to larval survival.
Introduction

Annual recruitment variability in fishes is often significantly affected by survival during the larval phase. Cumulative larval mortality can be 99% or more and relatively minor changes in this value can translate to large differences in the size of an annual cohort (Sissenwine 1984, Houde 1987, Houde 1989). One consequence of high mortality rates is that traditional approaches to analyzing patterns in survival based on the average characteristics of a cohort can be misleading because the 'average' larvae often does not survive (Sharp 1987). Instead, it may be more informative to ask whether the survivors of the larval phase are a random sub-group of the population or are a non-random group that possesses some inherent advantage when compared to other members of the cohort. In cases where selective mortality occurs, an analysis of the change in key characteristics of survivors has proven valuable for detecting the causes of selective mortality in larval fishes (e.g., Crecco and Savoy 1985, Rice et al. 1987, Leggett and Deblois 1994).

Larval mortality is typically size-dependent (Miller 1988, Sogard 1997). In particular, size dependent vulnerability to predation follows a complex pattern that is dependent on interactions between characteristics of both predators and their larval prey (Luecke et al. 1990, Cowan and Houde 1992). Factors that contribute to size variability within a larval cohort are an important part of this interaction (Rice et al. 1993).

Analysis of factors affecting size-dependent mortality in larval fishes is difficult because selective forces are hard to detect from field data (Miller 1997) and appropriate factorial experiments are often prohibitive due to time and expense. One approach that has born fruit in the past is the use of individual-based simulation models (IBMs). Individual-based models track individual members of a virtual cohort through time in order to better
understand how individual variability may interact with extrinsic factors to affect individual probability of mortality, and consequently cohort survival. Examination of general patterns in larval survival with IBMs has established several common threads such as the fact that the intensity of size-dependent vulnerability to predation in larval fishes can vary greatly based on changes in larval growth rate (Rice et al. 1993) and between predator types (Cowan et al. 1996).

In addition to growth rate variability, an often overlooked and potentially important source of size variability for a larval cohort is variation in individual hatchdate. Hatchdate often varies by days or weeks resulting in size differences among larvae due to differences in the amount of time they have had to grow. Interaction of growth rate and hatchdate may yield complex patterns in size variability. For instance, larvae with high growth rates should be less vulnerable to mortality than slower growing larvae hatched on the same day (Rice et al. 1993). However, a fast growing, late-hatched larva may be more vulnerable than a slow growing, early-hatched larva to predation occurring later in the larval period simply because the latter has had more time to grow and is therefore bigger. Previous analyses of size-dependent predation vulnerability in larval fishes have focused on variation in growth as a source of intra-cohort size variability (Rice et al. 1993, Letcher et al. 1996a). However, timing of hatch may be as important, or more important, than growth rate in the development of size variability within an annual larval cohort. In general, it is important to understand how all aspects of size variability contribute to size-dependent predation vulnerability in order to better understand variation in annual recruitment.

Hatchdate variability contributes to size variability, but individual hatchdate is also a stable characteristic of individual larvae, and changes in the hatchdate distribution can be
directly observed in a natural cohort (Rice et al. 1987, Schultz 1993, Mion et al. 1998).

Therefore, an individual-based model that includes hatchdate as a larval characteristic may be a valuable tool for linking patterns of change in hatchdate frequency with patterns of change in individual survival.

For instance, Rice et al. (1987) observed in an analysis of individual characteristics of larval bloater Coregonus hoyi that larvae hatched later in the larval period were over-represented in the hatchdate distribution of survivors, which indicated a survival advantage for later-hatched larvae by the end of the larval period. They attributed this survival advantage to higher growth rates observed for these later-hatched larvae, as size-dependent vulnerability to predation would decline more rapidly and be significant over a shorter period for faster growing larvae. The observed survival advantage for later-hatched bloater larvae is likely associated with observed higher growth rates, but other factors may have also been important in determining larvae survival. Any conditions that resulted in decreased mortality for later-hatched larvae relative to larvae hatched earlier would have contributed to this pattern.

A comparison of all potential contributing factors in a modeling framework could be more informative regarding the importance of particular factors than is possible from field data alone. In particular, the inclusion of variation in individual hatchdate in an individual-based model may allow for a clearer understanding of factors that cause observed patterns of change in hatchdate distributions; this would be a valuable tool for the interpretation of field data for characteristics of larval survival.

Variation in the timing and intensity of size-selective predation is likely to affect the relationship between larval probability of survival and hatchdate. Predator density can vary
significantly over the larval period for yellow perch resulting in differences in predation vulnerability over time for individual larvae due to changes in encounter rate with predators. Brandt et al. (1987) observed that alewife predation on larval yellow perch in an embayment of Lake Ontario occurred in a predation pulse associated with larval emergence rather than being constant over time. Further, the timing of this pulse affected its significance to larval survival. They found that alewife predation on larval yellow perch was significantly higher in a year when the timing of inshore migration for alewife occurred about two weeks after peak hatch for yellow perch, compared to years when alewife arrived later in the larval period. Early in the larval period variation in individual hatchdate is much more important to cohort size variability than variation in growth rate. If a predation pulse occurs during or soon after the hatching period has ended, larval size and vulnerability to size-dependent predation will be more dependent on variability in hatchdate than growth rate. Therefore if predator densities vary over time during the larval period for yellow perch this may make larvae hatched at particular times more vulnerable to predation than larvae hatched earlier or later in the hatching period. It is important to be able to distinguish the effects of a predation pulse on the hatchdate distribution of survivors from the effects of other factors such as growth rate variability in order to assess the importance of predation variability in determining larval survival.

My objective was to investigate patterns of size-dependent predation vulnerability for larval yellow perch, *Perca flavescens* in Lake Michigan. Yellow perch are a freshwater fish distributed throughout the Great Lakes region (Hubbs and Lagler 1964). Population levels of yellow perch in Lake Michigan have been highly variable over the last 30 years and have been in decline since 1990 (Francis et al. 1996). The present decline is widely thought to be
the result of increased mortality during the larval phase (Clapp and Makauskas 2002).

Increased vulnerability to size-dependent predation is one primary hypothesis for reduced survival during the larval stage. In particular, indirect evidence suggests predation by alewife, *Alosa pseudoharengus*, may be a significant factor limiting survival of larval yellow perch in Lake Michigan (Shroyer and McComish 2000). However, examinations of alewife diet in Lake Michigan have provided no direct evidence that larval yellow perch are a significant prey item for alewife (Clapp and Makauskas 2002). An IBM designed to identify links between observed patterns in characteristics of larval survivors and factors important to larval mortality would be of great benefit for identifying when size-dependent predation is likely to be important to recruitment and when it is not.

I evaluated the importance of size-dependent predation on yellow perch with this approach, using a predator-prey individual-based model that takes into account variability in both growth rate and hatchdate, as well as differences in size dependence of predation among three typical predators in Lake Michigan. Moreover, I used this individual-based model to examine changes in the hatchdate distribution of survivors resulting from two typical patterns of size-dependent mortality: changes in mortality due to changes in larval growth rate and due to changes in the timing and intensity of size-selective predation. Changes in the timing and intensity of predation are hypothesized to increase the importance of hatchdate in determining the predation vulnerability of individual larvae. I simulate a 5-day predation window in the model and look for differences in the hatchdate distribution as a function of when during the larval period the predation window occurs.

I conducted a series of laboratory experiments to quantify size-dependent vulnerability of larval yellow perch to three natural predators: alewife, white perch, *Morone*
*americana*, and adult yellow perch. I also examined how these relationships are affected by larval condition, larval density and the presence of alternative prey. I used these data to assess the hypothesis that predation limits survival of larval yellow perch in Lake Michigan. I also used these data to build a predator-prey IBM and used the model to analyze general patterns in hatchdate distribution resulting from size-dependent predation and whether these patterns may be useful for interpretation of hatchdate distributions of larval yellow perch survivors in Lake Michigan.

Methods

Larval yellow perch used in all of the experiments were hatched in the laboratory from egg skeins stripped and fertilized in the field during May from 1999 – 2001. These skeins were collected from ripe females captured in gill nets during the peak of spawning for yellow perch in Lake Michigan waters near Milwaukee, WI. Each female produces one skein per year. Up to ten skeins per day were collected over two sampling days and individually fertilized in the field with the milt from 3-6 males. Fertilized skeins were returned to the Great Lakes WATER Institute Aquaculture Lab and placed on plastic platforms in a 2.4-m diameter tank with minimal flow and ambient temperature conditions (10-11°C).

Beginning two days after egg fertilization, temperature was raised 1°C every other day until hatching was observed. This procedure decreases development time and increases hatching success in the laboratory (Fred Binkowski *unpublished data*). Hatching began within 10-14 days and larvae were maintained in the same tank at 15°C under flow-through conditions for the duration of the experimental season. Larvae were fed a staged diet
beginning with small cultured zooplankton, and followed by *Artemia* nauplii, ground up beef liver and finally a commercial pellet feed over the experimental period. A staged feeding protocol has been shown to maximize growth and survival for yellow perch larvae in the lab (Fred Binkowski *unpublished data*).

Predators used in these experiments were adult alewife, adult white perch and adult yellow perch. In the fall of the year preceding the experiments, juvenile alewives were captured with beach seines in water less than 1.5-m deep from various sites near Milwaukee, WI and maintained in the laboratory until the following spring. Adult white perch were captured with gillnets in Green Bay, WI in the late fall and maintained in the laboratory until the following spring. Yellow perch were available in the laboratory from previous years’ spawning activities (described above). All predators were maintained at 15°C in flow-through systems and fed a maintenance ration of commercial, pelleted food until the beginning of the experimental season.

*Probability of Capture* – This experiment was conducted in June-July 1999 and June-July 2001. In 1999 an experimental system was set up comprised of eight 145-L rectangular tanks each with a glass observation panel on one side. The tanks were isolated visually by surrounding them with a black plastic curtain. Each tank was covered with an opaque plastic lid fitted with a PVC tube extending from above the tank through the cover and into the tank interior. This tube was used to introduce fish larvae without disturbing the predators in the tank.

At the beginning of the acclimation period, each tank received five predators of a single species. White perch (150 – 193 mm TL) were placed in four tanks and adult yellow perch...
perch (144 – 157 mm TL) were placed in the other four; tanks were randomly assigned to species. Total length of each individual predator was measured to the nearest 1 mm prior to introduction. These predators were allowed to acclimate to the tank for 7 d prior to the beginning of a trial. Trial tanks were maintained at 17°C and a mean flow of 3.5 L/min. The acclimation period included the introduction of yellow perch larvae as a food source to re-acclimate the predators to live food. During the acclimation period, the fish were not disturbed unless a predator died and had to be removed. Predator mortality typically occurred only in the first 1-2 days after transfer. All feeding was conducted via the feeding tube, and all feeding was halted 24 hours prior to the beginning of an experimental trial.

At the beginning of an experimental trial 25-50 yellow perch larvae were introduced into an individual test tank. From the moment of introduction, an observer watched all activity in the tank through a small observation hole cut into the black plastic screen. A second participant stood behind the tank to introduce larvae through the PVC tube, keep time and record all observations. The observer would pick a single predator in the tank and verbally identify successful and unsuccessful strikes for 30 seconds; these strikes would be recorded by the second participant. At the end of 30 seconds, the observer would arbitrarily choose another predator and repeat the process. This single-predator observation method was used to minimize overestimation of capture success due to observer bias. Each trial lasted 30 minutes: an additional 25-50 larvae were introduced through the tube if larvae in the tank were more than 75% depleted prior to the 30-minute mark. If less than ten strikes were observed in any 30-minute trial, then that trial was not used for analysis. This procedure was then repeated in sequence for the remaining seven experimental tanks. Trials were conducted with larval yellow perch prey at 7 days post hatch (Mean TL 7.5 mm, SD
0.43 mm), 15 dph (9.2 mm, 0.82 mm) 30 dph (12.8 mm, 1.29 mm) and 45 dph (23.0 mm, 1.78 mm).

During pre-trial observations in 1999, I established that alewife would not acclimate to the rectangular tanks and begin feeding within a reasonable time. For this reason, alewife trials were conducted in 2.4-m diameter round tanks. I also noted that normal feeding activity was observed more often if alewife were kept in larger groups, so alewife trials were conducted with groups of 50 – 100 alewives per tank (113 – 180 mm TL) rather than five as with white perch and yellow perch. Alewife trials were conducted June-July 2001 in a manner similar to that described for other predator species, with the exception that a larger number of yellow perch larvae were introduced into each tank to maintain a comparable larval density between trials.

On all trial days a random sample of 25 larvae were removed from the main population and euthanized with MS-222. Total length was measured for each larva with an ocular micrometer to the nearest 0.1 mm. Mean TL from these larvae was used as the larval length for each trial tank on that day. Data from this experiment were predator capture success, defined as the number of successful strikes divided by total strikes, for each tank.

I used these data to test for a significant relationship between capture success and predator/prey size ratio. I also wished to establish whether this relationship differed among predator species. Two model functions were tested for best fit with a least squared deviation method and compared with a coefficient of multiple determination adapted to account for differences in the number of parameters in a particular model function ($R^2_a$, Neter et al. 1990). The parameter-weighted $R^2_a$ is comparable to the Akaike’s information criterion (AIC) parameter for comparing non-nested models, but allows for a clearer interpretation of
absolute model fit than is possible with AIC. The first model function was a logistic regression, which has two parameters and is the generally accepted approach for analysis of binary-type data such as capture success (Pampel 2000). The second model function was an inverse negative exponential model that has three parameters and has been used to describe the relationship between predator-prey relative size and capture efficiency for larval prey (Miller 1988). The Logistic model was fit to the data with the Logistic procedure in SAS (SAS 2002). The Miller model was fit to the data in the NLIN procedure with the Marquardt method of nonlinear estimation (SAS 2002). For both analyses data were weighted by the number of strikes observed in each replicate. Both models were fit to data for all predators combined and also to data for each predator species separately. I chose the best model fit for the data based on which modeling approach (Logistic vs. Miller and all data vs. predator-specific) resulted in the highest $R^2_a$ values. For the predator-specific models I also examined differences in the size-vulnerability relationship among predators based on changes in the model parameter estimates among predators.

*Condition-dependent selection* – Twelve 589-L round experimental tanks were set up in two sets of six and visually isolated behind a black plastic curtain. At the beginning of the acclimation period, ten yellow perch (144-157 mm TL) were placed in each of the six tanks in the first set and 20 alewives (110 – 180 mm TL) were placed in each of the six tanks in the second set. The TL of each predator was measured to the nearest 1 mm prior to this introduction. Predators were then allowed to acclimate to the trials tanks for seven days. This acclimation period included the introduction of yellow perch larvae as a food source to
re-acclimate the predators to live food. Predators were not otherwise disturbed except to remove any dead fish. All feeding ceased 24 hours prior to the experimental period.

On the same day that predators were moved into the trial tanks, 500 yellow perch larvae were removed from the main population and split between two 47-L aquaria. Temperature in the aquaria was maintained at 17°C with a flow of 0.3 L/min. These larvae were fed a similar ration as the main population and allowed to acclimate for two days, then were starved for the remaining five days prior to trials. A five-day starvation period caused a significant decline in larval nutritional condition without 100% mortality (Heyer 2000). On several occasions during the starvation period cannibalism by larger larvae on their smaller con-specifics was observed. In order to maintain a representative starved group, all cannibals were excluded from the trials.

During this five-day starvation period, otoliths of the starved larvae were marked with alizarin complexone (Letcher et al. 1996b). In order to minimize larval mortality due to excessive handling or an interruption of flow in the aquarium, the alizarin was introduced to each aquarium at 25 mg/L and flow was adjusted so that the alizarin was slowly diluted out of the system over twelve hours. In preliminary trials, this protocol resulted in a reliable mark being placed on otoliths that could be used for identification (R.S. Fulford unpublished data).

On each trial day a random sample of 25 starved, alizarin-marked larvae (hereafter 'starved larvae') were combined in a glass beaker with a random sample of 25 larvae from the main population that had been fed normally during the acclimation period. A trial was started by introducing this mixed group of larvae into one of the twelve experimental tanks selected at random. The predators in this tank were then allowed to feed for 30 minutes to 1
hour. The length of each trial was adjusted to insure a minimal amount of feeding activity but to stop the trial before excessive feeding masked the selective signature (i.e., predators may 'select' a larval type first but then continue eating, thereby eliminating evidence of selection). The target was a maximum of 50% consumption per trial. Trials were limited to one hour or less based on data suggesting larval yellow perch become hard to identify in predator guts after 1.5 – 2 hours (Appendix 2). All trials were observed in order to make these adjustments.

At the end of the feeding period, the predators were immediately removed from the tank and euthanized with MS-222. They were then placed on ice and their guts were removed and preserved in 95% ethanol for analysis. This procedure was repeated for each trial tank in random order. On each trial day, 25 larvae from both the main population and from the starved sub-group were euthanized in MS-222 and their total length was measured to the nearest 0.1 mm with an ocular micrometer. These data were used to calculate mean and standard deviation of larval size for each trial tank on that day. Experimental trials were conducted for larvae at 15, 30, 45 and 60 dph.

In the lab, all larvae were removed from the guts and both saggital otoliths were removed from all ingested larvae. These otoliths were observed immediately for an alizarin mark, which is clearly visible on freshly removed otoliths. The numbers of larvae with marked and unmarked otoliths consumed in each trial tank were analyzed for differences in percent occurrence of starved larvae in the guts with a Chi square analysis (Neter et al. 1990).

Alternative prey – Twelve 589-L round tanks were used in all trials involving alewife as a predator (hereafter 'alewife tanks'), and twelve 147-L rectangular tanks were used in all trials
involving yellow perch as a predator (hereafter 'perch tanks'). The use of different tanks was a compromise based on available space and previous observations regarding tank type and predator acclimation success. Both tank sets were visually isolated behind black plastic curtains.

Twenty alewife (110 – 180 mm TL) or eight adult yellow perch (144-157 mm TL) were placed in each tank within the respective sets and were maintained at 17-18°C with constant flow throughout the acclimation and experimental period. Flow in both tank types was maintained to allow for four complete exchanges of water per day. During the 7-day acclimation period, predators were not disturbed except to remove any dead fish. They were fed yellow perch larvae twice per day during the acclimation period to recondition them to a live food source. All feeding stopped 24 hours before the beginning of experimental trials. Tanks within each species block were randomly assigned to one of six possible treatments (zooplankton present/absent X Larval density 0.02, 0.09 or 0.16 mg/l).

Zooplankton used as alternative prey were collected once per week in Lake Nagawicka (surface area 3.7 km², mean depth 11 m), an inland lake located about 30 miles west of Lake Michigan near Milwaukee, WI. Zooplankton were collected by towing a 0.5-m diameter, 64-µm mesh plankton net 1 m below the surface for 10 minutes at a site in the middle of the Lake (site depth 30 m). Zooplankton was maintained in the laboratory with mild aeration until needed for experiments.

Collected zooplankton were filtered at 300 µm to remove small zooplankton from the assemblage prior to its use as alternative prey. Prior to the beginning of experimental trials, a mass-density relationship was established for the filtered zooplankton to ease the process of standardizing zooplankton density between trials. This mass-density relationship was
established by weighing out standard aliquots of zooplankton on a 64-µm filter and then counting the zooplankton in each aliquot under a dissecting microscope. Zooplankton density was set at 100 organisms per liter for all trials in the experiment. The mass-density relationship was calculated three times during the experimental period to adjust for any changes in zooplankton species composition.

Trials were initiated by introducing prey into the tank according to treatment. For tanks receiving only larvae, the required number of larvae was poured into a length of PVC pipe plugged with a rubber stopper mounted on a plastic rod. The pipe was lowered slowly into the tank until the bottom reached a depth of about 20 cm, and the larvae were introduced by forcing the stopper downward with the rod. For tanks receiving a mixture of larvae and zooplankton, a pre-weighed aliquot of zooplankton was added to the tube along with the larvae and introductions to the predator tank were done in a similar fashion. Trials were conducted one tank at a time in random order. Once prey were introduced to a tank, predators were allowed to feed for a pre-set period (30 minutes for alewife and 45 minutes for yellow perch). At the end of the feeding period, all predators were immediately removed from the tank and euthanized with MS-222. They were then placed on ice and their guts were removed for analysis. On each trial day a group of 25 larvae were removed from the main population, euthanized in MS-222 and TL was measured for these larvae to the nearest 0.1 mm with an ocular micrometer. These length data were used to calculate mean and standard deviation for larval size on that trial day. Trials were conducted for larvae at 15 dph (Mean TL 7.45 mm, SD 0.63 mm), 30 dph (9.7 mm, 1.1 mm) and 45 dph (16.4 mm, 2.3 mm).
In the lab, all larvae and zooplankton were removed from predator guts and counted. Data consisted of mean number of larvae and zooplankton consumed per predator per minute for each tank. Data were analyzed for a significant difference in feeding rate on either larvae or zooplankton between treatments and larval sizes. Statistical comparisons for a difference in feeding rate on larvae between larvae-only and zooplankton/larvae mix treatments were conducted with the Wilcoxin Rank Sum test. Comparisons for a difference in feeding rate on larvae and zooplankton between different larval densities were conducted with the Kruskal-Wallis test. Non-parametric tests were used due to heteroscedasity caused by high feeding variability between individual predators and low sample sizes within treatments (Hollander and Wolfe 1999).

*Individual-based Model* – The individual-based model was based on a general IBM describing size-selective predation on fish larvae (Letcher et al. 1996a). I adapted this model to account for multiple predators based on the approach of Cowan et al. (1996), and where appropriate I changed their general model functions to functions specific to larval yellow perch based on our laboratory experiments and data from the literature.

This model describes daily predation vulnerability of individual yellow perch larvae as a function of the relative size of predator and prey (Figure 2.1). Key parameters are expected daily encounter rate between a predator of size $l$ and the $i$th larva ($E_{i,l}$) and a size-based probability of attack and capture of a predator of size $l$ and species $k$ on the $i$th larva ($p_{k,i,l}$). Expected daily encounter rate is based on equations derived by Gerristen and Strickler (1977) and adapted for a non-trivial prey size by Breck and Gitter (1983). Expected daily encounter rate (number/day) is calculated in the model based on reactive distance (cm) of
both predator ($R_p$) and prey ($R_L$) and relative swimming speed (cm/s) of both predator ($ν$) and prey ($SS$)

\[
E_{i,t} = \pi (R_p + R_L)^2 \frac{SS^2 + 3ν^2}{3ν} * Den * Time
\]

where $R_p$ is equal to $0.8 *$ predator length (Cowan et al. 1996), and $R_L$ is equal to $2\times$larval length/$π^2$ (Bailey and Batty 1983). Larval swimming speed was calculated as a function of larval size based on laboratory observations of larval yellow perch (Houde 1969). Encounter rate is nearly constant with respect to the swimming speed of larval prey because predator swimming speed is so much higher over the range of relative sizes in the model. For equation (1), predator density ($Den$) is equal to $1/10^9$, where the denominator is the modeled water volume (ml). Because predator density ($Den$) equals the density of a single predator in the modeled volume of water equation (1) results in the daily encounter rate between an individual predator (randomly assigned species and length on each model day) and the $i$th larva (Cowan et al. 1996).

Modeled water volume was based on dividing the 10,000 larvae used in the model by mean larval density (number/ml) from field data for southern Lake Michigan and Green Bay ($1\times10^{-5}$/ml). I arbitrarily chose to use an initial larval population size of 10,000 because this number was high enough to allow sufficient survivors for analysis without resulting in excessive model run time. Actual number of predators in the modeled volume was based on density data from mid-water trawls and hydroacoustic analyses at several sites around Lake Michigan (30-60 fish/1000 m$^3$, Fabrizio et al. 1997) and adjusted within their range in our
model to achieve survival from 1 – 2% over the 45-day model period. Equation (1) was calculated separately for each predator on a given model day.

Encounter rate was converted to expected encounters per day by multiplying by total daily feeding time \((Time, 42,300 \text{ s})\). This value is based on predation occurring only during the twelve-hour daylight period. Realized daily encounter rate between the \(i\)th larva and a predator of size \(l\) \((ER_{i,l})\) is drawn randomly in the model from a Poisson distribution with \(E_{i,l}\) as the rate parameter. Encounter rate did not change among predator species.

The daily probability of attack and capture \((p_{k,i,l})\) for a predator of species \(k\) and length \(l\) in the model was a function of predator/prey size ratio defined empirically based on our laboratory results

\[
(2) \quad p_{k,i,l} = CS_{k,i,l} \times a_{k,i,l}
\]

where \(CS_{k,i,l}\) is the capture success given an attack on the \(i\)th larva by a predator of species \(k\) and length \(l\), and \(a_{k,i,l}\) is the relative attack rate on the \(i\)th larva by a predator of species \(k\) and length \(l\).

I used the results from the capture success experiment in two ways. First, I used these data to build a predictive function for capture success based on the predator/prey size ratio. This predictive function was the best-fit equation resulting from the capture probability analysis mentioned previously. Second, I used results from the capture success experiments in the form of number of strikes/trial (both successful and unsuccessful) to develop a functional relationship between predator relative probability of attack \((a_{k,i,l})\) and predator-prey size ratio. This approach rests on the assumption that the number of attacks observed in
a fixed period is an index of the relative probability of attack based on relative size of predator and prey. I can only estimate relative probability of attack because my experimental results cannot account for tank size effects on encounter rates or for differences in encounter rate between our experimental system and Lake Michigan.

I tested for a significant relationship between probability of attack and predator-prey size ratio for each predator type, and whether the slope of these relationships differed from zero using a simple linear regression analysis (SAS 2002). Probability of attack was set at 0.5 by Letcher et al. (1996a) for a general predator in order to achieve reasonable larval mortality rates in their model. I adapted this approach to allow the probability of attack to vary around a pre-selected mean value (0.5) based on the probability of attack-size ratio relationship established in our experiments. These two functions combined ($CS_{k,i,l} \ast a_{k,i,l}$) allowed me to incorporate size- and predator-specific differences in both attack rate and capture success into my model.

Daily vulnerability for the $i$th larva to a predator from species $k$ and of length $l$ ($V_{k,i,l}$) is defined as the probability of an individual larva not escaping all its encounters with that predator, based on a binomial probability function

\begin{equation}
V_{k,i,l} = 1 - (1 - p_{k,i,l})^{ER_{i,l}}
\end{equation}

where the number of trials is the realized daily encounter rate ($ER_{i,l}$) and the success probability is the probability of attack and capture ($p_{k,i,l}$). Vulnerability for each larva on each day was compared to a uniform random number ($x$) between 0 and 1, and if $V_{k,i,l}$ was more than $x$ then the $i$th larva was removed from the simulation.
Numerical Experiments – The predator-prey IBM was used to address questions regarding the influence of differences in individual hatchdate on size-dependent predation vulnerability of larval yellow perch. All model runs lasted 45 days based on the estimated length of the pelagic larval period for yellow perch (30-40 days). All numerical experiments were run with an initial cohort of 10,000 larvae with an initial size distribution (Mean initial length 5.7 mm, SD 0.13 mm) based on hatch size data collected in the laboratory (R. Fulford unpublished data). The 10,000 larvae were introduced into the model gradually over the first 24 days of each model run according to a hatchdate frequency distribution based on age data from field-collected larvae (Appendix 1). Both initial size and individual growth rate were randomly assigned to each larva at the beginning of the model run based on a normal distribution. Therefore, size variability for larvae in the model reflected the combined effects of variation in initial size, growth rate, and timing of hatch. Each numerical experiment consisted of three replicate model runs to account for model stochasticity.

First, I investigated how hatchdate distributions of survivors are affected by changes in size variability within cohorts caused by inter-annual changes in mean growth rate. Previous research has shown that changes in mean growth rate between cohorts can result in changes in the size dependence of larval vulnerability to predation (Rice et al. 1993, Cowan et al. 1996), and I wished to investigate how these changes are reflected in the hatchdate distribution. I conducted model runs at two mean growth rates (2% and 4% per day, SD 0.1% for both) representative of the range of mean growth rates I observed for larval yellow perch in Lake Michigan. I also conducted model runs in which larvae were exposed to mortality of a similar magnitude that was independent of larval size. These three scenarios
were hypothesized to result in a range of size-dependence measured as the daily mean difference in length between survivors and non-survivors. I further hypothesized that these differences in the size-dependence of mortality would be reflected as differences in the hatchdate distribution pattern of survivors. Output for the growth rate variability experiment was cohort survival, daily mean length of survivors and non-survivors, and hatchdate distribution of survivors. Simulations were conducted for each predator type (alewife, white perch and adult yellow perch) to assess predator-specific differences in size-selectivity. Predator density was set at 0.045 predators/m³ based on mean density data for predators in Lake Michigan (Fabrizio et al. 1997).

The second numerical experiment addressed how patterns in survival and hatchdate distribution of survivors were affected by a simulated predation pulse. Increased vulnerability to mortality was simulated with a five-day period of predation occurring at different times throughout the larval period (day 0-5, 6-10, 11-15, 16-20, 21-25, 26-30, 31-35, 36-40, 41-45). Predator density during the predation pulse was 0.045/m³ and mean larval growth rate was set at 4% per day (SD 0.1%/day) for all simulations. Output for the timing of predation experiment was total larval survival and hatchdate distribution of survivors for each model run.

Results

*Probability of Capture* – Capture success of individual predators feeding on larval yellow perch varied with predator/prey size ratio for all predator species tested (Figure 2.2). Capture success was low for the smallest size ratios and rose monotonically with increasing size ratio. For white perch and yellow perch predators, maximum capture success was achieved around
a predator-prey size ratio of 12-14 and remained high for all larger size ratios tested. Trials that involved predation by alewife at larger size ratios (i.e., smallest larvae) resulted in no attacks. As a consequence, alewife displayed a similar ascending pattern as the other two predators at lower size ratios, but no evidence that capture probability is maximized over a wide range of size ratios as was indicated for white perch and adult yellow perch. Capture probability also differed in variability between predator species. Maximum observed capture probability was high for all three predator species (Alewife 1.0, White Perch 1.0, Yellow Perch 0.94), however the observed values for alewife were much more variable than for the other two species.

I used these data for capture success as a function of predator/prey size ratio to develop a predictive relationship that could be used in the individual-based model. The Logistic model performed better than the Miller model when both functions were fit to the data for all three predators combined, but the R² value for both models was generally low (Table 2.1). However, model fit was noticeably improved when data for each predator species were fit separately, which suggests the capture success-size relationship differs between species. Further, R² values were higher for the species-specific fit of the Miller model for all three predators as compared to the species-specific fit for the logistic model (Table 2.1). Based on a comparison of parameter estimates for the predator-specific Miller model, differences in the relationship between capture success and relative size among predators are largely due to differences between alewife and white perch, with values for all three parameters for adult yellow perch falling between those of the other two predators (Table 2.1, Figure 2.2). Given these results, I used the predator-specific Miller model to
predict capture success as a function of predator/prey size ratio for each predator species in the model simulations.

*Relative probability of attack* – Predator interest measured as the number of strikes (successful and unsuccessful) observed in each 30-minute trial also differed among predator species (Figure 2.3). Predator interest of alewife feeding on yellow perch larvae declined significantly with increasing size ratio \( (\text{strikes} = -1.2 \times \text{size ratio} + 33.2, \ t\text{-test } p<0.001) \). In contrast, white perch showed a positive linear relationship between predator interest and size ratio, however the slope of this relationship did not differ from zero \( (\text{strikes} = 0.44 \times \text{size ratio} + 8.3, \ t\text{-test } p=0.18) \). Adult yellow perch showed no detectable change in their interest over the tested range of size ratios \( (\text{strikes} = 0.09 \times \text{size ratio} + 19.4, \ t\text{-test } p=0.62) \).

These data were used to adapt a general probability of attack parameter for predators preying on larval fishes into a size-based function that varied in shape among predator species, but had the same mean value. A function describing relative probability of attack \( (a_{k,i,l}) \) for the \( i \)th larva by all predators encountered of species \( k \) and size \( l \) was constructed by assuming relative probability of attack will be zero at size ratios where no strikes were observed and maximum probability of attack would occur at size ratios where the maximum number of strikes was observed for each predator species. Finally, the overall mean value of \( a_{k,i,l} \) across all predators and size ratios was set to 0.5 for all simulations. This relationship is based on the assumption that under constant conditions changes in predator interest with predator-prey size ratio reflect changes in relative probability of attack as a function of relative size. Only the strikes/trial – size ratio function for alewife displayed a slope significantly different from zero, so alewife relative probability of attack changed with size in
the model. Relative probability of attack for white perch and adult yellow perch was set to 0.5.

**Condition-dependent selection** – Mean length of larvae did not differ between the starved and fed treatment groups (t-tests, p<0.001 all dates; Table 2.2). Across all trials used for analysis, predators consumed an average of 37% (10-60%) of larvae in an individual trial. In most cases both alewife and adult yellow perch showed no significant selection for or against starved larvae (Figure 2.4). The only exception was that alewives captured starved larvae more often than un-starved larvae at 30 dph when predator/prey size ratios were between 11 and 14, which is near the optimal size ratio for attack and capture for alewives ($\chi^2 = 5.89, 1$ d.f., p<0.03). I did not detect significant condition-dependent selection by alewives at any other size ratio. Yellow perch displayed no significant condition-dependent selection at any size ratio tested ($\chi^2 < 3.4$ all sizes, 1 d.f., p>0.05).

**Alternative prey selection** - Both alewife and adult yellow perch fed during this experiment on both larval yellow perch and zooplankton. Zooplankton used as alternative prey consisted of more than 70% copepods with the remainder a mix of large and small cladocerans. Alewives fed consistently on zooplankton, but feeding rate showed no trend with larval biomass (Kruskal-Wallis H=0.52, p>0.3). Feeding rate for adult yellow perch on zooplankton was low, occurring in only 2 out of 18 trials, with no trends evident in these data as a function of larval biomass.

Feeding rates (larvae/min) as a function of size ratio for both predators were consistent with results from the capture success experiments. I observed maximum feeding
rate in this experiment at about the same size ratio at which I would predict maximum probability of attack and capture based on the results of the capture success experiment (Figure 2.5). A positive functional response was observed for alewife feeding on larval yellow perch (Figure 2.6), however this result was not statistically significant (Kruskal-Wallis H=0.92, p > 0.2). The presence or absence of alternative prey did not significantly affect alewife feeding rates on larvae (Wilcoxin statistic 0.63, p>0.05). I did not observe any trend in functional response for adult yellow perch feeding on larvae (Figure 2.6; K-W 0.52, p > 0.1). However, the feeding rate of adult yellow perch on larvae was 2-3 times higher in the presence of alternative prey (Figure 2.6; Wilcoxon statistic 1.8, p<0.05).

Numerical experiments

_Growth rate variability and predator species comparison_ – Vulnerability of larval yellow perch to predation generally increased with predator size and decreased with increasing larval size. The shape of these relationships shifted among predator species in accordance with predator-specific differences observed in the capture probability experiments. Vulnerability of larval yellow perch to both white perch and adult yellow perch rose monotonically as a function of predator size and was near the maximum vulnerability at a predator size of 160 mm TL for all larval sizes tested (Figure 2.7). However at predator sizes below 160 mm TL, larval vulnerability to predation dropped rapidly with increasing larval size when the predator was either alewife or adult yellow perch. In contrast, the slope of the relationship between vulnerability and larval size when the predator was white perch was much more shallow, suggesting that larval yellow perch grow out of the vulnerability window to predation by
white perch more slowly, and larvae are likely to remain vulnerable to white perch for more of the larval period.

Larval vulnerability to alewife predation was more parabolic in nature than vulnerability to white perch of adult yellow perch with a size refuge evident for both the smallest and the largest larvae (Figure 2.7). Larval vulnerability to predation by alewife was maximized for the smallest range of predator and larval sizes, and larval vulnerability to alewife dropped much more rapidly as larvae grew than did vulnerability to white perch or adult yellow perch. Vulnerability to predation by alewife appears the most strongly dependent on larval size of the three predators.

At comparable predator densities larval yellow perch survival over 45 days was lowest with white perch as predators (Mean survival = 0.007) and highest with alewife as predators (Mean survival = 0.02) across both growth rates tested. However, these differences in survival among predators did not translate to measurable differences in the size or hatchdate distributions of larval survivors (Kolmogorov-Smirnov test; p > 0.1 for size and hatchdate). Survival rate also changed as a function of larval growth rate. Mean survival was lower at the low growth rate (2%/day; S=0.008) than at the high growth rate (4%/day; S=0.018) across all predator types over 45 days.

The outcome of size-dependent predation, measured as the maximum daily difference in mean length between larval survivors and non-survivors, did not differ noticeably among predators but increased in response to increases in mean growth rate (Figure 2.8). As expected, non-selective model runs showed no size difference between survivors and non-survivors. Maximum size difference (mean across all predators) increased to 1.3 mm at a mean growth rate of 2%/day and 6.5 mm at 4%/day. Length differences between survivors
and non-survivors became positive around day 25 independent of changes in mean growth rate. These results are consistent with prior IBM analyses of larval vulnerability to predation (Rice et al. 1993, Cowan et al. 1996) based on size and demonstrate that the model is appropriately describing a range of intensity for size-selective predation against which I can compare patterns in the hatchdate distribution of survivors.

Observed changes in the hatchdate distribution of larval survivors on model day 45 (i.e., end of the larval period) were associated with observed changes in size-selectivity. Non-size-selective mortality in the model resulted in a hatch date distribution favoring later-hatched larvae by the end of the larval period due to their shorter duration of exposure to mortality (Figure 2.9). I observed minimal difference between the hatchdate distribution of survivors subjected to size-dependent predation at a larval growth rate of 2%/day and the hatchdate distribution of survivors subjected to non-size dependent mortality. In contrast, when the growth rate of the larval cohort was raised to 4%/day, the hatchdate distribution of survivors more closely resembled the initial hatchdate distribution.

However, a more detailed examination of hatchdate distributions over the simulation period revealed a more complex pattern. On model day 25, the hatchdate distributions of survivors were similar among the three scenarios (non-size selection, low growth and high growth), shifted somewhat to later hatchdates. In fact it appears that it was only in the later larval period between day 25 and 45 that hatchdate distributions in the high growth scenario deviated from the other two, shifting back towards earlier hatchdates. Day 25 is also close to the time that size-dependence became detectable in individual larval survival (Figure 2.8). When growth rate and hatchdate vary independently, non-size-dependent larval mortality
seems to favor later-hatched larvae, and the onset of size-dependence in larval mortality is correlated with a decrease in survival of late-hatched larvae.

*Predation pulse experiment* – For an analysis of the effects of a predation pulse on larval survival, I chose to use only alewife as a predator in model simulations. Alewife are of particular interest as a predator of larval yellow perch in several systems including Lake Michigan. Further, vulnerability of yellow perch larvae to alewife also appeared the most divergent from general vulnerability patterns described previously (Cowan and Houde 1992, Letcher et al. 1996a), and as such merits closer scrutiny.

The simulated five-day predation window resulted in hatchdate distributions of survivors with two basic patterns, depending on how close the predation window was placed to peak hatch. Survival was high when predation was focused during the early-larval period as most larvae had not yet hatched and fewer larvae were exposed to predation (Figure 2.10). When the predation window occurred between day 25 and the end of the simulation, cohort survival once again increased because as predation occurred later in the larval period more larvae had reached a size at which size-dependent vulnerability to predation was decreasing.

Timing of predation also affected patterns within the hatchdate distribution (Figure 2.11). Predation during the early hatching period generated little change in the hatchdate distribution, as most larvae were not available to be captured at this time. When the predation window occurred close to the timing of peak hatch (Day 11-15), later-hatched larvae were over-represented in the final hatchdate distribution, suggesting a survival advantage for these larvae. When the predation window occurred just after peak hatch (model day 16-20), later-hatched larvae were again over-represented, but the survival
advantage was reduced in comparison to predation around peak hatch. Finally, when the predation window occurred after day 20 in the model, the hatchdate distribution resembled the initial distribution with no apparent survival advantage as a function of hatchdate.

Discussion

Predation vulnerability of larval yellow perch is affected by larval and predator size, as well as predator species. Capture probability increased with increasing size ratio for all three predators in laboratory experiments, but unlike for white perch and adult yellow perch, interest in larval prey by alewife decreased and actually dropped to zero with increased predator-prey size ratio; that is they ignored small larvae. Larval vulnerability to predation by either white perch or adult yellow perch is largely a function of larval escape capacity, but larval vulnerability to predation by alewife is a function of both larval escape capacity and the probability alewife will attack. Therefore, vulnerability of larval perch to alewife predation as a function of size is more complex than vulnerability to other fish predators.

The relationship between predation vulnerability and relative size has been explored previously for larval prey and the pattern exhibited by white perch and adult yellow perch is similar to patterns described for generic fish predators. Vulnerability was high for newly-hatched larvae and dropped slowly as a function of larval size until larvae reached a threshold length when vulnerability dropped rapidly to zero (Cowan et al. 1996). In contrast, the pattern for alewife did not match these generic patterns well.

Alewife made no attacks on the smallest larvae. When they did attack, capture efficiency was maximized for only a narrow band of predator-prey size ratio (14-18). Through all of my experiments, alewife showed the highest capture efficiency for larvae
when the size ratio was in this range. Further, alewife were more selective at these size ratios for larvae in poor nutritional condition.

Janssen (1976) described two feeding modes for alewife: particulate feeding and filter-feeding. Particulate feeding is hypothesized to be more selective as alewife are choosing prey visually and are more likely to attack larger, more active prey items based on an optimal feeding model (Crowder and Binkowski 1983). Filter-feeding is largely non size-selective as the alewife are simply collecting all prey in their path and prey are captured or not based largely on their inherent escape abilities. The shift between feeding modes is based on prey density, prey size and predator size (Janssen 1976).

Alewife appear to feed on larval yellow perch in a particulate mode, and the lack of interest shown by alewife for the smallest larvae in our experiments may have resulted from these larvae being visually undetectable for alewife. Alewife do feed in a particulate manner on smaller organisms such as *Daphnia* and mysids, however these organisms have more pigmentation and rigid body parts that make them more easily detected. It is reasonable to assume that alewife might filter-feed on yellow perch larvae if they were present in sufficient densities, which would increase attacks on smaller larvae.

Alewife behavior also changed as larval density increased. Alewife always fed on larvae at densities above 100/m³, but they fed intermittently, if at all, below this density. Further, feeding rate was positively associated with larval density when larvae were between 7-9 mm TL. In general, a high level of alewife predation on larval yellow perch is predicted to occur if larvae and alewife interact at or near the optimal size ratio and if larval densities are high. This conclusion is supported by observations of alewife predation on larval yellow perch in other systems. Brandt et al. (1987) documented massive predation by alewife on
larval yellow perch in a small embayment adjacent to Lake Ontario. They reported that predation was highest in years when alewife interacted with larvae between 7-9 mm TL at a larval density of 79/m³, but they observed less predation when alewife did not appear until larvae were larger. Moreover, they reported that incidence of yellow perch larvae in alewife stomachs declined to less than 1% at a larval density of 11/m³ despite the larvae being an optimal size. Luecke et al. (1990) also observed that alewife show a positive functional response for larval bloater at densities exceeding 100/m³, but feeding rate was near zero by alewife at a larval density of 50/m³.

Larval yellow perch densities this high are rare in Lake Michigan. Larval densities in Green Bay, a shallow, productive embayment of Lake Michigan at the Lake’s northwest corner, have peaked at 18/m³ in recent years (WDNR unpublished data) and the maximum density for larval perch from our sampling in the main body of Lake Michigan in 1998 – 2001 was less than 1/m³ (See Chapter Five). These field densities support the results of our study that alewife predation is likely not a significant limiting factor for yellow perch larval survival at present.

Vulnerability of larval yellow perch to predation by both white perch and adult yellow perch remained high for a wider range of predator/prey size ratios in comparison to alewife. Moreover, larval vulnerability to these predators was not dependent on larval density. White perch and adult yellow perch should affect larval survival over a longer portion of the larval period than alewife, and have a more significant effect on year class strength when these predators are present. However, white perch are not abundant in the main body of Lake Michigan and adult yellow perch are found primarily in deeper water away from the pelagic zone, so these two predators are also not likely to have a strong
influence on the survival of larval yellow perch in Lake Michigan. Overlap between larval perch and both white perch and adult yellow perch is likely to be higher in smaller, shallower systems such as Green Bay. Both predators are abundant in Green Bay and the limited depth makes spatial overlap more likely as compared to a deeper, more open system like Lake Michigan. At present, predation does not appear to be a significant factor limiting larval yellow perch survival in Lake Michigan.

One interesting finding regarding larval vulnerability to predation by adult yellow perch was that feeding rate of adult yellow perch on larval yellow perch increased if alternative prey were present. Intra-cohort cannibalism has been reported for natural populations of European perch, *Perca fluviatilis* (Brabrand 1995), and for adult yellow perch feeding on young of year perch in Oneida Lake, NY (Tarby 1974), but the general importance of cannibalism to recruitment has not been well explored.

Two causes for an increase in feeding rate by adult yellow perch in the presence of alternative prey seem plausible. Either adult yellow perch were simply responding to a generic increase in prey density and this was a functional response, or the foraging activity of the larval yellow perch brought on by zooplankton being present made them more vulnerable to predation. It is not possible to draw conclusions regarding the veracity of these two hypotheses from my data because I did not monitor larval activity or examine the guts of larvae to check for feeding activity. However, in all of our trial tanks, only a few adult yellow perch fed on zooplankton and they showed no evidence of a functional response. These observations suggest that adult yellow perch were not responding to an increase in potential prey, and support the idea that larvae are more vulnerable to cannibalism when actively feeding. Anecdotal observations of feeding behavior during my probability of
capture experiments indicated that adult yellow perch remain near the bottom of the tank, while larvae occupied the upper 1/3 of the tank. As a result, adult yellow perch did not appear to actively search for prey near the surface, and observed attacks were initiated in response to some visual trigger, such as larval movement. In cases where predation by adult yellow perch is found to be significant, it would be fruitful to determine whether larvae develop a behavioral refuge from predation by reducing their movement and feeding activity in the presence of adult yellow perch. This behavior would indicate a compromise between maximizing growth rate and minimizing mortality risk, which has been observed in adult fish (Skalski and Gilliam 2002) but has not been reported for the larval stage. This finding merits further study, particularly in systems where cannibalism is thought to be important.

Individual-based model results suggest that hatchdate distributions of larval survivors change in response to increases in size variability resulting from variation in mean growth rate. When mortality is size-independent, survival to 45 days after peak hatch is higher for later-hatched larvae resulting in an over-representation of later-hatched larvae in the hatchdate distribution of survivors in comparison to the initial distribution. Size-dependent mortality acting on a cohort with a low mean growth rate (i.e., low size variability) resulted in a small difference in the maximum size between survivors and non-survivors, and a similar hatchdate distribution to that observed in the non-size-dependent simulations. However, when mean growth rate was doubled, the size difference between survivors and non-survivors tripled by the end of model runs. The resulting hatchdate distribution for survivors was similar to the initial distribution, which suggests that the increase in size-dependence of mortality in the later part of the larval period resulted in no net survival advantage for any particular portion of the cohort at the end of the larval period.
However, this is only part of the story. An examination of the hatchdate distribution of survivors on model day 25 indicated the hatchdate distributions resulting from my three size-dependent scenarios (size-independent, 2%/day, and 4%/day) were similar: all favoring later-hatched larvae. Only later in the larval period, about the time differences in mean length between survivors and non-survivors became detectable, did the hatchdate distribution of survivors growing at 4%/day began to deviate from the common pattern. Increased size variability within the larval cohort resulted in higher mortality for later-hatched fish, as they are the smallest larvae present at this time. These results suggest that when cohort survival is low due to a low mean growth rate, later-hatched larvae are more likely to survive, but when survival is higher due to a high mean growth rate, the increase in survival is mainly experienced by early-hatched larvae. Even when size-dependent vulnerability to predation is due largely to changes in growth rate, analysis of patterns in the hatchdate distribution are informative regarding the effect of size-dependent predation on individual survival.

The relationship between growth rate variability and the intensity of size-dependent predation has been observed in previous individual-based model analyses (Rice et al. 1993, Cowan et al. 1996). However, these analyses did not include an examination of the resulting patterns in hatchdate distribution, which are informative for the comparison of model results to similar data from natural populations. Size-independent mortality, as well as size-dependent mortality acting on low size variability, both favored survivors that hatched after peak hatch. In contrast, when size variability was increased by doubling the mean growth rate, the hatchdate distribution of survivors no longer favored later-hatched larvae.

One surprising result of the individual-based modeling analysis was that patterns in the characteristics of survivors did not change among the different predators
tested in this experiment. Cowan and Houde (1992) found differences in predators to be an important factor in larval survival, but their study involved comparisons of predators across a wider taxonomic and behavioral range than my work. Similarity in effect of predation among predators in my experiments was likely due to the fact that encounters between large alewife (> 160 mm TL) and small larvae (> 7 mm TL) in the model were rare and it was at the highest predator-prey size ratios (>20) that alewife capture efficiency and attack behavior deviated strongly from that of the other predators. At other size ratios, variance in larval size is likely more important to individual vulnerability to predation than variance in size-selectivity among these three fish predators.

When larvae were exposed to a predation pulse during the larval period, larval vulnerability to predation was highly dependent on hatchdate. Larvae hatched in the 5-7 days preceding the predation period were expected to be more vulnerable to size-dependent predation by alewife than larvae hatched significantly before the predation period. As expected, larvae hatched during or preceding the predation window had lower survival than larvae born at other times, but the impact this had on cohort survival and the hatchdate distribution of survivors depended on what portion of the cohort was affected. The lowest overall survival occurred when the predation window was near or immediately after peak hatch (Day 11-15 or 16-20). The hatchdate distribution of survivors from this predation scenario also exhibited the highest survival advantage for later-hatched larvae and closely resembled a non-size-dependent hatchdate pattern. As the predation window was placed successively later in the larval period, the non-selective signature (increased survival of later-hatched larvae), as well as the mortality rate, decreased. Just as with the growth rate
variability experiment, high mortality is associated with a survival advantage for later-hatched larvae and this advantage is reflected in the hatchdate distribution of survivors.

My results suggest that not only is variance in hatchdate important to the full description of size variability, but it may provide a valuable detection tool for the selective signature left in characteristics of survivors of the larval stage. Rice et al. (1997) stated that size-selective mortality may be masked and difficult to detect in size data of survivors if reversals in selection occur during the life-stage of interest. Hatchdate distributions would suffer from the same limitations, except they can be estimated at multiple points during the larval period and continually compared to the initial hatchdate distribution. Changes in the hatchdate distribution over the larval period observed in model simulations are also detectable in field data and may prove valuable for detecting size-selective mortality for a given cohort and making comparisons between cohorts. In this way, I can use the individual-based model as a tool for measuring the relative effects of sources of growth rate variation and sources of mortality on the hatchdate distribution of survivors. In turn I can provide information on the importance of these factors to year class strength based on how the hatchdate distributions resulting from model analysis match up to comparable field data.

In general, size-selective predation for larval yellow perch in Lake Michigan may be weakly correlated with yearclass strength at present due to low spatial overlap with predators at vulnerable sizes and densities. Size-selective predation is likely to play a stronger role in smaller systems that are more productive. Predation has been found to be important to yearclass strength in other populations of yellow perch (Campbell 1998, Mayer et al. 2001). My conclusions regarding the current importance of predation in Lake Michigan represent an important difference between Lake Michigan and other systems.
An analysis of these differences is warranted before applying lessons learned from examination of perch populations in other systems to our understanding of population dynamics of yellow perch in Lake Michigan. In particular, differences in the importance of sources of mortality such as predation between yellow perch populations in Lake Michigan and yellow perch populations in other systems may be associated with differences in the size of the pelagic habitat; an increase in available habitat will affect local larval retention and the amount of overlap between predator and prey. The application of both field data analysis and individual-based models to the examination of characteristics of larval survivors is a valuable tool for detecting differences in patterns of size-dependent larval mortality. The individual-based model developed as a part of this analysis will be coupled with field data from systems where predation is thought to be important to larval survival, such as Green Bay, in order to further improve our understanding of recruitment for larval yellow perch.

Literature Cited


Table 2.1. Results of model fit for the Logistic model and the Miller model for capture probability as a function of predator/prey size ratio from laboratory experiments. Each model was fit to the entire data set (all predators) and to data for each of the three predator species separately. Values in parentheses next to model parameters are the standard error for that parameter estimate. The value ‘Ratio’ in the model formula is predator/prey size ratio. R² values are the unweighted coefficient of multiple determination and the R²ₐ values are weighted by the number of parameters in the respective model (Neter et al. 1990).

<table>
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<th>Model Type</th>
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<th>Modeled Data</th>
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<th>β</th>
<th>R²</th>
<th>R²ₐ</th>
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<td></td>
<td></td>
<td>White Perch</td>
<td>-1.50 (0.13)</td>
<td>0.25 (0.01)</td>
<td>0.81</td>
<td>0.80</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Adult Yellow Perch</td>
<td>-2.88 (0.07)</td>
<td>0.26 (0.005)</td>
<td>0.85</td>
<td>0.85</td>
<td></td>
</tr>
<tr>
<td>Miller Model</td>
<td>[ P(\text{capture}) = 100 - \left( \frac{(\text{Ratio} + \beta_1)}{\beta_2} \right)^{-\beta_3} ]</td>
<td>All Predators</td>
<td>452.2 (4.7)</td>
<td>500 (0.5)</td>
<td>49.2 (6.1)</td>
<td>0.60</td>
<td>0.59</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Alewife</td>
<td>453.2 (80.8)</td>
<td>510.2 (89.0)</td>
<td>41.7 (0.6)</td>
<td>0.52</td>
<td>0.50</td>
</tr>
<tr>
<td></td>
<td></td>
<td>White Perch</td>
<td>180.9 (40.4)</td>
<td>204.9 (44.6)</td>
<td>35.7 (1.4)</td>
<td>0.85</td>
<td>0.83</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Adult Yellow Perch</td>
<td>325.4 (37.3)</td>
<td>367.3 (41.3)</td>
<td>40.2 (0.6)</td>
<td>0.92</td>
<td>0.91</td>
</tr>
</tbody>
</table>
Table 2.2. Summary data for mean size (mm) of larvae used in the condition-dependent selection experiment. Data are presented separately for the starved and fed treatment groups and p-values are given for a t-test for differences in mean length between treatment groups.

<table>
<thead>
<tr>
<th>Larval Age (dph)</th>
<th>Mean size (range) Fed larvae</th>
<th>Mean size (range) Starved larvae</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>8.7 (8.0 – 10.1)</td>
<td>8.6 (7.9 – 10.0)</td>
<td>0.52</td>
</tr>
<tr>
<td>30</td>
<td>12.7 (11.4 – 14.4)</td>
<td>12.2 (11.4 – 13.1)</td>
<td>0.23</td>
</tr>
<tr>
<td>45</td>
<td>20.2 (14.1 – 24.4)</td>
<td>20.1 (14.6 – 24.1)</td>
<td>0.95</td>
</tr>
<tr>
<td>60</td>
<td>36.6 (27 – 46)</td>
<td>33.4 (26 – 41)</td>
<td>0.21</td>
</tr>
</tbody>
</table>
Figure 2.1 Flow chart summarizing the predator-prey individual-based model used for the numerical experiments.
Figure 2.2 Capture success measured as the number of successful captures/number of strikes for alewife, white perch and adult yellow perch feeding on larval yellow perch. The diamonds are experimental data and the line is the best-fit of the Miller model. See Table 2.1 for model details. Black triangles on the alewife chart indicate size ratios at which all trials resulted in no attacks.
Figure 2.3  Predator feeding interest defined as the total number of strikes made in 30 minutes by alewife, white perch and adult yellow perch feeding on larval yellow perch as a function of predator-prey size ratio. The diamonds are experimental data and the line is a best-fit linear function. Formula and $R^2$ are given for significant trends and non-significant trends are labeled (NS).
Figure 2.4 Probability (± 1 SE) that a larva captured in mixed-condition prey experiments was starved. Trials were conducted at 15, 30, 45 and 60 days post hatch. Mean total length of larvae in each age treatment is given in parentheses. The reference line at 0.5 indicates random selection, however statistical results reported are based on a Chi-square analysis.
Figure 2.5 Probability of attack and capture estimated from capture success experiments (line) and feeding rates measured in the alternative prey trials (bars; ± 1 SE) for alewife and adult yellow perch as predators. Feeding rates are the combined mean of zooplankton present and zooplankton absent trials conducted at each predator-prey size ratio.
Figure 2.6  Feeding rate for alewife and adult yellow perch on larval yellow perch at three larval densities (0.02, 0.09, and 0.16 mg/L). Solid bars are zooplankton-absent treatments and open bars are zooplankton present treatments. Zeros on graph indicate treatments where no predator feeding occurred.
Figure 2.7 Larval yellow perch vulnerability to predation as a function of both predator and larval size (TL mm), for white perch, adult yellow perch and alewife predators. Surface plots are based on a deterministic calculation of model functions.
Figure 2.8 Daily mean difference across model runs (n=3/treatment) in total length between survivors and non-survivors for model runs conducted with size-independent mortality and size-dependent mortality at a mean growth rate of 4%/day and 2%/day. Results are given for simulations run separately for each of the three predator species.
Figure 2.9  Hatchdate distribution on model days 25 and 45 compared to initial hatchdate distribution for non-selective mortality simulations, as well as for selective predation by alewife simulations with a high (4%/day) and low (2%/day) mean larval growth rate.
Figure 2.10  45-day larval survival predicted in model runs simulating a 5-day period of predation occurring at different times throughout the larval period. Hatching period for larval yellow perch in the model is indicated by the gray bar and peak hatch is indicated by the black arrow.
Figure 2.11. Hatchdate frequency distributions of larvae surviving to the end of the larval period (30 days after peak hatch) predicted by the model from simulating a 5-day predation window on days 6-10, 11-15, 16-20, and 21-25. Distributions resulting from predation later in the larval period did not differ from that caused by predation during days 21-25 and therefore are not shown.
Predation Day 6-10

Predation Day 11-15

Predation Day 16-20

Predation Day 21-25

Recruitment of yellow perch is highly dependent on survival during the larval stage. Growth and survivorship of larval perch have been examined in many systems, but to what extent can conclusions from more thoroughly studied perch populations in smaller lakes be extended to populations in larger, more open systems such as Lake Michigan? I conducted a series of laboratory experiments with yellow perch from hatch to 35 mm TL to quantify larval selectivity for six major prey types. I used these data to develop an individual-based model of foraging and growth for larval yellow perch, in which I employed an empirical approach based on Chesson’s $\alpha$ to describe larval diet selectivity as a function of larval size and prey community composition. The model is optimized for comparing foraging decisions made by larvae in different systems so that I can address whether a single model can accurately predict changes in larval foraging behavior in response to changes in prey community composition. Larval perch made three transitions in selectivity during ontogeny from rotifers to copepods and then to cladocerans. However, the initial selection for rotifers and the final transition to cladocerans were both dependent on prey composition, and larvae exposed to prey assemblages that differed only in relative composition of prey types had different diets. Diet differences predicted in the model translated into predicted differences in individual larval growth and likelihood of starvation at prey densities from 50 to 250 prey/L. These findings suggest the importance of foraging success to larval survival will
differ between Lake Michigan and smaller systems; these results are important for comparisons of recruitment dynamics across the system size spectrum.
Introduction

Variability in mortality for larval fishes is often a significant factor driving variability in fishery recruitment, because larval fishes are small, widely dispersed and subject to a highly variable environment (Sissenwine 1984, Houde 1987). Mortality during the larval stage is affected by a variety of factors including predation (Cowan and Houde 1993, Rice et al. 1993), spatial or temporal mis-match with food resources (Cushing 1990), and hydrographic effects (Leggett et al. 1984). Predicting larval mortality has proven elusive as these factors interact in complex ways and different factors may be important at different times during the larval period. Such interactions are difficult to detect through field sampling (Miller 1997) and laboratory analysis is often prohibitive due to the size and expense of the necessary experiments.

Individual-based modeling (IBM) is an alternative approach for analyzing these complex interactions, which allows for a mechanistic analysis of links between larval behavior and survivorship (Murdoch et al. 1992). Individual-based modeling may also be more informative for questions regarding larval survivorship than models that are based on the average characteristics of larvae within a cohort. Mortality rates for larval fishes are often as high as 99%, and it is difficult to truly understand important relationships based on population-level averages because by the end of the larval stage the 'average' larva is likely dead (Sharp 1987). An IBM approach allows for a direct examination of characteristics of individual survivors, which may be helpful in relating larval experience to larval survival.

The IBM approach has been used successfully to understand broad patterns in larval growth and survival (Rice et al. 1993, Cowan et al. 1996, Letcher et al. 1996a, Paradis et al. 1999). These studies all indicate that an IBM approach combined with field sampling and
experimental analysis may lead to a clearer understanding of particular recruitment problems than is possible when these more traditional techniques are used alone. I have used an IBM approach combined with laboratory experiments to ask how changes in prey community composition may interact with changes in larval feeding selectivity during ontogeny to affect growth and survival for larval yellow perch, *Perca flavescens*. I then compared the potential importance of foraging success to larval survivorship for yellow perch between large and small systems, and examined the implications of these results for comparisons of data across the system-size spectrum.

Feeding selectivity in fish larvae is affected by endogenous factors such as sensory ability (Blaxter 1986), swimming performance (Webb and Weihs 1986, Fuiman et al. 1999) and foraging behavior aimed at maximizing net energy intake (Werner and Hall 1974, Ware 1982). Feeding selectivity is also affected by exogenous factors such as prey density and prey community composition. Prey types differ in size, but they also differ in behavior, morphology and relative density (Kerfoot et al. 1980). These additional differences make it likely that prey items from different taxonomic groups will differ in both ease of capture and value to larval fishes, even if they are of comparable size. Descriptions of larval selection based on endogenous factors only, or simplistic exogenous models based only on prey size, may fail to predict how changes in the prey community composition affect selection. Interactions of prey community structure with larval selectivity are particularly relevant for an analysis of foraging behavior of an opportunistic feeder such as larval yellow perch.

Yellow perch has a pelagic larval phase lasting 30-40 days, and is widely distributed throughout North America in aquatic systems from 0.1 to 52,000 km² in area (Jenkins and Burkhead 1994). Such a wide range in habitat size suggests that perch may be exposed to a
wide variety of foraging conditions throughout their distribution. Size-selective feeding patterns of larval yellow perch change with ontogeny (Schael et al. 1991). Changes in taxonomic selectivity have also been observed for larval perch in several smaller systems (surface area 0.1 – 392 km², mean depth 5 – 12 m). Larval yellow perch show a consistent pattern of selection for copepod nauplii at first feeding, followed by copepod adults, then small cladocerans and finally larger cladocerans when larvae are larger than 20 mm TL (Bulkley et al. 1976, Mills et al. 1984, Schael et al. 1991, Wahl et al. 1993). However in a comparative study of two lakes, Siefert (1972) found that yellow perch larvae in a shallow eutrophic lake (1.51 km², max depth 3.1 m) followed this selective pattern, but perch larvae in a deeper, oligotrophic lake (8.1 km², max depth 34 m) selected for rotifers at first feeding, and never showed positive selection for cladocerans. This observed shift in selective pattern for larval perch between systems suggests that larval yellow perch can respond to environmental variance by changing their feeding behavior.

Prey community composition has not been cited as a potential cause of annual variation in recruitment in any of these smaller systems. Still, there is a broad size gap between these systems and Lake Michigan (52,000 km², mean depth 89 m), as well as differences in the zooplankton community. The Lake Michigan zooplankton community is dominated by rotifers and calanoid copepods during the pelagic larval period of yellow perch (Madenjian et al. 2002). Further, cladocerans are a small proportion of the zooplankton assemblage and tend to be smaller in comparison to the cladoceran community in smaller lakes (Caceres 1998). The dominance of rotifers and the minor contribution of cladocerans are a significant contrast between Lake Michigan and many smaller systems where larval yellow perch have been studied. The significance of this difference for comparisons of
yellow perch feeding selectivity between systems, and the corresponding implications for recruitment, is unknown.

Another relatively small system that has been the focus of research on larval yellow perch is Green Bay (4212 km², mean depth 20 m), a shallow, productive embayment connected to Lake Michigan at the Lake’s northwest corner. Green Bay has a similar zooplankton composition to that observed in smaller systems described above where yellow perch feeding selectivity has been studied, such as Oneida Lake, NY (Wisconsin Department of Natural Resources *unpublished data*). Comparisons of perch foraging dynamics between the main body of Lake Michigan and Green Bay should be very informative regarding differences in larval yellow perch foraging behavior across the system-size spectrum.

Further, Green Bay is located adjacent to Lake Michigan and is exposed to similar regional conditions. The proximity of the two systems offers an opportunity to address differences between systems resulting from differences in system size without the confounding effect of larger-scale factors such as climate or geography.

I conducted a series of laboratory experiments to quantify larval selectivity as a function of larval size and prey type. I then used these data to build an individual–based foraging and growth model and used this IBM to ask how larval prey selection and diet may change between Lake Michigan and Green Bay and how these differences may translate to differences in growth rate and survival.
Methods

Selectivity experiments – A population (hereafter main population) of yellow perch larvae was established in the laboratory from egg skeins collected in Lake Michigan. Skeins were manually stripped from ripe females collected in gill nets about 1.2 km from shore at a depth of 10-20 m. Collected skeins were fertilized in the boat with milt from 3-6 males and returned to the lab for incubation. Hatching occurred within 12-14 days of fertilization and larvae were maintained in the lab in a 2.4 m diameter tank at 15-18°C under flow-through conditions. Larvae were initially fed a tank culture of rotifers and small zooplankton 4-6 times per day. Starting five days post hatch (dph) larvae were fed *Artemia* nauplii four times per day. At 10 dph food changed again to a commercial pellet food fed four times per day from automatic feeders.

Zooplankton prey were collected from two sites: nearshore Lake Michigan and Lake Nagawicka (3.7 km², mean depth 11 m), which is located 40 miles west of Milwaukee, WI. Zooplankton from nearshore Lake Michigan were collected 1.2 km from shore in waters 25 m deep by towing a 1-m diameter, 64-µm plankton net in a circular pattern 2 m below the surface. Two 15-minute tows were completed at each of two sites about 1 km apart along the same depth contour. Zooplankton were collected from nearshore Lake Michigan on each trial day and were transported live in ice chests back to the lab and maintained with mild aeration until used in selectivity trials. Zooplankton from Lake Nagawicka were collected at a site 0.5 km from shore in waters 20-30 m deep by towing a 0.5-m diameter, 64-µm mesh plankton net in a circular pattern 2 m below the surface. Four 5-minute tows were made at a single site on each collection day. Zooplankton from Lake Nagawicka were collected once
per week from mid-June until August and maintained in 1.25-m diameter tanks in the laboratory with mild aeration.

Experimental trials were conducted in 2000 and 2001. The length range for larval yellow perch used in selectivity trials combined over both years was 5.5 – 35 mm TL (2 – 50 dph). In 2000, trials were conducted with three larval ages: 2 dph (mean length 5.5 mm, SD 0.41 mm), 15 dph (8.6 mm, 0.91 mm), and 30 dph (12.3 mm, 1.4 mm). To begin each trial, 200 larvae were transferred from the main population to each of five 38-L aquaria and allowed to acclimate for seven days. These larvae were maintained at 15-18°C under flow-through conditions and were fed to satiation with live zooplankton collected from Lake Nagawicka for the first five days of the acclimation period. Feeding stopped on the sixth day of acclimation in order to ensure larvae would feed during the trial period and to minimize the presence of pre-trial zooplankton in the system. Pre-trial water samples indicated that no zooplankton remained in the trial tanks at the beginning of each trial period. For this experiment I wished to present yellow perch larvae with as wide a range of prey choices as possible to assess larval selectivity under optimal conditions. Therefore, to begin a trial, Lake Nagawicka and nearshore Lake Michigan zooplankton was mixed equally and introduced into each trial tank at a target density of 250 organisms/L. The number of zooplankton introduced into each tank was standardized based on zooplankton mass according to a predetermined mass-density relationship for mixed zooplankton (R. Fulford unpublished data).

In 2001, trials were conducted at four larval ages: 15 dph (mean length 7.9 mm, SD 0.6 mm), 30 dph (11.6 mm, 1.3 mm), 40 dph (15 mm, 1.4 mm) and 50 dph (21.5 mm, 3.0 mm). Seven days prior to each trial date, larvae were moved from the main population to the
trial tanks and the acclimation process proceeded as described above for the 2000 trials. In 2001, I wished to measure larval selectivity changes in response to differences in the zooplankton community between nearshore Lake Michigan and an inland lake (Lake Nagawicka). Therefore the experimental system was expanded to ten aquaria and two zooplankton treatments: nearshore nearshore Lake Michigan and Lake Nagawicka. Zooplankton from nearshore Lake Michigan and Lake Nagawicka were collected as described for the 2000 trials and maintained separately rather than being mixed as in 2000. For each trial, tanks containing acclimated larvae were randomly assigned to one zooplankton treatment or the other (nearshore Lake Michigan or Lake Nagawicka n=5/treatment). Zooplankton were introduced into each tank at a mean density of 250 organisms/L. Number of zooplankton introduced into each tank was standardized based on zooplankton mass and a predetermined mass to density relationship established separately for each treatment.

In both years, larvae were allowed to feed for 30 minutes and then they were removed from the tank, euthanized in MS-222 and preserved in 95% ethanol for stomach analysis. Zooplankton were sampled at the beginning and end of each 30-minute feeding trial by lowering a 4-cm diameter PVC tube onto four randomly place rubber stoppers on the bottom of each tank to collect four replicate 250-ml samples. Collected zooplankton were preserved in 95% ethanol for identification and enumeration. Data collected were used to calculate larval diet selectivity and the difference in zooplankton composition between treatments. Zooplankton samples collected at the end of each trial were also used to confirm zooplankton was not significantly depleted during the trial period. Maximum proportion of zooplankton consumed during any trial was 40% (Mean proportion 22%).
Sample analysis – Daily mean total length was calculated from length measured to the nearest 0.1 mm for 20 euthanized larvae from each trial tank. Stomach contents of preserved larvae (n=30) were identified and enumerated by taxonomic group at 8X magnification. Taxonomic zooplankton groups were defined as rotifers, copepod nauplii, cyclopoid copepods, calanoid copepods, small cladocerans and Daphnia spp. (Table 3.1). I chose to separate zooplankton into these groups based on consideration of differences in zooplankton size, morphology and what is typically reported in the diet of larval yellow perch (Bulkley et al. 1976, Schael et al. 1991). Lengths of whole prey items found in each stomach were measured to the nearest 0.1 mm with a digital imaging system (ImagePro 5.1, Media Cybernetics Inc.).

Zooplankton in samples collected from each tank were also identified and enumerated by taxonomic group based on a complete count of samples (n=8/tank) from both the beginning and end of the trial period. Mean size of zooplankton from the tanks was measured to the nearest 0.1 mm for common taxa with a digital imaging system. Differences in zooplankton community composition among treatments were examined with a MANOVA comparison (SAS 2002).

Diet Selectivity - Larval selectivity was quantified with the Chesson’s $\alpha$ statistic (Chesson 1983). Selectivity of larva $k$ for prey type $i$ is defined as:

$$\alpha_{i,k} = \frac{r_{i,k}}{\sum_{j=1}^{m} r_{j,k}} / \frac{p_j}{\sum_{j=1}^{m} p_j}$$
where $r_i$ is the proportion of prey type $i$ in the gut of larva $k$ and $p_i$ is the proportion of prey type $i$ in the tank for $m$ different prey types. Lockwood (1998) recommended using proportional data rather than absolute number for each prey item in experiments where it is difficult to control for variation in total consumption with a time-independent stopping rule. Alpha ranges from 0-1 with zero indicating complete avoidance, one indicating total preference and neutral selection defined as $1/m$.

This measure of larval selectivity has several advantages. First it is a maximum likelihood estimator (MLE) for population-level alpha. Manly (1974) established that this index is asymptotically normally distributed as would be expected from an MLE. Second, because this index is numerically associated with a measure of attack and capture probability, it can be used in the individual-based model to predict larval diet; this point will be expanded in a later section. Chesson’s alpha was calculated for each individual fish (n=30/tank) and a mean of these values for each tank represented a replicate value of $\alpha$ for each treatment (n=5/treatment).

**Zooplankton sampling** - Data regarding the zooplankton community of Lake Michigan were obtained from samples collected every three days from June to August in 2000 and 2001. Sampling was conducted with triplicate vertical hauls of a 0.5-m diameter, 64-µm mesh plankton net at each of four sites between 1 and 5 km from shore. The sampling depth was 10 m. Zooplankton were preserved in 95% ethanol and returned to the lab for identification and enumeration of taxonomic groups (Table 3.1). Three 5-ml sub-samples from each main sample were enumerated at 20X magnification in a counting wheel and the combined count
for all three sub-samples was converted to density for each prey type based on a constant sample volume (sample depth X net mouth area).

Zooplankton community data for Green Bay were based on samples collected in 1998 and 1999. Samples were collected weekly in May and June with a 0.5-m diameter, 64-µm mesh plankton net lifted from the bottom to the surface at a site 6 m deep and 0.5 km from shore near Little Tail Point, WI (Figure 1.1; Brian Belonger, Wisconsin Department of Natural Resources). The larval period for yellow perch begins about a month earlier in Green Bay compared to Lake Michigan due to earlier spring warming, so sampling periods were slightly different in Green Bay. Zooplankton were identified and enumerated as described for samples from Lake Michigan (John Dettmers, Illinois Natural History Survey). Data from different years were used because comprehensive zooplankton data were not available for both systems in the same years. All zooplankton groups collected in zooplankton samples in Green Bay and Lake Michigan were present in collections used in laboratory experiments.

*Individual-based foraging model* - In order to examine the relationship between diet and growth for larval yellow perch, I adapted a general larval fish foraging IBM (Letcher et al. 1996a) to predict growth and starvation rates of larval yellow perch from hatch to 45 dph (Figure 3.1). This model predicts daily consumption of each prey type (Table 3.1) for each individual larva \( k \) based on larval length \( l \) (mm) and a stochastic sized-based encounter rate \( (ER_{i,k}) \), handling time \( (HT_{i,k}) \) and probability of attack and capture \( (Q_{i,j}) \).
Mean encounter rate (prey/s) of larva $k$ with prey type $i$ is based on a general calculation of search volume (ml/day) multiplied by the density ($d_i$, prey/ml) of prey type $i$ in the environment (Letcher et al. 1996a):

$$\text{(2) } \text{ER}_{i,k} = \text{SV}_{i} * d_j$$

$$\text{(3) } \text{SV}_{i,k} = \text{SS}_k * \text{RA}_{i,k}$$

where search volume ($\text{SV}_i$, ml/s) is a function of larval swimming speed ($\text{SS}_k$, cm/s) and larval reactive area ($\text{RA}_{i,k}$, cm$^2$). Larval swimming speed is based on laboratory observations of larval yellow perch (Houde 1969); larval swimming speed is around 1 body length/s at hatch, rises linearly to 3 body lengths/s at 8 mm TL and remains at 3 body lengths/s for all larger larvae. Reactive area is a function of larval reactive distance ($\text{RD}_i$, mm) for a given prey type developed by Blaxter (1986). This general function assumes the reactive area for a larval fish is a semicircle:

$$\text{(4) } \text{RA}_{i,k} = (\text{RD}_{i,k})^2 * \pi * 0.5$$

where reactive distance is a function of body size for prey type $i$ and the minimum angle of acuity ($a_k$, radians) of larva $k$ based on larval length (Breck and Gitter 1983).

$$\text{(5) } \text{RD}_{i,k} = \frac{\text{PL}_i}{2 * \tan\left(\frac{a_k}{2}\right)}$$
The relationship between angle of acuity and larval length is based on laboratory observations of yellow perch larvae feeding on natural zooplankton prey (Wanzenbock et al. 1996). The mean number of prey type $i$ encountered by larva $k$ is quantified based on the number of prey type $i$ predicted to be present in the volume of water that a larva searches per second. Realized encounter rate per second ($E_{i,k}$) is randomly assigned each day based on a Poisson distribution with the rate parameter equal to $E_{i,k}$.

Probability of attack and capture for larva $k$ on prey item $i$ in a given day is given by an empirical function derived from my size-based selectivity experiments. Probability of attack and capture is a function of a joint estimation of larval preference and capture efficiency for a given prey type ($a_{i,k}$), as well as relative density ($p_i$) of that prey item in the environment. The probability ($Q_{i,k}$) that the next prey item attacked and captured by larva $k$ will be of prey type $i$ can be expressed as a function of larval selectivity ($a_{i,k}$) and the relative proportion of that prey type in the environment:

\[
Q_{i,k} = \frac{\alpha_{i,k} \cdot p_i}{\sum_{j=1}^{m} \alpha_{k,j} \cdot p_j}
\]

if the relative abundance of all prey types is equal, this function reduces to $Q_{i,k} = a_{i,k}$, (Chesson 1983). Defined in this way, the probability of attack and capture has two
components. The selectivity of the larva defined empirically in my experiments and expressed as \( \alpha_{i,k} \), and the relative abundance \( p_i \) of prey type \( i \) on a given model day.

The best-fit function between \( \alpha_{i,k} \) and larval size (5 – 35 mm TL) was found separately for each prey type \( i \) based on a comparison of the least-squared fit to the data for a series of common functions. Function types tested were linear, logarithmic, exponential, 2\(^{nd}\) order polynomial, generalized logistic and double Weibull. No single function fit the data best for all prey types. The best function for each prey type was established based on a coefficient of multiple determination (R\(^2\)) adjusted for the number of parameters in the model (Neter et al. 1990). The best-fit function for each prey type \( i \) was then used in the IBM to predict \( \alpha_{i,k} \) for prey type \( i \). Data used for calculations of \( \alpha_{i,k} \) for larvae larger than 25 mm TL included diet and field zooplankton data from the literature (Bulkley et al. 1976, Mills et al. 1984). Diet selectivity indices were calculated for yellow perch in these studies, but in cases were the index was not Chesson’s \( \alpha \), I converted the selectivity index to Chesson’s \( \alpha \). In the model, probability of attack and capture (\( Q_{i,k} \)) is calculated each day for each larva \( k \) and each available prey item \( i \).

Handling Time (HT\(_{i,k}\)) is defined as the sum of pursuit, attack and capture times and is calculated for each prey item \( i \) as a function of larval length. While data regarding prey handling time for larval yellow perch have been reported (Mills et al. 1984, Miller et al. 1992), no relationship between relative predator/prey size and handling time has been presented. Further Miller et al. (1992) noted that handling times for *Artemia* nauplii as a function of larval size for three species of larvae including yellow perch were well described by a general function. Walton et al. (1992) reported a general function describing handling time for fish larvae feeding on natural prey that has been used previously in individual-based
models (Letcher et al. 1996a). Therefore, handling time was calculated for each prey type based on size of both larva and prey with the general empirical function for larval fishes derived by Walton et al. (1992):

\[ HT_{i,k} = e^{0.264*10^{7.0151} (PL_i / l)} \]

where \( PL_i \) is the mean length of prey type \( i \) and \( l \) is the length of larva \( k \) on a given model day.

The total number of a given prey type \( i \) consumed by larva \( k \) per second of search time was calculated with a binomial probability equation with realized encounter rate \( (E_{i,k}) \) as the number of feeding events and probability of attack and capture \( (Q_{i,k}) \) as the success probability. The result from the binomial calculation was a stochastic estimation \( (x_{i,k}) \) of the number of prey type \( i \) captured by larva \( k \) per second of search time. However, this estimation of total captures per second of search time must be adjusted to account for any time spent handling captured prey. The number of successful captures \( (x_{i,k}) \) per second of search time for each prey type was reduced to account for handling time by dividing \( x_{i,k} \) by the total feeding time \( (FT_k, s) \) per second of search,

\[ FT_k = 1 + \sum_i E_{i,k} * Q_{i,k} * HT_{i,k} \]

which is equal to search time \((1 \text{ s})\) plus the combined handling time per second of search time of all prey types captured by larval \( k \) on a given day. Total feeding time \( (FT_k) \) per
second of search is based on the assumption that 1 second of successful search represents more than 1 second of feeding time as the prey item captured must be handled prior to the onset of a search for more prey. The adjusted \( x_{i,k} \) was then converted to successful captures per day by multiplying the result by the number of seconds available for foraging in a day (42,300 s) to give the number of prey type \( i \) actually eaten (\( n_{i,k} \)) per day by larva \( k \). Larval foraging was limited to the daylight period (12 hr) based on the observation that larval yellow perch are not active at night.

The number of prey type \( i \) successfully captured in a given day was then converted to mass (\( \mu g \), dry mass) by multiplying the number of each prey type \( i \) eaten in a day by the mean mass of prey type \( i \). Mean mass for each prey type was derived from a prey type-specific length-mass relationship and mean length for each prey type taken from zooplankton collected in Lake Michigan (Table 3.1). Input to the foraging model was zooplankton density (\( d_i \)) and relative abundance (\( p_i \)). Zooplankton relative abundance was based on the average seasonal pattern observed during the yellow perch larval period over two years for each prey type taken from the field data for either Green Bay or Lake Michigan respectively. Zooplankton density was manipulated as a part of the numerical experiments (described below).

*Individual-based bioenergetics model* - Total mass consumed by larva \( k \) each day was converted to individual daily growth (\( \mu g \) dry mass) in a bioenergetics sub-model adapted from two models, one developed previously for larval yellow perch (Hanson 1997) and a general larval bioenergetics model developed specifically for an IBM approach (Letcher et
The combined model predicts daily growth \( G, \mu g/day \) from predicted daily consumption \( C, \mu g/day \) from the foraging sub-model with a mass balance equation:

\[
G = (C \cdot AE) - (R + (C \cdot (U+SDA))
\]

where \( AE \) is assimilation efficiency (proportion), \( R \) is the energetic cost (\( \mu g/day \)) of respiration including both standard and active metabolic rates, and \( U (\mu g) \) and \( SDA (\mu g) \) are the proportion of daily consumption lost to excretion and standard dynamic action respectively.

Predicted daily consumption from the foraging sub-model was first compared to a maximum daily consumption value that is based on larval mass and temperature:

\[
C_{\text{max}} = 2.82 \cdot W_k^{0.85} \cdot f(t)
\]

where \( W_k \) is the mass of larva \( k \) and \( f(t) \) is a function of daily water temperature and is based on optimal and maximum temperature for consumption in larval yellow perch. Mass specific exponents in this function are from Letcher et al. (1996a) and the water temperature dependence function \( f(t) \) was presented by Hanson (1997). I used the maximum consumption – mass relationship provided by Letcher et al. (1996a) because it predicts consumption of the smallest larvae to be close to 200% of their body weight per day. The similar function provided by Hanson (1997) is for later life stages of yellow perch and underestimates maximum daily consumption for larvae. Higher consumption rates are in agreement with laboratory observations of larval feeding (Letcher et al. 1996b) and were
necessary for larval fish growth in the model. If predicted daily consumption exceeded Cmax, daily consumption was set equal to Cmax for that larva on that day. Daily consumption was then adjusted for assimilation efficiency (AE), which ranged from 0.6 at hatch to a maximum value of 0.8 for larvae larger than 15 mm TL (Letcher et al. 1996a). Assimilation efficiency is given by

\[ AE_k = 0.8 \times (1 - 0.25e^{-0.0002(W_k - 10)}) \]

where \( W_k \) is the mass of larva \( k \). This general model for assimilation efficiency was used because comparable values in the yellow perch specific model given by Hanson (1997) did not change with ontogeny, and assimilation efficiency typically does change with size for larval fishes.

Total respiration costs (R) are a function of specific metabolic rate (SMR, \( \mu g/\mu g \) /day) and larval mass. SMR is given by the mass- and temperature-dependent function for larval yellow perch presented by Hanson (1997). Respiration costs are adjusted for active metabolic costs with an activity multiplier for larval yellow perch (4.4, Post 1990).

\[ R = SMR \times W_k \]
\[ SMR = 0.0065 \times W_k^{-0.2} \times f(t) \times 4.4 \]

Losses to excretion (U) and standard dynamic action (SDA) are each fixed at 15% of consumption (Hanson 1997). Caloric density of both larvae and prey was set at 600 cal/g (Post 1990).
Input to the bioenergetics sub-model was daily mass of prey consumed by larva $k$ and daily mean temperature. Daily mean temperature data were taken from a variety of sources depending on the system being modeled. Temperature data for nearshore Lake Michigan were taken from hourly temperature records collected 1 m below the surface at a site located 1.2 km from shore due east of Texas Rock near Milwaukee, WI (42°59’60” N, 87°50’38” W) from June to August 1999 – 2001 (Fulford unpublished data). Temperature data for Green Bay were taken from temperature data collected hourly at the surface in the intake canal for the Pulliam power plant in Green Bay, WI, and from weekly temperature measurements taken at the surface 0.5 km from shore near Little Tail Point on the southwestern side of Green Bay. Little Tail Point is located 15 km north of the City of Green Bay (Figure 1.1). The area around Little Tail Point is a known spawning area for yellow perch (Wisconsin Department of Natural Resources unpublished data).

Each model simulation began with 1000 larvae and initial size was randomly assigned to each larva from a normal distribution (Mean=5.7 mm, SD=0.3 mm). Initial mass was calculated from randomly assigned length according to a larval yellow perch specific mass-length formula:

\[
W_k = 0.519 \times \text{Length}^{3.293}
\]

where length is larval total length (mm) and $W_k$ is dry mass (µg) of an individual larva (C. Heyer, T. Miller and B. Letcher unpublished data, Mills and Forney 1981). During a model run, a larva could not lose length but could lose mass based on the difference between total daily consumption predicted by the foraging submodel and calculated daily metabolic costs.
Each model day, larvae were allowed to forage to predict total daily consumption from the available prey assemblage. Predicted consumption was then converted to individual growth in the bioenergetics sub-model. At the end of the bioenergetics sub-model run, the model checked to see if each larva gained mass or lost mass and if each larval starved to death based on the ratio of its current mass to its previous maximum mass (Letcher et al. 1996a&b). If a larva lost more than 53% of its previous maximum mass at any point in a model run, then that larva starved to death. If the larva lived, individual larval mass was then updated for the next model day. If the larva gained mass, then length was updated based on the length to mass relationship under the constraint that a larval cannot lose length and can only increase in length if its present mass exceeds its previous maximum mass. Model output was larval size-specific diet data, individual and cohort mean growth rate over the period from hatch to 45 days, distribution of size at age for the entire cohort and the proportion of larvae that starved to death during each model run.

**Numerical experiments** - I conducted two numerical experiments with the foraging and growth IBM to address two questions. First, I wanted to establish that the model would accurately predict diet for larvae exposed to different prey assemblages. In order to accomplish this, the functions relating $\alpha_{i,k}$ to larval total length were fit to a sub-set of the selectivity trial data (n=45). I then used the model to predict the diet of larvae exposed to the prey assemblage in the remaining set of reference data (n=10). These predictions were then compared to observed diet for larvae used in the reference trials with a Chi-squared analysis.

Second, I asked how larval growth rate, size at age and likelihood of starvation are affected by differences in zooplankton community composition between Green Bay and Lake
Michigan. The model was run with two separate prey assemblages consisting of zooplankton composition observed in nearshore Lake Michigan in 2000-2001, or in Green Bay in 1998-99. Simulations were conducted at 50, 100, 150, 200 and 250 prey/L for each zooplankton assemblage. A broad range of zooplankton densities was used in order to explore more generally relevant patterns in growth and survival as a function of prey density than observed in just the two years for which I had data. I also wanted to explore more directly how the interacting effects of prey density and composition on larval growth and starvation mortality differ between nearshore Lake Michigan and Green Bay. The range of zooplankton density used in this experiment approximates the full range of daily and site-specific mean zooplankton densities observed in both nearshore Lake Michigan and Green Bay (Wisconsin Department of Natural Resources unpublished data). Three replicate model runs were conducted for each combination of zooplankton density and zooplankton assemblage to account for variability due to stochastic functions in the model.

Results

Selectivity experiments – The three zooplankton assemblages used in selectivity trials (nearshore Lake Michigan, Lake Nagawicka, and Mixed) differed significantly in composition (Wilks’ Lambda $F_{12,94} = 12.34$, $p<0.0001$). The Lake Michigan treatment was dominated (>70%) by rotifers, while the Lake Nagawicka assemblage was comprised largely of daphnia and cyclopoid copepods. The mixed assemblage was the most balanced among prey types but remained high in rotifers (>40%). Mean initial zooplankton density in the trials tanks was 382 prey/L and ranged from 112 – 782 prey/L. The higher than expected mean and variance in zooplankton density in the tanks was due largely to variance in rotifer
density because rotifers can vary in number without having a significant affect on total mass of a zooplankton sample. High zooplankton density in the tanks should not bias my measurements of selectivity as long as density is high enough to generate larval feeding activity.

Chesson's $\alpha$ values higher than $1/m$ (0.166) are interpreted as positive selection by larval yellow perch for a given prey type and values below $1/m$ are interpreted as negative selection. For the analysis of selectivity patterns, selection was interpreted as neutral if the 95% confidence interval for $\alpha_i$ at a particular larval size included $1/m$ and either positive or negative if the 95% confidence interval was higher or lower than $1/m$ respectively. Mean larval length on each trial day was 5.5, 8.6 and 12.4 mm TL respectively in 2000, and 7.9, 11.6, 15 and 21.5 mm TL respectively in 2001.

Larval yellow perch displayed size-based selectivity patterns that were specific to individual prey types (Figure 3.2). Values of $\alpha$ for rotifers indicated strong positive selection by 5.5 mm larvae, but dropped quickly to near zero indicating negative selection at all larger larval sizes. Values of $\alpha$ for copepod nauplii were also highest for larvae at 5.5 mm TL, but selection was neutral rather than positive. Selection for nauplii was generally neutral up to 15 mm TL and then became negative, but $\alpha$ values showed no trend with size (Figure 3.2A).

Selection differed for cyclopoid and calanoid copepods (Figure 3.2B). Values of $\alpha$ for cyclopoid copepods were near $1/m$ for the smallest larvae suggesting selection for cyclopoids was initially neutral. Alpha values rose sharply for larvae at 8 mm TL indicating a period of strong positive selection for early feeding larvae, then overlapped $1/m$ for larvae larger than 12 mm TL suggesting a generally neutral selectivity pattern at larger larval sizes. Alpha values were generally below $1/m$ for larvae at 20 mm TL, but the 95% confidence
interval included $1/m$ so selection was still interpreted as neutral at this larval size. Data from the literature also suggest that selectivity for cyclopoid copepods by larvae at 26.5 mm TL is neutral (Bulkley et al. 1976).

Values of $\alpha$ for calanoid copepods were near zero for the smallest larvae suggesting negative selection for calanoids by yellow perch larvae at 5.5 mm TL (Figure 3.2B). Values of $\alpha$ rose with larval size beginning around 8 mm TL, but the 95% confidence interval included $1/m$ for larvae up to 11.6 mm TL indicating rising but generally neutral selectivity by larvae up to this size. Values of $\alpha$ were clearly above $1/m$ for larvae at 15 mm TL indicating positive selection for calanoid copepods by larger larvae (Figure 3.2B). Data from the literature suggest that selection for calanoid copepods by larvae at 26.5 and 35 mm TL is consistently positive (Bulkley et al. 1976, Mills et al. 1984).

Values of $\alpha$ for cladocerans all showed similar patterns with slightly different shapes (Figure 3.2C). Values of $\alpha$ for small cladocerans were below $1/m$ for all larvae < 12 mm TL, but were close to $1/m$ for larvae between 12 and 20 mm TL. Values of $\alpha$ rose above $1/m$ for larvae at 21.5 mm TL and data from the literature (Bulkley et al. 1976) suggest that values of $\alpha$ for larvae between 26 and 35 mm TL are above $1/m$ indicating that selection for small cladocerans by yellow perch larvae larger than 21.5 mm is consistently positive.

Values of $\alpha$ for Daphnia spp. were below $1/m$ for larvae at 5.5 and 8 mm TL, but were near or above $1/m$ at 11.6 and 12.2 mm TL suggesting that selection for Daphnia spp. by larvae became positive for larvae around 12 mm TL. Values of $\alpha$ for larger larvae did not rise above $1/m$ in this experiment, but mean relative density of daphnia spp. ranged from 0.01% to 0.03% in replicate tanks at all larger larval sizes tested. These low density values suggest that negative selection in these trials for daphnia was due to low encounter rates.
rather than larval preference. Selectivity data from the literature for larvae at 26.5 and 35 mm TL suggest positive selection for daphnia by larger larval yellow perch (Mills et al. 1984, Schael et al. 1991) and I used the literature data in describing selectivity for Daphnia spp. in the model.

Parameterizing the IBM – I developed prey type-specific functions relating Chesson’s α to larval total length for the six prey types used in this analysis (Figure 3.3, Table 3.2). Selectivity was always near zero for any prey type in my selectivity trials when its relative abundance was below 0.03%. When relative density for a particular prey item was below this threshold low selectivity for that prey item likely occurred because larvae did not encounter this rare prey type, not due to negative selection. Therefore, trials for which any prey item was less than 0.03% of the assemblage were not used to fit the larval size – selectivity relationship for that prey item.

Selectivity for rotifers was best described by a power function. The model fit (measured by coefficient of multiple determination adjusted for the number of parameters in the model) was highest for rotifers among all prey types. I observed no relationship between larval selectivity for copepod nauplii and larval size; selectivity for nauplii in the model was described with the mean value of α for nauplii across all larval sizes (0.07). Selectivity for cyclopoid copepods was best described by a second-order polynomial function with a minimum α-level set at 1/m. This function allowed for the steep rise in α for larvae around 8 mm TL and predicted neutral selection for larvae larger than 12 mm TL. Selectivity for calanoid copepods was best described by a logarithmic function with a maximum α value of 0.4 for larvae larger than 15 mm TL. Selectivity for both small cladocerans and daphnia
were best described by a generalized logistic function. Values of $\alpha$ for both cladoceran groups were low initially and rose with increasing larval size.

**Zooplankton community composition** - The nearshore Lake Michigan zooplankton assemblage was dominated numerically by rotifers (80%; Figure 3.4). Prey densities across sites in nearshore Lake Michigan in 2000-01 were between 50 and 200 prey/L with a mean density of 75 prey/L between years. In contrast, the prey assemblage of Green Bay was more diverse. Cladocerans and copepods were nearly equal in abundance and no prey type represented more than 50% of the total assemblage at any time over the larval period (Figure 3.4). Prey densities in 1998-99 in Green Bay were between 50 and 300 prey/L with a mean density of 124 prey/L over both years.

**Numerical experiments** - Larval diet data from the independent reference dataset were used to test the predictive ability of my empirical selectivity model. These data were for larvae between 7 and 15 mm TL and were broken into two sets: larvae exposed to a zooplankton community from nearshore Lake Michigan and larvae exposed to a zooplankton community from Lake Nagawicka. The nearshore Lake Michigan assemblage was dominated by rotifers and calanoid copepods, and the Lake Nagawicka assemblage was dominated by *Daphnia* spp. The model predicted larval diet well for both prey assemblages (Figure 3.5).

Model predictions did not differ significantly from observed diet ($\chi^2 = 1.23$, d.f. = 5, p > 0.1), which suggests the model performed well. Diets for larvae exposed to the nearshore Lake Michigan assemblage were dominated by calanoid and cyclopoid copepods with rotifers and cladocerans being a minor dietary component. In contrast, diets of larvae
exposed to the Lake Nagawicka assemblage were comprised mostly of *Daphnia* spp. with calanoid copepods a distant second in relative dietary abundance. There were noticeable differences between what was available and what was eaten by larvae, particularly for the nearshore Lake Michigan treatment where larvae avoided rotifers despite their high relative abundance. However, available prey composition did not differ significantly from either observed diet or model predictions ($\chi^2 = 1.3$, d.f. = 5, $p > 0.1$).

Larvae exposed to the nearshore Lake Michigan assemblage in the model fed mainly on rotifers and copepods initially and made a transition to mainly larger calanoid copepods as they grew, mainly at the expense of rotifers (Figure 3.6). Larvae exposed to the Green Bay assemblage in the model fed largely on cyclopoid copepods initially, avoided the smaller rotifers, and shifted gradually to a diet split between small cladocerans and *Daphnia* spp. as they increased in size. The transition to small cladocerans and *daphnia* was predicted to occur around 20 mm TL and these two items dominated larval diet in Green Bay for the remainder of the model run (Figure 3.6).

These observed differences in diet between larvae exposed to different prey assemblages translated into differences in both growth and survivorship in the model. Larvae allowed to forage on the Green Bay assemblage had a higher predicted mean growth rate compared to nearshore Lake Michigan larvae at all prey densities except the lowest (50/L). Growth rates for larvae exposed to the nearshore Lake Michigan assemblage did not rise substantially until prey density rose above 100 prey/L (Figure 3.7). Growth rates for larvae exposed to a Green Bay prey assemblage were also low at a prey density of 50/L but rose more rapidly between 50 and 200 prey/L. Further, more than 50% of simulated larvae exposed to the nearshore Lake Michigan assemblage starved at prey densities <150 prey/L.
(Figure 3.8). Starvation rates for larvae exposed to the nearshore Lake Michigan assemblage declined linearly with increasing prey density over the entire density range (50 – 250 prey/L). In contrast, larvae exposed to the Green Bay assemblage had a high starvation rate at the lowest density, but it dropped rapidly to around 20% or lower for prey densities at or above 150 prey/L (Figure 3.8).

These differences in growth and survivorship were reflected in larval size distributions at the end of the model runs (Figure 3.9). Larvae exposed to the Green Bay assemblage at a prey density of 250 prey/L were generally larger than those larvae feeding on the nearshore Lake Michigan assemblage at the same prey density. Both distributions were bimodal, but the major mode in the length distribution for larvae exposed to the Green Bay assemblage (mode centered on 34 mm TL) included most of the larval survivors. The minor mode in the length distribution of the Green Bay assemblage (at ~20 mm TL) overlapped the major mode in the length distribution of the nearshore Lake Michigan assemblage (at ~18 mm TL). The minor mode in the length distribution of larval survivors exposed to the nearshore Lake Michigan assemblage (7 mm TL) was comprised of larvae demonstrating little or no growth over the model period. These slow growing larvae were not predicted to starve, but they would have been highly vulnerable to size-dependent predation and most likely would not have survived if exposed to predation in the model (Chapter 2). The size distribution of larvae exposed to the Green Bay assemblage was also bimodal, but both groups showed positive growth indicating a more consistent growth rate between individuals.

The size distribution of larval survivors exposed to both prey assemblages at a lower mean density (100/L) had similar length ranges as observed at the higher prey density, but the peaks were at a smaller larval size in both cases (Figure 3.9). For larvae exposed to the
nearshore Lake Michigan assemblage, the larger length peak dropped from 18 mm TL to 13 mm TL. For larvae exposed to the Green Bay prey assemblage the larger length peak dropped from 36 mm TL to 23 mm TL. Further, in the case of larvae exposed to the nearshore Lake Michigan assemblage, the distribution was not bimodal as observed in this distribution at a high prey density. Prey density appears to affect how many individuals achieve the maximum observed growth rate, while prey community composition affects the larval length range and the magnitude of the maximum observed growth rate.

The bimodality in the size distributions of larval survivors predicted by the model appears to be the result of an interaction between zooplankton community composition and timing of individual hatch. Larvae hatched at times when small copepods were abundant selected for copepods at smaller larval sizes than larvae hatched when small copepods were rare relative to other available prey. This diet shift resulted in a higher initial larval growth rate and this early growth advantage was still detectable in the size distribution of larvae 30 days after peak hatch.

Discussion

Diet composition of larval yellow perch is well described in the model by a set of empirical functions based on larval selectivity and prey community composition. Larval yellow perch appear to make three distinct transitions in selection throughout ontogeny. Larval yellow perch initially showed positive selection for rotifers (Figure 3.3). This early preference for rotifers has been observed in other oligotrophic systems (Siefert 1972). Surprisingly, model results suggest that rotifers have limited value for growth of larval yellow perch. Larvae that switch to small copepods quickly have a distinct growth advantage
over larvae that do not, but this energetic conclusion does not translate to a high preference for copepods in early-stage larvae. In fact, the results from selectivity experiments and numerical simulations suggest that rotifers are initially more desirable than copepods despite the fact that they do not result in high or even positive growth. It may be that larval yellow perch select rotifers simply because they are much more abundant and easy to catch, and that this initial positive selection is dependent on limited foraging ability rather than true preference. The full recruitment of visual acuity occurs significantly after first-feeding in larval yellow perch (Wahl et al. 1993); first-feeding larvae are likely to select prey based more on availability than optimality. This conclusion is supported by the fact that larvae exposed to a Green Bay prey community (i.e., low rotifer abundance) switched to small copepods earlier than larvae exposed to a nearshore Lake Michigan prey community (i.e., high rotifer abundance). These results suggest that individual larvae that are exposed to higher relative densities of small copepods close to the time of first feeding should have a significant growth advantage over larvae that are not.

A second selective transition was a shift from neutral to positive selection for copepods that occurred for larvae between 8 and 12 mm TL. Selection first became strongly positive for cyclopoid copepods for larvae at 8 mm TL, and this shift appeared independent of copepod relative abundance. Cyclopoid copepods are a medium sized prey type. Mean size for cyclopoid copepods collected in nearshore Lake Michigan and Green Bay was 0.44 mm and the size range for the combined zooplankton community was 0.08 – 1.28 mm. The gape size of an 8-mm larval yellow perch is around 0.5 mm (Schael et al. 1991) so an increased preference for cyclopoid copepods at this point is expected based on increases in capture efficiency.
However, the strong increase in selection for copepods in early feeding larvae is not predicted by a foraging model based on size alone (Letcher et al. 1996a). Strong positive selection for copepods observed in my experiments and predicted by the empirical selectivity model suggests that cyclopoid copepods possess characteristics that make them a highly desirable and obtainable prey type for early feeding stage yellow perch larvae. However, the brief larval size window of this positive selection suggests that cyclopoid copepods are largely a transitional food resource and that larval perch prey selection is shifting rapidly with growth during this period. Selection for calanoid copepods changed from negative to neutral and finally became positive for larvae around 12 mm TL. Calanoid copepods likely possess many of the positive attributes of cyclopoid copepods in a slightly larger package, and larvae appear to make this selective transition as soon as possible.

A final selective transition was observed for larvae around 15-20 mm TL that was dependent on prey relative abundance. At this size, larval perch begin to show a change in selectivity from negative to positive selection for cladocerans. Selection was increasing more rapidly for \textit{Daphnia} spp. but smaller cladocerans were always more abundant. As a result, smaller cladocerans begin to appear earlier in larval diets. Larval perch switched to eating cladocerans at intermediate sizes even when cladocerans comprised only 1% of the prey assemblage. However, the nearshore Lake Michigan prey assemblage frequently had less than half a percent cladocerans in 2000-01, and larvae exposed to this prey community shifted their selection to larger calanoid copepods. Larval yellow perch larger than 16 mm TL showed positive selection for calanoid copepods in all assemblages but the importance of calanoids tended to vary based on the relative abundance of cladocerans. This
cladoceran/calanoid tradeoff was a selection pattern that remained constant for larval sizes larger than 20 mm TL.

Positive selection for cladocerans has been observed for yellow perch larvae in other systems including Lake Mendota (Schael et al. 1991), and Oneida Lake (Hansen and Wahl 1981, Mills et al. 1984), but the timing of this transition with respect to larval size varies greatly. Variance in the observed onset of positive selection for *daphnia* may be due in part to variance in the composition of the *daphnia* complex between systems. *Daphnia* collected in Green Bay, Lake Nagawicka and nearshore Lake Michigan were mainly medium-bodied *daphnia* (0.62 - 1.17 mm). In contrast, Oneida Lake is dominated by *Daphnia pulex*, which has a size range of 0.7 – 2.1 mm (Mills et al. 1984). Positive preference for daphnia was evident at a smaller larval size in my data compared to similar data from other systems; this difference is most likely due to observed differences in the size of the *daphnia* complex. Such differences are an important reason to understand both size and taxonomic selectivity for larval perch.

Prey selection is a complicated process made up of prey preference, capture efficiency, and prey availability. Traditional approaches to modeling larval foraging have used optimization rules such as maximization of the benefit/cost ratio (Eggers 1977). This approach has two distinct disadvantages for comparing feeding selectivity between different prey assemblages. First, optimization rules are frequently based only on inherent and readily measurable quantities of prey such as size. In other words, decisions regarding prey type *i* are based on a measure of profitability of prey type *i* that does not directly account for the relative abundance of all available prey types. As a result, optimization rules are not well suited to predicting gradual shifts in selection such as shifts caused by subtle changes in prey
relative abundance. Changes in diet composition in optimality models often occur abruptly when prey density crosses a discrete threshold. Such changes result in prey types being included or not included in the diet in a 'knife-edge' fashion not representative of the real world (Stephens and Krebs 1986).

A second disadvantage of optimization rules is that they require an assumption regarding what criteria would be of value to the larva in order to rank prey types. This criterion is usually size, as this is the only numerically and biologically tenable metric available (Eggers 1977). Prey frequently differ in other significant and non-quantifiable ways such as behavior and morphology (Kerfoot et al. 1980).

My empirical approach to predicting prey selection for larval yellow perch allows for selection without assumptions regarding optimal criteria. That is, size is considered as a criterion for selection just as it is in an optimality model, but it is bundled with other less mathematically tenable characteristics of prey that may also be important. This approach exploits a selectivity metric (Chesson's alpha) that describes changes in larval preference, is mathematically tenable, and is resistant to most changes in the prey assemblage. There is a minimum relative abundance greater than zero below which selectivity data are affected, but it was extremely low in this study (0.03%) and is only likely to be important for extremely simple prey communities (Confer and Moore 1987). By utilizing empirical data I was able to more accurately describe how selection for a particular prey item may change both as a function of larval size and as larvae are exposed to different prey assemblages.

Two potential sources of bias exist in this empirical approach to measuring larval selectivity. First, a significant amount of variation among prey may exist within the taxonomic prey types (Table 3.1). I have tried to define prey types in my model so that this
bias is minimized. It does appear that variation among species of *daphnia* may be important. The onset of positive selection for *daphnia* occurred relatively early in my selectivity trials compared to observations of yellow perch in smaller systems, likely due to differences in the dominant *daphnia* species between systems like Oneida Lake and Lake Michigan. Differences within the *daphnia* species complex would need to be addressed in order to increase the generality of model results. These differences strengthen the argument that comparisons of selectivity data for larval yellow perch between systems warrant greater scrutiny.

A second potential source of bias in this analysis is differential digestion of hard-bodied vs. soft-bodied zooplankton in larval guts (Sutela and Huusko 2000). Smaller, softer-bodied prey such as rotifers would be less likely to be present in the gut, so selection for these prey types might be underestimated. By limiting the foraging experiments to half an hour, I likely minimized the impact of this bias in comparison to field-collected larvae, for which total digestion time is unknown. Digestive bias may also be a reason why rotifers are not often cited as a significant item in larval guts from field data.

Diet of larval yellow perch has been shown to change during ontogeny (Bulkley et al. 1976, Mills et al. 1984, Schael et al. 1991). Both mean size and size distribution of selected prey items increase with larval total length. However, upon closer inspection, it is evident that larvae of comparable size in different systems can make very different foraging decisions. For instance, larval perch in Clear Lake, IA fed primarily on copepods up to a larval size of 25 mm TL (Bulkley et al. 1976), but larvae of similar size in Oneida Lake, NY showed a strong positive selection for *Daphnia* spp. (Mills et al. 1984). Such data suggest that it may be important to account for prey community composition, as well as inherent
preferences, when using selectivity criteria to predict diet of larval yellow perch. Moreover, the importance of community composition to a comparison of larval diet between foraging habitats will only increase as differences in community composition increase, which is more likely with increasing differences in geography and size between systems.

Larval response to changes in prey community composition between nearshore Lake Michigan and Green Bay resulted in significant changes in patterns of growth and survival as a function of prey density. Model results suggest that larval fish in Green Bay grow faster and are less likely to starve to death than in nearshore Lake Michigan at comparable prey densities. Based on differences in the size distribution of survivors, larval yellow perch growth rates in Green Bay are also predicted to be more variable among individuals, resulting in a higher maximum growth rate among individuals. High growth variability among individuals means that larvae in the upper portion of the growth rate distribution are likely to reach a refuge from size-dependent predation faster; this may increase overall survival (Rice et al. 1993).

Larvae in nearshore Lake Michigan are also predicted to be less responsive to changes in prey abundance than larvae in Green Bay. Starvation rate was over 80% and mean growth rate was less than 0.1 mm/day for larvae in both Green Bay and nearshore Lake Michigan at the lowest prey density modeled. Starvation rate decreased and growth rate increased with increasing prey density for nearshore Lake Michigan in the model, but growth rates did not approach observed growth rates from the field (0.12 – 0.57 mm/day) until prey densities exceeded 150/L. In contrast, both growth rate and starvation rate of larvae exposed to a prey assemblage from Green Bay improved more rapidly as prey density increased. These differences in response of larval vital rates to changes in prey density between systems
are particularly significant in light of observed differences in prey density between Lake Michigan and Green Bay.

Based on conditions in 1998-1999 mean prey density in Green Bay (125/L, SD 59/L) was high enough that a substantial portion of larval yellow perch (i.e., at least half) would have encountered prey densities adequate for high growth rates and low risk of starvation in these years. In contrast mean prey density in nearshore Lake Michigan was lower (75/L, SD 19/L) and places a larger proportion of the population in conditions that are predicted to result in low growth and a nearly total loss to starvation, due in part to a lower mean prey density in nearshore Lake Michigan. However equally important is that prey community composition in Lake Michigan causes larval growth rates and risk of starvation to change slowly in response to changes in prey density, so local prey density must rise substantially above the mean to result in good larval survival. In nearshore Lake Michigan 25% of my prey density samples exceeded 150/L. These locally high densities are high enough to predict good growth and low starvation in nearshore Lake Michigan for some portion of a larval perch cohort, but growth and starvation are predicted to be less consistent when compared to conditions in Green Bay.

These results suggest that in years when other forms of mortality such as predation are low in Green Bay, larval survival will likely be high, but variability in these other forms of mortality will likely be less important to larval recruitment in nearshore Lake Michigan. Larval survival in nearshore Lake Michigan is primarily dependent on larvae finding high-density patches of prey in order to grow. A strong initial dependence on foraging success means that in years when larval overlap with optimal prey is low year class strength will likely be low, but in years when this overlap is high year class strength could be high or low,
depending on the importance of other forms of mortality. Consequently, good larval survival and a subsequent strong year-class will occur less often in Lake Michigan than in Green Bay, increasing the dependence of longer-term population stability for yellow perch in Lake Michigan on extrinsic factors affecting larval survival.

These findings are based on prey community differences at a large scale (i.e., between systems). I did not attempt to take into account small-scale factors such as changes in foraging efficiency due to water clarity or turbulence. Furthermore, because I am comparing the zooplankton assemblages of Green Bay in 1998-99 to nearshore Lake Michigan 2000-01, I cannot make predictions about the year-class in Green Bay being better than that in Lake Michigan in any particular year. Nonetheless, by studying the effect of community composition across multiple years and a range of zooplankton densities, it is possible to address the larger question of whether a single model of foraging behavior is sufficient to describe larval diet across a range of prey communities. Model results suggest this is the case.

Several key elements of behavior have come out of this prediction as well. First, initial foraging choices may be more dependent on capture efficiency than a strategy of optimizing energetic benefit. First feeding larvae may be forced to make a choice between sub-optimal prey and no prey at all until they achieve some optimal foraging threshold. In fact, the model results suggest that larvae that achieve this threshold soonest have a large energetic advantage over smaller members of their cohort. This notion of the ‘haves’ and ‘have nots’ during the early larval stage has been observed in field data. Post et al. (1997) observed a bi-modality in the size structure of perch populations in Lake St George, Ontario in some years but not in others. They attributed this within-cohort size difference to density-
dependent competition, but this splitting of a cohort into two size groups is also consistent with an early growth advantage for part of the cohort that may be related to earlier onset of optimal feeding.

Between 8 and 12 mm TL, yellow perch larvae make a transitory shift to copepods and then make a third shift to cladocerans during the later larval period if these prey are available. This preference for cladocerans has been observed in both field sampling and laboratory analysis of larval diet (Hansen and Wahl 1981, Mills et al. 1984, Mills et al. 1989). Yet the density of cladocerans in Lake Michigan is low at present (<1%) particularly in the nearshore region, and this results in a trade-off in which later-stage larvae feed primarily on calanoid copepods. This strong preference for cladocerans during the later larval stage suggests that they are an optimal prey item for larval yellow perch growth and survival, and the poor cladoceran community in Lake Michigan may limit larval growth making larvae more susceptible to mortality.

The cause of the present low abundance of cladocerans has been blamed on alewife predation, but competition from larger invasive cladocerans and low productivity caused by zebra mussels and reductions in important nutrients such as phosphate during the late 1980s are probable contributing factors (Madenjian et al. 2002). In particular, efforts to reduce the delivery of phosphate into Lake Michigan have been very successful. However, it is important to acknowledge that this success may have contributed to a reduction in fish production. Population recovery for yellow perch may be closely associated with our ability to increase lake productivity by increasing the concentration of limiting nutrients such as phosphorus, as well as to decrease the impact of invasive species. Such actions should help
the zooplankton community shift back to a more diverse cladoceran assemblage observed historically in Lake Michigan (Makarewicz et al. 1995).

It is important to have an understanding of how different factors affecting growth and survival of yellow perch populations may differ in importance between systems prior to making comparisons between those systems. Factors found to be important to growth and survival of larval yellow perch in smaller systems include density-dependence (Post and McQueen 1988, Sanderson et al. 1999), predation (Campell 1998, Mayer et al. 2000), inter-specific competition (Roseman et al. 1996), and over-winter mortality (Post and Evans 1989). Due to the size and depth of Lake Michigan, density-dependent effects are going to be ameliorated by larval dispersion, and long-term survey data indicate that year-class strength is highly correlated with juvenile abundance in the fall (Clapp and Makauskas 2002), which suggests that over-winter mortality is not a significant factor. The importance of predation and competitive interactions with other species such as alewife remains open. Nevertheless, my results suggest that the interaction of prey community composition in Lake Michigan with larval yellow perch selectivity patterns results in a strong relationship between prey availability and larval survival not observed in smaller systems.

Yellow perch life history seems optimized for smaller, more productive systems where survival during the pelagic phase is more consistent between years. For populations of yellow perch in systems such as Green Bay or Oneida Lake that exhibit higher larval survival population regulation is more dependent on factors regulated by perch density such as over-winter mortality or predation during the juvenile stage (Mayer et al. 2001). In Lake Michigan where annual recruitment appears dependent on density-independent factors such as spatial and temporal overlap with prey, recruitment patterns observed in smaller systems
would have less value for predicting annual recruitment. In such cases, the individual-based modeling approach is a valuable and flexible tool for a comparative assessment of factors important to larval survival.

For larval yellow perch the importance of diet choice made based on limited ability (e.g. first feeding) and limited availability of optimal prey items (e.g., Lake Michigan) can be both strong and important for describing patterns in annual recruitment success. Under these conditions, it is vital to describe changes in prey community composition throughout the pelagic zone of Lake Michigan to better characterize how foraging-mediated recruitment patterns may be important to predicting population recovery.

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selection of cladocera, copepoda and rotifera from the plankton, periphyton, and


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Table 3.1 Mean lengths of zooplankton were taken from field samples collected in Lake Michigan and Green Bay 1998 – 2001. Lengths were converted to mass with length-dry mass relationships taken from the literature. Function used is \( \text{Mass} = a \times \text{length}^b \).

<table>
<thead>
<tr>
<th>Prey Item</th>
<th>Mean Length (mm)</th>
<th>intercept (a)</th>
<th>exponent (b)</th>
<th>Mass (µg)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rotifers</td>
<td>0.13</td>
<td>1.84</td>
<td>1.44</td>
<td>0.10</td>
<td>Dumont 1975</td>
</tr>
<tr>
<td>Copepod nauplii</td>
<td>0.2</td>
<td>3.0</td>
<td>1.71</td>
<td>0.19</td>
<td>Culver et al. 1985</td>
</tr>
<tr>
<td>Calanoid copepods</td>
<td>0.54</td>
<td>6.19</td>
<td>1.96</td>
<td>1.85</td>
<td>Culver et al. 1985</td>
</tr>
<tr>
<td>Cyclopoid copepods</td>
<td>0.43</td>
<td>6.66</td>
<td>2.89</td>
<td>0.58</td>
<td>Culver et al. 1985</td>
</tr>
<tr>
<td>Sm. cladocerans</td>
<td>0.3</td>
<td>17.74</td>
<td>2.22</td>
<td>1.2</td>
<td>Culver et al. 1985</td>
</tr>
<tr>
<td><em>Daphnia</em> spp.</td>
<td>0.9</td>
<td>7.50</td>
<td>1.56</td>
<td>6.4</td>
<td>Culver et al. 1985</td>
</tr>
</tbody>
</table>
Table 3.2. Summary data for the model fit between Chesson’s $\alpha$ and larval total length (L, mm) based on experimental data. Larval size range was 5.5 – 35 mm TL for all functions and data for larvae > 25 mm TL include data from the literature (see text).

<table>
<thead>
<tr>
<th>Prey Item</th>
<th>Model Type</th>
<th>Parameters</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rotifers</td>
<td>Power: $\alpha = a*L^b$</td>
<td>$a = 193499$</td>
<td>0.89</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$b = -7.64$</td>
<td></td>
</tr>
<tr>
<td>Copepod Nauplii</td>
<td>No trend</td>
<td>Mean $\alpha = 0.07$</td>
<td>N/A</td>
</tr>
<tr>
<td>Cyclopoid Copepods</td>
<td>Polynomial: $\alpha = a_1<em>L^2 + a_2</em>L + a_3$</td>
<td>$a_1 = -0.042$</td>
<td>0.67</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$a_2 = 0.75$</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$a_3 = -2.60$</td>
<td></td>
</tr>
<tr>
<td>Calanoid Copepods</td>
<td>Ln(x): $\alpha = a*\ln(L) + b$</td>
<td>$a = 0.272$</td>
<td>0.68</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$b = -0.3834$</td>
<td></td>
</tr>
<tr>
<td>Small Cladocerans</td>
<td>Logistic: $\alpha = \frac{a_1}{1 + \left( \frac{a_1}{a_2} - 1 \right) e^{-a_4L}}^{1/a_4}$</td>
<td>$a_1 = 0.40$</td>
<td>0.65</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$a_2 = 0.09$</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$a_3 = 13$</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$a_4 = 0.031$</td>
<td></td>
</tr>
<tr>
<td>Daphnia spp.</td>
<td>Logistic: $\alpha = \frac{a_1}{1 + \left( \frac{a_1}{a_2} - 1 \right) e^{-a_4L}}^{1/a_4}$</td>
<td>$a_1 = 0.445$</td>
<td>0.86</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$a_2 = 0.092$</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$a_3 = 20$</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$a_4 = 0.029$</td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.1 Flow chart summarizing the foraging and growth individual-based model used for the numerical experiments.
Figure 3.2 Chesson’s $\alpha$ for larval yellow perch feeding on $m=6$ prey types; rotifers and copepod nauplii (A), cyclopoid and calanoid copepods (B), or small cladocerans and *Daphnia* spp. (C). Data are for laboratory observations of larval perch feeding on three different prey assemblages at four larval sizes (see text). The horizontal line represents no selection and is set at $1/m$ (0.16667). Solid circles are offset by +1 mm on the x-axis for clarity.
A

B

C

Larval TL (mm)

Rotifers
Nauplii
Neutral

Chesson's alpha

Calanoids
Cyclopoids
Neutral

Sm. cladocerans
Daphnia spp.
Neutral
Figure 3.3 Chesson’s $\alpha$ data (♦) and best model fit to the data for a prey-type specific function (solid line) relating Chesson’s $\alpha$ to larval length (mm). Error bars for data are 95% confidence intervals. Details regarding the specific model formulas and parameter values are given in Table 3.2.
Rotifers

Cyclopoid copepods

Small cladocerans

Copepod nauplii

Calanoid copepods

Daphnia spp.

Chesson's α

Larval TL (mm)
Figure 3.4 Relative abundance of six prey types in field samples collected during the pelagic larval period for yellow perch in Green Bay (1998-1999) and nearshore Lake Michigan (2000-2001).
Figure 3.5 Comparison of observed diet (± 1 SE) for larval yellow perch (7-15 mm TL), diet predicted by our individual-based foraging model and prey availability for either a nearshore Lake Michigan (top panel) or Lake Nagawicka (bottom panel) prey assemblage (See methods for details).
Figure 3.6 Mean diet composition for larval perch from model runs (N=3, 1000 larvae/run) exposing larvae to a zooplankton assemblage from either nearshore Lake Michigan or Green Bay. Data are separated into four larval size groups: 5-7 mm, 7.1-10 mm, 10.1-20 mm and 20.1-30 mm TL.
Figure 3.7 Mean growth rate (± 1 SE) from model runs comparing larvae exposed to a zooplankton assemblage from nearshore Lake Michigan (●) or Green Bay (△) over a range of zooplankton densities. N=1000 larvae per model run.
Figure 3.8 Proportion of larvae that starved to death per model run (N=1000) for larvae exposed to a zooplankton assemblage from nearshore Lake Michigan (●) or Green Bay (△) over a range of prey densities.
Figure 3.9 Size-frequency distribution of surviving yellow perch larvae at 30 days after peak hatch (simulation day 45) based on model simulations (N=3, 1000 larvae/run) at 100 prey/L and 250 prey/L from the individual-based foraging model. Larvae were exposed to a prey assemblage from either nearshore Lake Michigan or Green Bay at both prey densities.
To understand larval survival, ask the survivors: An individual-based model analysis of larval yellow perch, *Perca flavescens*, in Green Bay, WI based on characteristics of individual larvae.

Variability in annual recruitment is strongly related to variability in larval survival for many fishes including yellow perch, *Perca flavescens*. I used an individual-based modeling approach combined with field data analysis to investigate factors important to larval yellow perch growth and survival in Green Bay, WI. I examined characteristics of larval survivors in a good recruitment year (1998) and a poor recruitment year (1999) and asked whether observed differences in temperature, prey community composition and timing and intensity of size-selective predation were important in describing differences in characteristics of surviving larvae between years. Mean growth rate was higher in 1998 than in 1999; model results suggest this was due to higher abundance of copepods and more consistent seasonal warming in 1998. High relative abundance of copepods and lower abundance of rotifers results in higher growth rates for early-stage larvae. Larvae hatched after peak hatch were over-represented in the hatchdate distribution of survivors in 1998 compared to the initial distribution. This advantage was not apparent in the hatchdate distribution of larval survivors in 1999. Model results suggest that growth rate differences between years were not sufficient to predict either the differences in survival or differences in the hatchdate distribution that were observed 30 days after peak hatch between years. Patterns in survival and hatchdate distribution of larval survivors were well described when observed variation in timing and intensity of predation between years was added to the model. Selection for hatchdate through variable timing of predation, as well as variation in growth rate among individual
larvae within a cohort, can be important to variability in year class strength for yellow perch in Green Bay. The combination of field data analysis and individual-based modeling is a valuable tool for the comparison of multiple confounding factors and their respective influence on larval survival.
Introduction

Variability in recruitment of fishes is strongly influenced by variability in mortality during the larval phase. The life history of many fishes involves the production of numerous small offspring that are dispersed into the environment and offered little or no parental protection. As a consequence, mortality during initial life stages is high and the resulting adult cohort is a very small percentage of the population size at hatching (Sissenwine 1984, Houde 1987).

With so few larvae surviving to the adult stage it is difficult to describe annual recruitment patterns with population–level averages, such as average growth rate, because by the time a year class is formed the 'average' larvae is usually dead (Sharp 1987). Do larvae that survive in any given year possess unique characteristics that are related to survival, or are survivors randomly selected from the original population? Such characteristics of survivors may be intrinsic traits such as increased swimming ability (Fuiman et al. 1999), or they may be extrinsic factors such as spatial or temporal overlap with food resources (Cushing 1990). Whether, intrinsic or extrinsic, characteristics of survivors offer a window into factors influencing recruitment that may be important for management.

Detecting these characteristics of survivors can be a challenge. High larval mortality rates make selective forces that favor particular characteristics difficult to detect in field data (Miller 1997), and the short larval stage, combined with the potentially complex interactions of important factors, make designed experiments prohibitive (Letcher et al. 1996a). Nonetheless, it is of interest to fisheries management to understand what factors may lead to high larval survivorship and recruitment. One approach that has shown promise for
elucidating the relationships between characteristics of survivors and larval survival is individual-based modeling.

Individual-based models (IBMs) differ from traditional deterministic population models in that they follow the fate of each individual for the entire model period. By tracking individual fate, we can examine patterns of variability in relevant characteristics for the surviving cohort and compare these patterns over time or to patterns observed in field data. Moreover, individual-based models are flexible and allow for factors of interest (e.g., timing of predation) to be added to the model sequentially so that potentially important relationships can be distinguished from unnecessary complexity. Further, IBMs can be developed to address general questions such as patterns in size-dependent mortality (Rice et al. 1993b) and relative importance of starvation vs. predation to larval survival (Letcher et al. 1996a), or they can be developed to address particular questions relevant to specific species and systems. I used an individual-based modeling approach, combined with field data analysis, to ask what factors are most important to larval survival for yellow perch, *Perca flavescens*, in Green Bay, WI based on characteristics of larval survivors.

Larval vulnerability to mortality is often size-dependent (Luecke et al. 1990, Letcher et al. 1996b, Sogard 1997). In particular, size dependent vulnerability to predation is likely to have an influence on cohort survival in a system like Green Bay where the favorable composition of prey resources decreases the likelihood of significant larval starvation (Chapter 3). Potential for size-dependent mortality is dependent on the amount of intra-cohort size variability present (Rice et al. 1993b). The two most important factors affecting intra-cohort size variability are variation in individual growth rate and variation in date of hatch.
Rice et al. (1993b) found that small changes in both mean growth rate and growth rate variance within a single cohort could change both total survival and the growth rate of survivors. However, date of hatch is frequently overlooked as a factor in cohort size variability in IBM analyses, with analysis often limited to a single daily sub-cohort (e.g., Rice et al. 1993b, Cowan et al. 1996, Letcher et al. 1996a, Paradis et al. 1999). While this is a valid simplification for examination of other factors in isolation, these authors acknowledged that this approach does not fully describe the development of size variability in a natural cohort. Hatchdate and growth rate interact to generate the size distribution of a natural cohort, and it is of interest to explore this interaction and its impact on characteristics of survivors.

Hatchdate distributions also represent a characteristic of survivors that can be compared directly to the initial hatchdate distribution to look for important changes, which is not possible with size or growth distributions because they have no stable reference point; these characters can only be compared to a reference distribution in a model environment. I can compare the hatchdate distribution of survivors to the initial distribution both in a modeling environment and in field data, which means that I can examine relationships between characteristics of survivors and causative factors in an IBM and then assess the relative importance of these factors by comparing model results to character distributions observed in natural populations.

Hatchdate distributions of survivors can differ from the initial distribution in response to both changes in growth rate within a larval cohort and changes in sources of mortality such as predation that may target particular hatchdates (Chapter 2). These two factors may affect larval survival in different ways. Predation is a potential selective force,
whereas changes in growth rate affect the amount of intra-cohort size variability upon which such selective forces may act. Field data on both growth variability and the timing and intensity of predation offer a window into the relative effects of these factors, which can be simulated in an IBM analysis. The resulting predictions regarding larval characteristics of survivors can then be used to make inferences about how these factors affect larval survival in the field. In this way, the combination of field data and modeling analysis will generate a clearer picture of important relationships than would be possible from field data alone.

I examined how characteristics of survivors may change between a good recruitment year (e.g., 1998) and a bad recruitment year (e.g., 1999) in Green Bay and whether these changes are informative regarding the relative importance of environmental factors to larval survival. I used the characteristics of survivors approach within a foraging-growth-predation IBM developed specifically for larval yellow perch (Chapters 2 & 3) to compare differences in the characteristics of survivors between the 1998 and 1999 yellow perch year classes in Green Bay. I tested the hypothesis that growth rate variability and variation in the timing of predation are both important in determining larval survival and characteristics of survivors for yellow perch.

Specifically, I had three objectives. First, I examined differences in larval hatchdate distribution, growth rates, mortality rates, and size at age of survivors between the 1998 and 1999 cohorts. Second, I examined differences in larval prey community composition, prey density, and water temperature between these years. These factors are mostly likely to impact larval growth rates. I also examined differences in the timing and intensity of predation on larval yellow perch between years. Finally, I examined mechanistic links between these environmental factors and larval survival in the individual-based model by
comparing observed characteristics of survivors from field data to characteristics of survivors predicted by the model under 1998 and 1999 conditions.

Methods

*Study area* - Green Bay (surface area 4212 km², mean depth 20 m) is a relatively shallow, productive embayment connected to Lake Michigan at the lake’s northwest corner (Figure 1.1). Like the main body of Lake Michigan, Green Bay has historically supported a profitable commercial and recreational fishery for yellow perch (Walters and Punt 1994). Commercial catch peaked in the late 1980s after strong year classes of yellow perch were produced in 1983 and 1985, but yellow perch catch in Green Bay has been declining for the last twelve years (Wisconsin Department of Natural Resources *unpublished data*). The yellow perch fishery in the main body of Lake Michigan has also been in decline since 1990 and was closed to commercial fishing in 1994 (Francis et al. 1996), while the Green Bay fishery has stabilized and remains open. Despite the relative stability of the Green Bay yellow perch population, inter-annual variability in recruitment has been high (Figure 4.1) even during the 1980s when the spawning stock biomass was large.

*Field sampling* – All field sampling in Green Bay was conducted by Wisconsin Department of Natural Resources (WDNR) personnel in cooperation with the Yellow Perch Task Group (See Chapter 1) at Little Tail Point (44°39’07” N, 87°58’39” W; Figure 1.1) on the southwestern side of Green Bay 15 km north of the city of Green Bay. Little Tail Point is a known yellow perch spawning area and the location of long-term index sampling conducted by WDNR. Samples were collected weekly from late April until mid-June in both years.
Larval fish were collected by towing a 1 X 2-m neuston net with the top of the net frame 1 m below the surface (median sample depth 1.5 m) for 5 minutes along two 200-m transects about 0.5 km from shore in waters 6 m deep. Mesh size was initially 500 µm and was increased to 1000 and then 1800 µm over the sampling period to track larval perch growth. All larval fish collected were flash frozen in dry ice-alcohol slurry and delivered to the Great Lakes WATER Institute in Milwaukee, WI. Samples were flash-frozen because some larvae collected were used for an analysis of nutritional condition (C. Heyer and T. Miller *in prep*). Frozen samples were defrosted in the lab and all larval yellow perch were removed. Fifty larvae were randomly selected from each sample and separated for age and growth analysis. Total length of each of these larvae was measured to the nearest 0.1 mm with an ocular micrometer and both sagittal otoliths were removed for age and growth analysis.

Juvenile yellow perch were sampled with triplicate hauls of a 7.6-m beach seine from a depth of 1.5 m straight back to shore for two sites about 1 km apart at Little Tail Point. Juvenile perch captured were preserved in 95% ethanol. In the lab, up to 25 juveniles were randomly selected from each sample; total length of each selected fish was measured to the nearest 0.1 mm with a digital imaging system (Image Pro 5.1 Media Cybernetics Corp.) and both sagittal otoliths were removed for age and growth analysis.

Zooplankton were sampled with triplicate hauls of a 0.5-m, 76-µm mesh hoop net from bottom to surface at the beginning of each larval transect. Zooplankton collected were preserved in 95% ethanol and delivered to John Dettmers, Illinois Natural History Survey in Zion, IL for analysis. Zooplankton were identified and enumerated by taxonomic group, and measured to the nearest 0.01 mm with a digitizing board. Taxon-specific counts were based
on the examination of triplicate 5-ml sub-samples from a known concentration of each main sample at 20X magnification (J. Dettmers personal communication). Taxonomic groups of interest were rotifers, copepod nauplii, cyclopoid copepods, calanoid copepods, small caldocrans and *daphnia* spp. based on the taxonomic distinctions used in the individual-based model (Chapter 3).

Predators of larval yellow perch were sampled with 1-hour sets of a 15.2-m, variable mesh (2.5 – 7.6 cm) gillnet on the bottom. All gillnet sampling was conducted at night 0.5 km west of Little Tail Point in 4-6 m of water. All fish captured were measured to the nearest 1 mm and guts were removed and preserved in 95% ethanol for later analysis. Contents of predator guts were identified and all larval yellow perch found were counted; the length of all whole larvae was measured to the nearest 0.1 mm.

*Temperature data* - Temperature data for Green Bay were collected weekly during fish sampling with a field thermometer within 0.5 m of the surface and from daily readings at the inflow pipe of the Pulliam Power Plant near Green Bay, WI (Brian Belonger, WDNR personal communication).

*Age and Growth Analysis* – Larval and juvenile fish collected from Green Bay in both 1998 and 1999 were used for analysis of patterns in age and growth rate. Otoliths were prepared for examination with different methods depending on fish size. Otoliths from perch larvae up to 15 mm TL were mounted in clear mounting medium (Cytoseal, Fisher Scientific Inc.) on glass slides for examination. Otolith rings were counted at either 400 or 1000X under immersion oil by two independent readers. Otoliths from larvae over 15 mm TL and from
juvenile perch were mounted on 1 cm x 1 cm glass squares with thermoplastic cement and flat polished with fine-grit sand paper until the rings were visible from the core to the edge. Otolith rings were then counted at 400X under immersion oil by two independent readers. Discrepancies between independent readings were corrected with an additional joint reading. Mean ring count from all readings (n=4) for an individual otolith was converted to an estimate of individual age with a relationship between ring count and larval age based on an inverse regression analysis of ring count data on age for known-aged larvae raised in the laboratory (Rice 1987, Appendix 1).

Hatchdate estimates for individual fish were calculated by subtracting age from sample date. Individual hatchdates were compiled into a hatchdate frequency distribution for each sample and annual cohort (Appendix 1); hatchdate frequency distributions were adjusted for variability in age estimates based on a 95% confidence interval for individual estimates of larval age from the inverse regression analysis. Individual growth rates were calculated based on the following formula:

\[
GR = \frac{TL - 5.7}{\text{age}}
\]

where TL is the total length of a larva measured in the laboratory and 5.7 is the mean initial length of yellow perch larvae based on examination of newly hatch fish in the laboratory (R. Fulford unpublished data).

Instantaneous daily mortality rate (M) was estimated for arbitrary 4-day sub-cohorts within each year based on abundance data for each sub-cohort from larval sampling over the period between peak hatch and 30 days post peak hatch. The estimate of M is based on an
adapted catch curve analysis (Hilborn and Walters 1992) in which M is equal to the slope of a linear regression between ln(abundance) and age in days for each sub-cohort.

*Year class comparison* – The 1998 and 1999 larval cohorts were compared with field data for individual growth rate, as well as hatchdate and size distributions at 30 days post peak hatch. Differences in mean growth rate between years were examined with a t-test (Neter et al. 1990). I tested for a significant difference in the hatchdate distribution at 30 days after peak hatch between years, and for differences in hatchdate distributions within year between the initial distribution and the distribution at 30 days after peak hatch. Both hatchdate comparisons were conducted with a Kolmogorov-Smirnov test (Hollander and Wolfe 1999).

*Individual-based model analysis* - For the IBM analysis I used a foraging-growth-predation IBM described previously (Chapters 2 & 3; Figure 4.2). Briefly, The model uses inputs of daily zooplankton density and relative abundance to predict daily larval consumption based on sized-based estimates of encounter rates and probability of attack and capture between larvae and zooplankton prey. Prey types were rotifers, copepod nauplii, cyclopoid copepods, calanoid copepods, small cladocerans and *daphnia* spp. (Table 3.1). Encounter rate of larva $j$ with prey type $i$ is based on a function relating larval search volume (SV, ml) and prey density ($d_i$, prey/ml) to encounter rate (ER$_{ij}$, prey/s):

\[
ER_{ij} = SV_i \cdot d_j
\]
where search volume is a size-based function of larval swimming speed and reactive area for prey type $i$ (Formulas 2 to 5, Chapter 3). Realized daily encounter rate ($E_{i,j}$) of larva $j$ with prey type $i$ was determined stochastically from a Poisson distribution with $ER_{i,j}$ as the rate parameter.

Probability of attack and capture ($Q_{i,j}$) is a function of larval selectivity ($\alpha_{i,j}$) for prey type $i$ and the relative abundance ($q_i$) of prey type $i$ in the environment:

$$
Q_{i,j} = \frac{\alpha_{i,j} \cdot q_i}{\sum_{k=1}^{m} \alpha_{k,j} \cdot q_j}
$$

and selectivity of larva $j$ for prey type $i$ is described with Chesson’s $\alpha$ (Chesson 1983), which was calculated with a size-based function derived empirically for each prey type (Figure 3.2). Daily relative abundance ($q_i$) for prey type $i$ was obtained from field data.

Daily consumption of each prey type was calculated stochastically with a binomial probability model with realized daily encounter rate ($E_{i,j}$) as the number of foraging events and $Q_{i,j}$ as the success probability. Daily consumption could not rise above an estimate of maximum consumption, which was a function of larval mass ($\mu g$, dry mass) and daily mean temperature (Letcher et al. 1996a, Hanson 1997).

Estimates of daily consumption were then used to predict individual growth in a bioenergetics sub-model. Growth ($G$, $\mu g$/day) was calculated as consumption ($C$, $\mu g$/day) multiplied by assimilation efficiency minus total daily metabolic costs.

$$
G = (C \cdot AE) - (RM + AM + (C \cdot (U + SDA))
$$
where assimilation efficiency (AE) was a proportion of daily consumption described with a function based on larval size (Letcher et al. 1996a). Assimilation efficiency was 60% for first feeding larvae and rose to a maximum of 80% at a larval size of 15 mm TL. Routine metabolic cost (RM, µg/day) was a function of larval mass and daily mean temperature, and active metabolic cost (AM, µg/day) was a constant multiple of routine metabolic costs (4.4, Post 1990). Costs of excretion (U, µg) and standard dynamic action (SDA, µg) were set at 15% of consumption each.

Individual larvae died in the model from either starvation or predation. Daily vulnerability to starvation was based on a comparison of larval mass to a starvation threshold (Threshold) derived from experimental observations for larval yellow perch (Letcher et al. 1996b):

\[
(4) \quad \text{Threshold} = 0.47 \times \text{Maxwt}
\]

where Maxwt is the previous maximum mass (µg, dry mass) attained by a larva for that model run. Previous maximum mass was updated for each larva as it grew and vulnerability to starvation declined with increasing larval mass.

Daily vulnerability to predation was a function of both larval and predator total length and was described in the model with size-based functions of larval-predator encounter rate and probability of attack and capture. Daily encounter rate \((E_{j,z})\) of larva \(j\) and predator \(z\) was calculated based on swimming speed of both larva (SS, cm/s) and predator (\(v\,\text{cm/s}\)) and reactive distance of both larva (\(R_{j}\,\text{cm}\)) and predator (\(R_{z}\,\text{cm}\)). Daily encounter rate was also
a function of predator density \((\text{Den}, \text{ml}^{-1})\) and total available feeding time in a day \((\text{Time}, 42,300 \text{ s})\):

\[
E_{j,z} = \pi (R_z + R_j)^2 \cdot \frac{SS^2 + 3 \cdot \nu^2}{3 \cdot \nu} \cdot \text{Den} \cdot \text{Time}
\]

where feeding time was limited to the 12-hour daylight period based on the observation that all predators in the model search for prey visually and larval yellow perch are inactive at night. Predator density was set equal to \(1/10^9\) where the denominator is the modeled water volume (ml). This calculation for predator density makes equation (5) equal to the encounter rate between an individual larva \(j\) and an individual predator \(z\) (randomly assigned size and species each model day). In model simulations the actual number of predators present was set based on field data for predator densities and equation (5) was calculated separately for encounters between larva \(j\) and each predator on each model day. Larval swimming speed was a yellow perch-specific function of size described by Houde (1969) and predator swimming speed was \(3 \times \) predator length as described for planktivorous fish by Cowan et al. (1996).

Probability of attack and capture \((a_{j,z})\) was derived empirically for two predators, alewife \(Alosa\ pseudoharengus\) and white perch \(Morone\ americana\), feeding on larval yellow perch (Figure 2.1). Daily vulnerability to predation in the model was defined as one minus the probability a larva escaped all encounters with a predator for that day based on a binomial probability model,
\[ V_{j, z} = 1 - (1 - a_{i, z})^{E_{i, z}} \]

with the number of encounters equal to \(E_{j, z}\) and success probability equal to \(1 - a_{j, z}\). Mortality occurred for larva \(j\) if \(V_{j, z}\) was higher than a uniform random number between 0 and 1 generated for each encounter in the model.

Output for comparison between years was individual growth rates, hatchdate distributions of survivors and total cohort survival. I also conducted model runs that simulated non-size dependent mortality of the same magnitude observed in size-dependent model runs. Output from the non size-dependent simulations was hatchdate distribution of survivors that I used for comparison to size-dependent output to gauge the effect of size-dependence on model results.

I conducted a numerical experiment comparing perch growth rates, survival, and hatchdate distributions predicted by the model under both 1998 and 1999 conditions in Green Bay. I compared growth predictions to field data to assess model performance and then tested for differences in predicted cohort survival and hatchdate distributions between years.

I also used a layered approach to the examination of important factors affecting characteristics of survivors. Initial model runs were conducted with only differences in temperature, prey density and prey community composition between years. Predation was constant over the model run at a density of 0.045 predators/m\(^3\). This value is based on available density data for alewife in Lake Michigan (Fabrizio et al. 1997). I then added differences in the timing and intensity of predation based on changes in catch per unit effort for predators from the gillnet survey data in Green Bay.
Results

*Year class comparison* – Differences in total mortality between the 1998 and 1999 year classes were evident from catch per unit effort (CPUE) data for juveniles collected in the fall of each year (CPUE$_{1998}$ = 1004, CPUE$_{1999}$=80; Figure 4.1). The 1998 year class was over an order of magnitude larger than the 1999 year class at the end of the pelagic larval period. Higher year-class strength for the 1998 cohort was also evident in mortality rate estimates for the larval period. Mean instantaneous daily mortality rate across all 4-day sub-cohorts within year was twice as high in 1999 as in 1998 (M$_{1998}$ = 0.02; M$_{1999}$ = 0.04) over the larval period.

Growth rate estimates for survivors of the larval period were significantly higher for the 1998 year class than for the 1999 year class (Mean GR$_{1998}$ = 0.49 mm/day; GR$_{1999}$ = 0.27 mm/day; t =10.3, 78 df, p<0.0001). As a result, survivors were considerably larger in 1998 than in 1999 (Figure 4.3).

Growth rate also changed as a function of hatchdate within year. Growth rates were higher for larvae with a hatchdate after peak hatch in both years; this difference was most evident when larvae were between 11 and 20 dph in age (Figures 4.4 and 4.5). This trend was stronger in 1999 with mean growth rate of larvae hatched after peak hatch (0.42 mm/day) nearly twice as high as growth rate of larvae hatched prior to peak hatch (0.27 mm/day). However, this trend weakened for older larvae in both years, suggesting an early growth advantage for later-hatched fish that was ameliorated by other factors by the end of the larval period.

Initial hatchdate distributions were similar between the 1998 and 1999 year classes, except the 1999 distribution was slightly wider and peak hatch in 1998 occurred 4-5 days
earlier than in 1999 (Figure 4.6). In contrast, hatchdate distributions of survivors to 30 days after peak hatch were significantly different between years (Kolmogorov-Smirnov J=2.00, p=0.007). Larvae hatched later in the larval period were over-represented in the hatchdate distribution of survivors in 1998 in comparison to the hatchdate distribution of survivors in 1999. Moreover, the hatchdate distribution for survivors to 30 days after peak hatch for the 1998 year class was significantly different from the initial hatchdate distribution for this year class (Figure 4.6; K-S J=2.28, p<0.0001); more later-hatched than early-hatched larvae survived to 30 days after peak hatch in 1998. In contrast, the hatchdate distribution of survivors to 30 days after peak hatch for the 1999 year class was not significantly different from the initial hatchdate distribution for that year (Figure 4.6; K-S J=0.81, p=0.41).

Zooplankton community – Zooplankton density in Green Bay was highly variable over the course of the pelagic larval period in both years (Figure 4.7). Daily mean density ranged from 46 – 244 prey/L in 1998 and from 14 – 351 prey/L in 1999. Daily mean zooplankton density was less than 100 prey/L early in the larval period in both years, which is a density level predicted to result in low larval growth rates (Chapter 3). Zooplankton density rose rapidly above 100 prey/L beginning 10-14 days after peak hatch in 1998 and 7-10 days after peak hatch in 1999. The rise was stronger in 1999, and maximum density was 30% higher in 1999 and maintained for a longer period than in 1998.

There were also detectable differences in zooplankton community composition between years. The 1998 zooplankton community showed more evenness between taxonomic groups (Figure 4.7). Both cyclopoid copepods and small cladocerans were significant components of the assemblage beginning 10-12 days after peak hatch and there
was a detectable pulse of *Daphnia* spp. at this time as well. In contrast, the 1999 zooplankton community was dominated early by copepod nauplii and rotifers and later by small cladocerans such as *Bosmina* and *Eubosmina*. In fact, density differences between years were primarily due to the pulse of small cladocerans in May of 1999.

*Temperature* – Daily water temperature data also differed between years (Figure 4.8). An increase in water temperature above 10°C occurred prior to peak hatch in both years, but seasonal warming was more erratic and occurred more slowly in 1999 than in 1998.

*Predator sampling* - Predator relative abundance changed over the larval period in both 1998 and 1999 (Figure 4.9). Based on gillnet data and stomach analysis, two predators were both abundant and observed to feed on larval perch: alewife and white perch. Alewife were not abundant in the study area prior to May 21st in 1998 or May 16th in 1999. When these data are combined with differences in peak hatch between years, this difference in arrival time means that alewife became abundant 20 days after peak hatch in 1998 and 12 days after peak hatch in 1999. The magnitude of the change in alewife catch per unit effort around these dates was comparable between years (80-100 fish/0.5 hr set).

White perch were more abundant after the pelagic larval period for yellow perch in both years. Relative abundance of white perch was low (<5 fish/0.5 hr gillnet set) during the pelagic larval period in 1998 and 1999 (Figure 4.9). The exception was a significant pulse (>20 fish/0.5 hr set) of white perch around May 22nd in 1999. Incidence of larval yellow perch in the guts of both predators was consistent (daily mean 9-14 larvae/stomach) during periods of high relative abundance for both alewife and white perch (WDNR *unpublished data*).
Numerical experiments – The constant predation experiment involved a comparison of individual growth rate and hatch date distributions of survivors to 30 days post peak hatch between 1998 and 1999 based only on observed differences in temperature, zooplankton density and zooplankton community composition, with predator abundance constant through time and between years. The constant predation simulation predicted differences in individual and mean growth rate of survivors between years. The simulation predicted mean growth rate of survivors in 1998 was nearly twice as high as mean growth rate in 1999. Predicted mean growth rate of survivors at 30 days after peak hatch was 0.47 mm/day (SD = 0.15) in 1998 and 0.24 mm/day (SD = 0.14) in 1999. This predicted difference in growth rate between years agreed well with observed difference in growth rate of survivors between years. The observed mean growth rate of survivors at 30 days after peak hatch was 0.49 mm/day (SD = 0.13) in 1998 and 0.27 mm/day (SD = 0.05) in 1999.

The constant predation simulation correctly predicted that individuals born just after peak hatch were growing faster than larvae hatched earlier in 1998, and the lack of a trend for growth rate with hatchdate in 1999 (Figure 4.10). This simulation also predicted a slow-growing group and a fast-growing group for each year class. This bimodality was not observed in field data, but there was still good agreement between the distribution of simulation results and the distribution of individual growth rates from field data.

Differences in growth rate of survivors to 30 days post peak hatch between annual cohorts predicted by the model were not sufficient to generate observed differences in 30-day survivorship or changes in the hatchdate distribution at thirty days after peak hatch (Figure 4.11 upper panel). The simulation predicted similar survival in both years despite the fact that larvae were growing much faster in 1998 than in 1999 in the simulation (Model results:
$M_{1998} = 0.07$; $M_{1999} = 0.08$). In contrast, observed mortality for the 1998 cohort was twice as high compared to the 1999 cohort. The simulation also predicted that larvae born after peak hatch were over-represented in the hatchdate distribution of survivors to 30 days post peak hatch in both years; this pattern was observed in field data for 1998 but not in 1999. These results suggest that the difference in growth rate observed between years was by itself not sufficient to generate observed differences in mortality or hatchdate distribution of survivors.

In the variable predation experiment, I used observed patterns of predator abundance and species composition through time from field data in each year. Background predator density was set at $0.01/m^3$ for alewife and $0.005/m^3$ for white perch and peak density was ten times this value for alewife and five times this value for white perch.

The variable predation simulations correctly predicted mortality rates almost twice as high in 1999 as in 1998 ($M_{1998} = 0.06$; $M_{1999}=0.10$). The simulation predictions were higher than my estimates of $M$ from the field based on catch-curve analysis ($M_{1998} = 0.02$; $M_{1999}=0.04$), but the relative differences between years corresponded with field observations. Further, hatchdate distributions of survivors predicted in the variable predation simulations more closely resembled observed hatchdate distributions of survivors in both years (Figure 4.6 & 4.11). Later-hatched larvae were over-represented in the hatchdate distribution for the 1998 cohort. This pattern was observed in the hatchdate distribution of survivors for field data from 1998; it also closely resembled the pattern predicted by non-size selective mortality simulations. In contrast, the hatchdate distribution of survivors predicted for 1999 was less dominated by later-hatched larvae and agreed well with the observed hatchdate distribution in 1999; this distribution deviated from the pattern observed in non-size selective simulations.
Discussion

The 1998 and 1999 year classes for yellow perch in Green Bay differed in several significant respects. Most importantly, the 1998 year class was much larger than the 1999 year class at the end of the larval period. Further, this difference in year class strength persisted into the adult population based on annual gillnet surveys conducted in Green Bay from 1999 to 2003 (WDNR unpublished data), which suggests that differences in larval survival are important in determining the contribution of an annual cohort to the population.

Individual growth rates were higher in 1998 resulting in a noticeable increase in mean size at the end of the larval phase. Model results suggest that these growth differences were due to both temperature differences and differences in prey community composition between years. Timing of yellow perch spawning is strongly related to the occurrence of water temperatures above 10°C (YPTG unpublished data). Further, optimal hatching success and early growth in the laboratory occurs at temperatures above 15°C (Fred Binkowski Great Lakes WATER Institute personal communication). Water temperatures in 1999 were close to 15°C at peak hatch but daily temperature dipped below 15°C several times after peak hatch and seasonal temperature increase was both slower and more erratic than in 1998.

Changes in prey community composition also had an effect on growth. Prey resources were actually more abundant in 1999 overall, largely due to an increase in small cladocerans that occurred about 10 days after peak hatch. Larval yellow perch selectivity for smaller cladocerans is positive once they grow larger than 15-18 mm TL, but negative for smaller larvae (Figure 3.2). Therefore, it is unlikely that an increase in cladoceran abundance would bestow an advantage on larvae prior to about 20 dph. In fact, previous model results
suggest that the relative abundance of small copepods is more important to early-stage growth (Chapter 3) and copepods were more abundant in 1998.

Modeling results based on differences in both mean daily temperature and mean prey community composition and density yielded good predictions of differences in mean growth rate between years. The model results did predict bimodality in the distribution of individual growth rates for both years that was not observed in field data. This bimodality was due to differences in the prey assemblage that larvae hatched at different times had to prey upon in the model, which had a strong impact on the growth rate of newly hatched larvae. Larvae exposed to an assemblage with a high proportion of copepods early were predicted to have an early growth advantage compared to larvae that fed largely on rotifers during the early larval period. This advantage is reflected in model results by a fast growing larval group exhibiting growth rates similar to growth rates observed in field data, and a slow growing larval group exhibiting little or no growth over the larval period. The slow growing group was reduced in size, though not eliminated, in simulation results by including data on predator relative abundance in the variable predation simulations, which suggests that under natural conditions survivors would include fewer individuals from the slow growing group as they remain vulnerable to size-selective predation for the entire larval period. Nonetheless, model results did predict that individual growth rates of survivors were higher in 1998 than in 1999.

Food abundance and temperature have both been cited as factors affecting growth in larval fishes (Leggett and Deblois 1994, Rutherford and Houde 1995, Secor and Houde 1995). However it is extremely difficult to delineate the relative effects of these two factors as they interact in natural populations in complex ways hard to distinguish in field data (Dower et al. 2002). Our model required both temperature and prey community differences
to accurately predict growth, which suggests that the interaction, rather than either factor in isolation, was the dominant influence on growth of yellow perch in Green Bay.

I also observed differences in the hatchdate distribution of survivors between years. In 1998 a larger proportion of larval survivors were hatched after peak hatch than before peak hatch. In 1999 no survival advantage was apparent as a function of hatchdate. It is important to understand how hatchdate distribution patterns may develop in response to various factors of interest. Mortality need not be size-dependent in order to cause a shift from initial conditions. Model simulations that included a non-size-dependent mortality pattern predicted survival was more likely for larvae hatched later in the hatching period, very similar to the hatchdate distribution pattern observed in field data for the 1998 cohort.

In a natural cohort, non-size-dependent mortality is expected early in the larval period because size-variability among larvae requires time to develop, but if predation levels are high mortality should become more size-dependent as size differences increase, because larger larvae are less vulnerable to predation than smaller larvae (Rice et al. 1993b). Previous modeling results indicate that early in the larval period, when mortality is largely non-size-dependent, later-hatched larvae are initially over-represented in the hatchdate distribution. However as intra-cohort size variability increases and size-dependent predation increases in importance, predation vulnerability of later-hatched larvae increases, as they are the smallest larvae present. This shift in vulnerability from early-hatched larvae to later-hatched larvae was predicted to result in no net survival advantage for individual larvae as a function of hatchdate by the end of the larval period (Chapter 2). These results suggest that if predation is high and constant over the larval period, a higher growth rate should result in a hatchdate distribution of survivors at the end of the larval period that resembles the initial
hatchdate distribution for that cohort. The observed hatchdate distribution of survivors in 1998 did not fit this pattern despite the high growth rate observed for this cohort. Further, the constant predation simulations predicted that the hatchdate distribution in both 1998 and 1999 favored later-hatched larvae. These results suggest that predation was low in 1998 and that observed differences in the hatchdate distribution of survivors between the 1998 and 1999 cohort were not likely to result solely from differences in growth rates between years.

Larvae may also have a survival advantage as a function of hatchdate when there is variability in the timing and intensity of size-dependent predation. Results from general model simulations examining the effect of timing of predation suggest that later-hatched larvae are more likely to survive to the end of the larval period if predation is focused near peak hatch. In contrast, predation focused later in the larval period should result in no net survival advantage to individual larvae based on hatchdate (Figure 2.11). Increased predation intensity after peak hatch was the pattern observed in 1999. When this pattern was included in model simulations, the predicted hatchdate distribution of survivors in 1999 was similar to the hatchdate distribution of survivors observed for the 1999 cohort.

These data suggest that the timing and intensity of predation was important in shaping characteristics of survivors that differed between a good year class and a poor year class. Moreover, in order to distinguish growth rate-dependent patterns in the hatchdate distribution from patterns resulting from timing of predation, it was necessary to have data about both the growth rate and hatchdate distribution of survivors and the relative intensity of predation over the larval period.

Modeling results support the hypothesis that in Green Bay, the timing and intensity of predation was more important than growth rate differences in explaining differences in
mortality between the 1998 and 1999 year class. Differences in mortality of this magnitude have been correlated with differences in growth rates alone in general larval models (Rice et al. 1993b, Cowan et al. 1996). However, these studies were based on analysis of a single daily sub-cohort exposed to constant predation and either a constant growth rate or a growth rate that varied daily based on a correlated random walk. Such models suggest that if predation is relatively stable over the larval period, it is advantageous for an individual to grow through the predation window quickly as all larvae are exposed to a window of similar duration and the individuals that pass through it the quickest are most likely to survive. However, for the youngest larvae, hatchdate variability generates much more size variability than growth rate. When predation is variable in intensity over the larval period, larvae hatched at different parts of the larval period will be exposed to different levels of predation and the relationship between high growth and high survival will be weakened.

It is axiomatic that an individual larva will increase its chances of survival if its growth rate is maximized and its exposure to predation is minimized. However, it can be important to address these two factors more independently than has been done in the past. When growth rate is the only factor affecting size variability in a model, then size-dependent mortality becomes growth rate-dependent mortality. Under these conditions, growth rate and vulnerability to predation are tightly linked. However, in nature individual size and growth rate are uncoupled during the early-larval stage. Based on my IBM analysis of field data for both growth rate and timing of predation, it seems that vulnerability to predation can be a function of hatchdate, and a good year class can result from larvae hatched into favorable conditions either for maximizing growth or for minimizing vulnerability to predation.
In the case of yellow perch larvae in Green Bay, favorable conditions seem more likely for larvae hatched in the later portion of the larval period. These larvae are likely to have an inherent growth advantage in most years because water temperatures are more likely to be favorable to optimal growth later in the larval period. If these later-hatched larvae are not exposed to higher densities of predators, or low prey abundance, they are more likely to be survivors. Rice et al. (1987) also observed a higher relative abundance of later-hatched larvae based on hatchdate distributions for bloater, *Coregonus hoyi*, in their analysis of characteristics of survivors. They attributed this survival advantage to higher growth rates observed for later-hatched larvae, particularly during the period prior to 20 dph. Their findings agree in general with mine regarding growth rate differences, but it is worth noting that their analysis did not include an examination of predation intensity. My results suggest that growth rate variability alone does not result in a survival advantage to later-hatched larvae sufficient to explain differences in year class strength for larval yellow perch between the two year classes I examined.

These results are based on data from only two years and do not provide definitive evidence that predation timing and intensity are the pivotal factors controlling long-term recruitment patterns of larval yellow perch in Green Bay. However, multiple simulations under various growth and predation scenarios suggest that these results are not unique. In fact, the results of this study suggest that factors important to variability in growth rate and predation intensity will interact to affect larval survival in complex ways that are hard to simplify down to one common pattern. Under such conditions, our ability to observe these interactions in a modeling environment is a valuable tool for disentangling these synergistic effects.
The IBM approach in particular has proven useful for understanding the relative importance of starvation and predation (Letcher et al. 1996a), understanding the relative importance to predation of size-based larval vulnerability and encounter rate (Paradis et al. 1999), and describing size-based interactions when both predator and prey are growing at a significant rate (Rice et al. 1993a). In my analysis, a multi-cohort IBM approach has proven useful for disentangling the relative importance of larval growth and the timing of size-selective predation.

Both variation in hatchdate and variation in growth rate affect size variability in natural fish populations. However, variation in hatchdate can be much more important to size variability early during the larval period when larvae haven’t had much time to grow. In some fishes, the hatching period may extend over several months (e.g., centrarchids, Jenkins and Burkhead 1994) or have two distinct peaks within each year (Gadus morhua, NMFS 1999). In cases like these, the timing of high predation relative to individual hatchdate can be much more important to year-class strength than growth rate. Yellow perch have a relatively short hatching period at the local scale (e.g., 14-30 days), and even under these conditions, variation in the timing of predation was necessary to explain observed patterns in characteristics of survivors. Such hatchdate-dependent mortality must be identified and understood if we are to draw links between larval survival and annual year class strength for fishes such as yellow perch that display significant variation in recruitment even when the spawning stock is large. My individual-based model is an effective tool for the analysis of these links. In the future we can expand this analysis to include longer-term datasets and work to generalize our understanding of how hatchdate and growth rate-dependent mortality interact to affect survival of larval yellow perch.
Literature Cited


Hanson, P. C. 1997. Fish Bioenergetics. University of Wisconsin Sea Grant Institute, Madison, WI.


Figure 4.1 Annual mean catch per unit effort (catch/trawl hr) for YOY yellow perch in Green Bay from 1980-2001. Sampling was conducted in September and October of each year by Wisconsin Department of Natural Resources personnel. Chart courtesy of Justine Hasz, WDNR Peshtigo, WI.
Figure 4.2  Flow chart summarizing the foraging/growth/predation individual-based model used for the numerical experiments.
Figure 4.3  Size distribution at 30 days post peak hatch for the 1998 and 1999 yellow perch cohorts in Green Bay.
Figure 4.4 Individual growth rate as a function of hatch date for yellow perch larvae at three ages, 0-10, 11-20 and 21-30 dph collected in Green Bay in 1998. Trend in data is indicated by solid line and mean growth (GR) is given for each age-group. If the trend was significant, the $R^2$ value for the trend is given and the mean growth rate is given for pre-peak hatch and post-peak hatch separately. Date of peak hatch is indicated by the solid arrow below the middle chart.
Figure 4.5 Growth rate distribution as a function of hatchdate for yellow perch larvae at three ages, 0-10, 11-20 and 21-30 dph collected in Green Bay in 1999. Trend in data is indicated by solid line and mean growth (GR) is given for each age-group. If the trend was significant, the $R^2$ value for the trend is given and the mean growth rate is given for pre-peak hatch and post-peak hatch separately. Date of peak hatch is indicated by the solid arrow below the middle chart.
Figure 4.6 Hatch date distributions for larval survivors to 30 days post peak hatch for the 1998 and 1999 cohorts from Green Bay, WI. Initial hatchdate distribution of each cohort is given for reference.
Figure 4.7  Daily mean zooplankton density and community composition for Green Bay during the pelagic larval period for yellow perch in 1998 and 1999. Data were collected weekly by Wisconsin DNR personnel, and samples were analyzed by staff of the Illinois Natural History Survey in Zion, IL. Date of peak hatch indicated in each year with a black arrow below the x-axis.
Figure 4.8 Daily mean temperature data for lower Green Bay collected at Pulliam power plant and at Little Tail Point. Data are for 1998 and 1999. Lines are best-fit linear regressions for 1998 (solid) and 1999 (dashed).
Figure 4.9  Catch per unit effort (catch/0.5 hr gillnet set) for alewife and white perch in Green Bay in 1998 (▲) and 1999(□). Pooled results of two gillnet samples per day collected by staff from the Wisconsin Department of Natural Resources. Date of peak hatch is indicated on the alewife chart by a black arrow for 1998 and a gray arrow for 1999.
Figure 4.10  Comparison of individual growth rate estimates from larvae in Green Bay to those predicted by the model for 1998 and 1999. Both field data and model estimates are measured 30 days after peak hatch. Date of peak hatch in each year is indicated by a black arrow below the x axis.
Figure 4.11  Hatchdate distributions of larval survivors predicted by the individual-based model for the constant predation experiment (upper panel) and for the variable predation experiment (lower panel) under 1998 and 1999 conditions. A hatchdate distribution of survivors resulting from non-size-selective mortality is given on each chart for reference.
A big lake or a small ocean? Predicting growth and survival of larval yellow perch, *Perca flavescens*, in offshore Lake Michigan and implications for recruitment.

Annual variability in year class strength is closely linked to larval survival in fishes with a pelagic larval stage. Yellow perch, *Perca flavescens*, has a pelagic larval stage and has experienced sustained recruitment failure in Lake Michigan since 1990. I used field sampling and an individual-based modeling approach to test the hypothesis that yellow perch larvae are being transported from nearshore spawning areas to offshore pelagic habitat, and that this movement has consequences for larval survival. Larval perch were found at all sites between 1 and 32 km from shore, and larval length showed a significant positive relationship with capture distance from shore. The offshore zooplankton community was similar to the nearshore community in 2000, but in 2001 the offshore zooplankton community contained a higher percentage of copepods and a lower percentage of rotifers compared to nearshore waters. Copepods are an optimal prey item for early-larva growth and will be selected more often by early-stage larvae when copepod abundance is high relative to rotifer abundance. Model results suggest that advection offshore would not have resulted in higher larval survival in 2000. In contrast, offshore advection would have resulted in higher larval survival and growth rates in 2001, but only if advection occurred within two weeks after peak hatch. Physical data suggest that larval transport was not adequate in 2001 resulting in low larval survival and a weak 2001 year class. In larger systems like Lake Michigan the interaction of physical advection and spatial differences in zooplankton community composition at the whole-lake scale can have a strong impact on year class strength of yellow perch. Further, offshore advection of larval yellow perch limits the effect of density-
dependent predation on larval survival. Density-independent factors such as advection and
overlap with favorable prey are not commonly cited as important to yellow perch larval
survival in smaller systems. Lake Michigan more closely resembles an oceanic environment
with regards to larval recruitment processes; this resemblance should be taken into account
when applying lessons learned in smaller systems to understanding larval recruitment in Lake
Michigan.
Introduction

Annual recruitment variability in fishes has been closely tied to survival during the larval phase (Sissenwine 1984, Houde 1987), particularly for fishes with a pelagic larval stage as they are generally smaller, more widely dispersed and subject to higher rates of mortality than other types of larvae (Houde 1989). Variation in larval mortality has been found to be particularly important to recruitment in fishes from a variety of marine habitats including estuary-dependent fish such as menhaden, *Brevoortia tyrannus* (Warlen et al. 2002), tropical reef fishes (James et al. 2002) and Atlantic cod, *Gadus morhua* (Bradbury et al. 2000). Density-independent factors such as physical transport between good and poor habitat and variable food supply are commonly cited as important to larval recruitment in marine systems (Houde 1974, Alexander and Roughgarden 1996, Hare et al. 1999).

A pelagic larval phase is not unique to marine fishes. Freshwater species such as yellow perch, *Perca flavescens*, also have a pelagic larval phase that is sensitive to similar factors as their marine counterparts. However, analysis of recruitment for larval yellow perch has largely been conducted in small (< 1500 km²), productive systems that are generally dissimilar to a marine environment. Analysis of yellow perch populations in these smaller systems has largely focused on density-dependent factors important to larval and juvenile survival, such as predation and competition (Kelso and Ward 1977, Whiteside et al. 1985, Post et al. 1997, Rose et al. 1999, Mayer et al. 2000). These and similar studies have become the foundation for our understanding of yellow perch recruitment dynamics.

Questions regarding the growth and survival of pelagic-stage yellow perch are significant at present in Lake Michigan. The Lake Michigan yellow perch population has experienced sustained recruitment failure since 1990 that is widely believed to be due to low
survival during the pelagic larval phase (Clapp and Makauskas 2002), but those factors most important to variation in survival among annual cohorts in Lake Michigan are unknown.

Pelagic larvae in Lake Michigan reside in an open environment where physical transport of larvae away from nearshore (< 5 km) spawning sites is highly likely. Seasonal current patterns and episodic wind events in Lake Michigan during the larval period for yellow perch are both significant and highly variable (Mortimer 1971, Beletsky and Schwab 2001). Episodic events such as upwelling force nearshore water away from shore and have the potential to move yellow perch larvae away from shore through passive advection. Further, abundance data for larval yellow perch from 1998 – 2001 indicate that larvae are present in the nearshore region of Lake Michigan for only 5-7 days after hatching (R. Fulford unpublished data, Clapp and Makauskas 2002). There is little information regarding larval densities farther offshore, but Nash and Geffen (1991) documented the presence of yellow perch larvae in their mid-lake (20-30 km from shore) samples along a cross-lake transect. These data suggest that in Lake Michigan larval yellow perch may spend a significant portion of the larval period away from the nearshore zone.

In general, data are limited regarding the dynamics of larval perch in Lake Michigan and we must often rely on lessons learned from examination of the larval stage in other freshwater systems to fill important knowledge gaps (Rutherford et al. 2001). This practice can be a valuable and efficient tool for elucidating population dynamics, but it assumes that Lake Michigan can be characterized simply as a larger lake. This assumption requires caution, because Lake Michigan has a substantially larger pelagic zone (59,000 km²) in comparison to most other freshwater systems; the open pelagic habitat of Lake Michigan may more closely resemble an oceanic habitat than a lake habitat for larval fishes,
particularly in terms of variability in prey community composition. Movement into offshore
habitat not available to larvae in smaller systems is likely to have consequences for growth
and survival not observed in smaller systems, which may change as a function of when
during the larval period advection occurs.

Currently, both management agencies and the public are highly interested in
information about larval perch survival in Lake Michigan (Francis et al. 1996), and this has
focused research attention on the pelagic larval phase. However, my investigations also
address the more general question of how our understanding of larval recruitment in Lake
Michigan should be influenced by life history characteristics of the species and how much it
should be influenced by the physical characteristics of the available habitat.

One potentially useful method for examining factors important to larval survival in
Lake Michigan is individual-based modeling. Individual-based modeling is optimal for
investigating links between habitat characteristics, individual behavior and individual fate in
situations where either system complexity or system size makes a direct examination via
sampling or experimentation prohibitive. The individual-based modeling approach is also
well suited for analysis of patterns of variability in characteristics of survivors when
mortality rates are high such as with larval fishes.

In this chapter I address four questions. First I test the hypothesis that larval yellow
perch are using both nearshore and offshore habitat by sampling larval abundance, size and
age as a function of both depth and distance from shore. I also examine potential
mechanisms of larval advection into the offshore zone by measuring the frequency of
upwelling and downwelling events on the western side of Lake Michigan. Second, I test the
hypothesis that the nearshore and offshore habitats differ in significant ways for larval yellow
perch by sampling zooplankton community composition and water temperature as a function of distance from shore. In chapter three, I demonstrated that both growth rates and mortality rates of larval yellow perch change as a function of prey composition. Larval yellow perch choose prey based on relative abundance as well as innate preferences, resulting in predictable changes in larval diet between habitats. In this chapter I use data on prey community composition and temperature from nearshore and offshore Lake Michigan within the framework of a foraging-growth-predation individual based model to examine potential consequences of offshore advection for larval growth and survival. Finally, I address the general question of whether Lake Michigan is best characterized as a large lake or a small ocean for analysis of larval fish recruitment.

Methods

Study area – All field sampling was conducted along eight 1.6-km transects located from 1 to 32 km from shore extending southeast from Milwaukee, WI (Figure 5.1). Transects were evenly split between a nearshore set (n=4) and an offshore set (n=4). The nearshore transects were located 2, 3, 4 and 5 km from shore and overlaid Green Can Reef, a known yellow perch spawning area located 2 km southwest of Milwaukee Harbor (WDNR unpublished data). The offshore transects were located 8, 16, 24 and 32 km from shore and were oriented east west to maximize available vessel time. Sampling was conducted every four days from June 15 to July 17 in 2000 and from June 15 to July 31 in 2001. Due to vessel time constraints I could only sample four transects on each trip. From June 15 – 22 sampling was limited to the nearshore transects. Beginning on June 27-28, daily sampling was split evenly between nearshore and offshore transects and each transect was sampled every other trip.
Field sampling – Larval yellow perch were collected with either a 1 x 2-m neuston net or a 1 x 1.2-m multiple net tucker trawl. The dimensions of the tucker trawl are such that its oblique orientation in the water results in a functional mouth area of 1 m². In 2000, sampling was conducted with two neuston nets towed at the surface for 1 hr along each transect. In 2001, one neuston net was replaced with the tucker trawl in order to investigate depth distributions of larval perch. Total flow through the neuston net was measured with a propeller-type flowmeter (General Oceanics Inc.). Neuston net sample depth was 1-2 m (median depth 1.5 m).

Tucker trawl samples were collected by towing the trawl obliquely from the thermocline back to a depth of 2 m. Thermocline depth was established at each site on each day by taking a thermal profile prior to sampling. The net was raised ¼ of the thermocline depth every 15 minutes resulting in four depth strata being sampled. The tucker trawl was equipped with two nets: the first net was closed remotely after 30 minutes, resulting in separate lower epilimnion and upper epilimnion samples. Mesh size for both net types was initially 500 µm but was increased to 1000 µm on sample trip four and 1800 µm on sample trip eight to maximize capture efficiency for the largest larvae. I did not have two 1000- or 1800-µm tucker-trawl nets, so beginning on trip four, one composite epilimnion sample was collected rather than separate upper and lower samples.

Samples collected with all gear types were flash frozen in dry ice/alcohol slurry, returned to the Great Lakes WATER Institute and stored frozen at –80º C. Flash freezing was used as a preservation method because some of the larvae collected were used for a separate analysis of nutritional state. In the laboratory, samples were defrosted and searched
for larval yellow perch. All yellow perch larvae found were counted and measured to the nearest 0.1 mm with an ocular micrometer and both saggital otoliths were removed and prepared for age and growth analysis. Gut contents of all larvae were examined under a dissecting microscope at 20X magnification and all prey were identified and counted by taxonomic group. Taxonomic groups of interest were rotifers, copepod nauplii, cyclopoid copepods, calanoid copepods, small cladocerans and Daphnia spp. These groups include all major zooplankton available as prey for larval fishes in Lake Michigan (Madenjian et al. 2000).

Zooplankton were sampled with triplicate vertical hauls of a 0.5-m diameter, 64-µm mesh hoop net from a depth of 10 m back to the surface. Samples were collected at the beginning and end of each larval tow. All zooplankton collected were preserved in 95% ethanol and returned to the lab for enumeration. With the exception of rotifers, zooplankton were examined at 20X magnification and counted by taxonomic group. For each sample, at least three 5-ml sub-samples were examined from a known-volume dilution of the sample for density estimates. More sub-samples were examined if the prior three did not contain a combined 100 individuals from the taxonomic groups. Rotifers were enumerated at 400X and at least three 1-ml sub-samples were examined. Twenty individuals per sample from each taxonomic group, including rotifers, were measured to the nearest 0.1 mm with a digital imaging system.

*Age and Growth Analysis* – Otoliths removed from yellow perch larvae collected in both years were processed according to larval size. Otoliths from larvae less than 15 mm TL were mounted in Cytoseal (Fisher Scientific Corp.) on microscope slides. Otoliths from larvae
larger than 15 mm TL were mounted in thermoplastic cement on 1 cm X 1 cm glass squares and hand polished with fine grit sandpaper to clarify rings from the edge to the core. Individual age estimates were a function of mean ring counts (n=4) made at 400X magnification by two independent readers (Secor et al. 1995). Discrepancies in count between readers for an individual otolith were corrected with an additional joint reading. Mean ring count for an individual larvae was converted to an estimate of age based on an inverse regression analysis of ring count on true age for known-age larvae raised in the laboratory (Rice 1987, Appendix 1)

\[
\text{AGE} = \frac{\text{COUNT} - 0.83}{0.82}
\]

where COUNT is the mean ring count for an individual larva and AGE is the age estimate (days) for that larva.

These age estimates were used in two ways. First, growth rate (mm/day) was estimated for each individual over 7 mm TL based on the following formula:

\[
\text{GR} = \frac{\text{TL} - 5.7}{\text{AGE}}
\]

where TL is the total length (mm) measured in the laboratory and 5.7 mm is the mean length at hatching of perch larvae from my lab populations (See Chapter 2). Growth rates were not estimated for larvae less than 7 mm TL as the variability in mean initial length makes these growth rate estimates unreliable (Growth rate standard deviation: 0.22 mm/day below 7 mm and 0.023 mm/day above 7 mm; R. Fulford unpublished data). Hatchdate estimates for
individual fish were calculated by subtracting age from sample date. Individual hatchdates were compiled into a hatchdate frequency distribution for each sample and annual cohort (Appendix 1); hatchdate frequency distributions were adjusted for variability in age estimates based on a 95% confidence interval for individual estimates of larval age from the inverse regression analysis. Hatchdate distributions were used to simulate daily hatching frequency in the numerical experiments.

*Wind and temperature data* – I collected temperature data hourly 1 m below the surface and 1 m above the lake bottom at two sites from May 20 to July 17 in 2000 and from May 20 to July 30 in 2001. The two sites were located 1 km (depth 10 m) and 2 km (depth 25 m) from shore on Green Can Reef. I also collected surface water temperature data from hourly readings taken at an offshore weather buoy located 42 km southeast of Milwaukee, WI (Buoy 45003; National Data Buoy Center *archived data*). Data on hourly wind speed and direction during the larval period in each year were also collected from the offshore weather buoy.

I used wind and temperature data in two ways. First I used surface water temperature data to calculate daily mean surface water temperature for the nearshore and offshore zone of Lake Michigan during the pelagic larval period in each year. These data were used as input for individual-based model analysis.

I also used both surface and bottom water temperature data collected at my two stations, along with data for wind speed and direction collected at the offshore weather buoy, to identify upwelling and downwelling events on the western side of the Lake in 2000 and 2001. Upwelling is characterized by a rapid decrease in surface water temperatures to near bottom water temperatures and consistent wind from the south-southeast for 6-8 hours prior
to the period of interest. Downwelling events are characterized by a rapid increase in bottom
water temperature to near surface water temperatures and consistent wind from the north for
6-8 hours prior to the period of interest (Mortimer 1971). Both event types should be
detectable at the shallow site first and move gradually to the deep site. I examined the wind
and water temperature profiles for each year and identified potential events (upwelling or
downwelling) qualitatively as an index of advection potential for larvae in each year.

*Statistical analysis* – I tested for a difference in larval size as a function of capture distance
from shore with a linear regression analysis of larval length data from all gear types (N=735).
I tested for both a size and age difference for larvae as a function of capture depth by
comparing larvae captured in the tucker trawl to larvae captured in the neuston nets with an
ANOVA (SAS 2002). Tucker trawl data from all depth strata were pooled for analysis.

*Individual-based model analysis* - For the IBM analysis I used a foraging-growth-predation
IBM described previously (Chapters 2 & 3; Figure 4.2). Briefly, The model uses inputs of
daily zooplankton density and relative abundance to predict daily larval consumption based
on sized-based estimates of encounter rates and probability of attack and capture between
larvae and zooplankton prey. Prey types were rotifers, copepod nauplii, cyclopoid copepods,
calanoid copepods, small cladocerans and *Daphnia* spp. (Table 3.1). Encounter rate of larva
$j$ with prey type $i$ is based on a function relating larval search volume (SV, ml) and prey
density (d$_i$, prey/ml) to encounter rate (ER$_{i,j}$, prey/s):

\[
(2) \quad ER_{i,j} = SV_i * d_j * \text{Time}
\]
where search volume is a size-based function of larval swimming speed and reactive area for prey type \(i\) (Formulas 2 to 5, Chapter 3) and \(Time\) is available feeding time (42,300 s).

Available feeding time was limited to the 12 hr daylight period based on the observation that larval yellow perch are not active at night. Realized daily encounter rate \((E_{i,j})\) of larva \(j\) with prey type \(i\) was determined stochastically from a Poisson distribution with \(ER_{i,j}\) as the rate parameter.

Probability of attack and capture \((Q_{i,j})\) was a function of larval selectivity \((\alpha_{i,j})\) for prey type \(i\) and the relative abundance \((q_i)\) of prey type \(i\) in the environment:

\[
Q_{i,j} = \frac{\alpha_{i,j} \cdot q_i}{\sum_{k=1}^{m} \alpha_{k,j} \cdot q_j}
\]

where \(\alpha_{i,j}\) of larva \(j\) for prey type \(i\) was described with Chesson’s \(\alpha\) (Chesson 1983). Chesson’s \(\alpha\) was calculated with a size-based function derived empirically for each prey type (Figure 3.2). Daily relative abundance \((q_i)\) for prey type \(i\) was obtained from field data.

Daily consumption for each prey type was calculated stochastically with a binomial probability model with realized daily encounter rate \((E_{i,j})\) as the number of foraging events and \(Q_{i,j}\) as the success probability. Daily consumption could not rise above an estimate of maximum consumption, which was a function of larval mass (\(\mu g\), dry mass) and daily mean temperature (Letcher et al. 1996a, Hanson 1997).
This estimate of daily consumption was used to predict individual daily growth in a bioenergetics sub-model. Growth (G, µg/day) was daily consumption multiplied by assimilation efficiency minus total daily metabolic costs:

\[
G = (C \times \text{AE}) - (RM + AM + (C \times (U + SDA)))
\]

where assimilation efficiency (AE) was a proportion of daily consumption described with a function based on larval size (Letcher et al. 1996a). Assimilation efficiency was 0.6 for first feeding larvae and rose to a maximum of 0.8 at a larval size of 15 mm TL. Routine metabolic cost (RM, µg/day) was a function of larval mass and daily mean temperature, and active metabolic cost (AM, µg/day) was a constant multiple of routine metabolic cost (4.4, Post 1990). Costs of excretion (U, µg) and standard dynamic action (SDA, µg) were each set at 15% of consumption.

Individual larva died in the model from either starvation or predation. Daily vulnerability to starvation was based on a comparison of larval mass to a starvation threshold (Threshold) derived from experimental observations for larval yellow perch (Letcher et al. 1996b):

\[
\text{Threshold} = 0.47 \times \text{Maxwt}
\]

where Maxwt is the previous maximum mass (µg, dry mass) attained by a larva for that model run. Previous maximum mass was updated as larvae grew and vulnerability to starvation declined with increasing larval mass.
Daily vulnerability to predation was a function of both larval and predator total length and was described in the model with size-based functions of larval-predator encounter rate and probability of attack and capture. Daily encounter rate \( (E_{j,z}) \) of lava \( j \) and predator \( z \) was calculated based on swimming speed of both larva \( (SS, \text{cm/s}) \) and predator \( (\nu, \text{cm/s}) \) and reactive distance of both larva \( (R_j, \text{cm}) \) and predator \( (R_z, \text{cm}) \). Daily encounter rate was also a function of predator density \( (Den, \text{ml}^{-1}) \) and total available feeding time in a day \( (Time, 42,300 \text{ s}) \):

\[
E_{j,z} = \pi(R_z + R_j)^2 \cdot \frac{SS^2 + 3\nu^2}{3\nu} \cdot Den \cdot Time
\]

where feeding time was limited to the 12-hour daylight period based on the observation that all predators in the model search for prey visually and their larval prey are not active at night. Predator density was equal to \( 1/1\times10^9 \) where the denominator is the modeled water volume (ml). This calculation for predator density makes equation (5) equal to the encounter rate between an individual larva \( j \) and an individual predator \( z \) (predators were randomly assigned size and species each model day). In model simulations the actual number of predators present was set based on field data and the encounter rate between larva \( i \) and each predator was calculated separately with equation (5). Larval swimming speed was a yellow perch-specific function of size described by Houde (1969) and predator swimming speed was \( 3 \times \) predator length as described for planktivorous fish by Cowan et al. (1996).

Probability of attack and capture \( (a_{j,z}) \) was derived empirically for predators feeding on larval yellow perch (Chapter 2). The main predator of interest in Lake Michigan is
alewife, *Alosa pseudoharengus*. Alewife have been observed to feed on larval yellow perch in the laboratory (Chapter 2) and in natural populations (Mason and Brandt 1996). Moreover, a large body of anecdotal evidence exists to support the hypothesis that alewife have been significant predators of larval yellow perch in Lake Michigan (Crowder 1980, Eck and Wells 1987, Shroyer and McComish 2000). Daily vulnerability to predation ($V_{j,z}$) in the model was defined as one minus the probability a larva escaped all encounters with a predator for that day based on a binomial probability model

\[(9) \quad V_{j,z} = 1 - (1-a_{i,z})^{E_{i,z}}\]

with the number of encounters equal to $E_{j,z}$ and success probability equal to $1 - a_{j,z}$. If $V_{j,z}$ for larva $j$ on a given day exceeded a uniform random number between 0 and 1 generated in the model then larva $j$ died. If larva $j$ survived predation, then both size and mass were updated according to predicted growth and the larva continued to the next day.

All model simulations were run with 10,000 individual larvae drawn from a normal distribution of initial sizes with mean 5.7 mm TL and SD = 0.3 mm. Larvae were introduced into the model based on the initial hatchdate distribution estimated for newly-hatched larvae captured from Lake Michigan in 2001. The hatching period lasted from day 1 to day 24; 15% of the population had been hatched by day 9, 50% by day 13, 90% by day 18 and 100% by day 24. The model was run until 30 days after peak hatch (45 days total).

The IBM was used to conduct a numerical experiment to examine the consequences of the timing of offshore advection for perch larvae in both 2000 and 2001. Annual conditions were based on field data for daily mean water temperature and zooplankton
community composition collected in 2000 and 2001 respectively. The nearshore (0-5 km) and offshore (8-32 km) zones were defined in the model as described for field sampling. For each model simulation, conditions were set to either ‘2000’ or ‘2001’ at the beginning of the model run and all larvae were initially hatched into the nearshore zone.

A series of model runs were conducted in which timing of advection from nearshore into offshore waters was set to day 0, 10, 20, 30 or never. Nearshore and offshore waters varied in daily mean temperature and zooplankton community composition. The objective of these numerical experiments was to test the importance of changes in prey community composition between nearshore and offshore waters, so zooplankton density was set at 100 organisms/L in both zones. This value is representative of zooplankton densities observed in both years and results in enough survivors for analysis in the model. Predator density was set at 36 alewife/1000 m³ for all runs based on alewife density estimates for Lake Michigan (Fabrizio et al. 1997).

Model output for comparisons between years and timing of larval movement into the offshore zone was mean diet composition as a function of larval size for all larvae in the model, total survival, and growth rate and size distributions of survivors. All results were based on triplicate model runs to account for stochastic variability. Diet proportions, as well as growth rate and size distributions of survivors were summarized across replicate model runs by calculating combined distributions with data from all three replicates.

Results

Larval sampling– Larval abundance in 2000 was two orders of magnitude lower than in 2001 (Figure 5.3). Peak abundance was 0.35/1000 m³ in 2000 and 40/1000 m³ in 2001. However,
the timing of peak abundance was very similar between years. In 2001, larvae were captured at all sites from 1 to 32 km from shore. Further, there was a significant positive relationship between larval total length and capture distance from shore ($R^2 = 0.86$; Figure 5.4). Larvae took two weeks to appear at the 12-km site and a month to appear at the 32-km site, which is near the middle of the lake. I also detected a significant difference in larval total length between depth zones (ANOVA $F=416$, $p<0.001$; Figure 5.4). Larvae larger than 15 mm TL were only captured in tucker trawl samples (both upper and lower epilimnion), which were collected at depths greater than 2 m. These data suggest that larvae smaller than 15 mm TL are distributed from the surface to the thermocline, but larger larvae are only found in waters deeper than 2 m. The age-depth relationship showed a similar pattern with larvae older than 18 days post hatch (dph) avoiding surface waters.

Otolith analysis indicated that larvae captured in 2001 hatched from June 15 to July 8 with around 85% of the hatch occurring between June 12 and June 28. Peak hatch was on June 20th. Mean growth rate of survivors to 30 days after peak hatch from the 2001 cohort was 0.65 mm/day (SD = 0.08). Insufficient otolith data were available to generate a hatchdate distribution or growth rate estimates for 2000. However, based on a comparison of temperature data and data for larval abundance as a function of sample date between years, 2000 and 2001 were similar in the timing of hatch, so the 2001 hatchdate frequency was used in the model simulations for both years.

Only later-stage larvae (N=16, mean size 20.8 mm SD=7.3 mm) were captured with food in their guts. Diet for these larvae was dominated by calanoid copepods (Mean proportion 0.97, SD=0.02) with cyclopoid copepods (0.02, 0.02) and *Daphnia* spp. (0.003, 0.006) comprising a small dietary component.
Zooplankton sampling – Density and community composition varied with sample date in both seasons. Density peaked at 70 organisms/L nearshore in 2000 and was only below 50/L on one date (6/22; Figure 5.5). Densities were lower offshore in 2000 with a peak density of 48/L. Densities were higher in 2001 with a peak density of 165/L nearshore and 104/L offshore (Figure 5.6). Zooplankton density changed with sample date within zone and year, but these patterns were not consistent between years. However, zooplankton density was consistently lower in the offshore zone compared to the nearshore zone in both years.

Community composition differed between nearshore and offshore sites in 2001 but not in 2000. The ratio of rotifer to copepod abundance has been found to be particularly important to the growth and survival of early-larval stage yellow perch (Chapter 3). Larval yellow perch positively select rotifers at first-feeding, but the appearance of copepods in larval diets increases with copepod relative abundance; copepods are a better prey item than rotifers for maximizing growth. Therefore I am particularly interested in changes in the relative abundance of copepods and rotifers between nearshore and offshore habitat.

The early nearshore assemblage in 2000 was composed mostly of cyclopoid and calanoid copepods, but the assemblage shifted to dominance by rotifers around the time of peak hatch for yellow perch (6/20). Rotifers dominated the nearshore assemblage in both years accounting for up to 75% of the total abundance (Figure 5.5 and 5.6). The offshore assemblage in 2000 was very similar to the nearshore assemblage (Figure 5.5) with the exception that small cladocerans were more abundant in the nearshore zone in 2000 later in the larval period. However, the offshore assemblage in 2001 differed from the nearshore assemblage in that it was dominated by copepods until about four weeks after peak hatch for
yellow perch. Prior to July 15th calanoid and cyclopoid copepods made up as much as 50% of the offshore assemblage in 2001. This difference between the nearshore and offshore in 2001 is likely to be important.

Relative abundance of small cladocerans rose to about 11% of the assemblage in the nearshore zone in 2000. At all other times, cladocerans were only a minor portion of both nearshore and offshore assemblages accounting for less than 1% of the zooplankton community.

**Temperature** - General patterns in surface water temperature were similar between years (Figure 5.7). Mean daily temperature was 10-12°C on June 15 and warmed slowly to 20-23°C over the pelagic larval period. This warming pattern was also observed in surface water temperature data for this period collected at the offshore data buoy in 2000. The observed trend offshore in 2001 was generally similar, but inshore and offshore surface temperature were 5-10°C different during two periods. The first was June 26-31 when offshore surface water increased in temperature. The second event was July 17-27 when nearshore surface temperature abruptly dropped (National Data Buoy Center archived data).

Comparison of surface and bottom water temperature data between the shallow- and deep-water sites indicated no potential upwelling or downwelling events in waters near Milwaukee, WI during the larval period for yellow perch in 2000. Two upwelling events were evident in temperature data during the pelagic larval period in 2001 (Figure 5.8). The first event in 2001 began on June 18th indicated by a decline in surface water temperature to near bottom water temperature, and subsided 24-36 hours later. Data for wind speed and direction collected at the data buoy were consistent with these results. Wind speeds
maximized at over 10 m/s predominantly from the south-southeast during the 24-hr period leading up to this event. This upwelling event was early in the hatching period for yellow perch. It was also strong as evidenced by the rapid 7-8°C temperature decrease in nearshore surface waters, but it was short (< 36 hours) in comparison to historical data (Mean length of upwelling 1992 – 2000 15 days; D. Mason personal communication). The second upwelling event began on June 25th and lasted for 4-5 days (Figure 5.8). Wind direction in the 24-hr period leading up to June 25 was primarily from the south-southeast and supports the existence of an upwelling event on the western side of Lake Michigan on these dates. However, this event was not strong (2-3°C drop in surface water temperature) with a maximum wind speed (4.5 m/s) nearly equal to the seasonal average wind speed (4.3 m/s).

There was also evidence for three downwelling events later in the larval period in 2001. The first occurred on July 1st, the second on July 9th and the third began on July 25th. The events on July 1st and 10th were brief, but the downwelling event on July 25 was strong and lasted for 10-12 days. Downwelling events would be more likely to retain larvae nearshore than to facilitate transport into offshore waters. However, both of the measurable downwelling events occurred late in the larval period when they are not predicted to have as strong an effect on larval survival as events which occurred closer to the hatching period. It is worthy of note that the two periods of observed deviation between surface water temperatures nearshore and surface water temperatures offshore (Figure 5.7) coincided with an upwelling event on June 25th and a downwelling event on July 25th (Figure 5.8).

**Numerical experiments** – Mean survival of simulated larval yellow perch under 2000 conditions was 0.02% when larvae were transported from nearshore to offshore habitat after
Mean survival was three times higher (0.07 %) when larvae where transported offshore on day 0 or 10. Mean larval survival under 2001 conditions was always higher than mean larval survival under 2000 conditions, but it followed a similar pattern with respect to when larvae were transported offshore. Mean survival in 2001 was over 4% when larvae were transported into the offshore zone prior to day 20 (5 days after peak hatch). Mean survival in 2001 dropped to less than 2% when larvae were transported offshore on day 30 and it was below 1% if larvae remained in the nearshore zone for the whole model run (Figure 5.9). Predation mortality was high in all model simulations (>80% of mortality), but differences in survival both between years and between timing of larval advection within year were due largely to changes in predicted starvation rates. The higher offshore abundance of copepods seems to have been the pivotal advantage of early larval transport into offshore habitat.

Both mean and distribution of larval growth rates changed between years and as a function of when larvae were transported from nearshore to offshore waters (Figure 5.10). In 2000, mean growth rate of survivors was 0.43 mm/day when larvae were transported offshore for at least part of the larval period. Mean growth rate dropped to 0.23 mm/day when larvae remained in the nearshore zone for the entire larval period. In 2001, larval survivors had a higher mean growth rate (0.68 mm/day) in comparison to 2000 when larvae were advected offshore either on day 10 or day 20, but a lower mean growth rate if advection occurred on day 30 (0.34 mm/day) or never (0.15 mm/day). The distribution of individual growth rates showed a similar pattern. Distributions of growth rates in 2000 were not strongly affected by the timing of larval transport, although the maximum observed growth rate was predicted to be higher if larvae were advected offshore in 2000 compared to larvae
that remained nearshore. In contrast growth rate distributions in 2001 differed markedly as a function of timing of larval transport into offshore waters. Individual growth rates for larvae that remained in nearshore waters for the entire model run in 2001 were much lower in comparison to the growth rate of larvae that were transported offshore prior to day 20 in that year; there was minimal overlap between these two distributions. The growth rate distribution for larvae that remained in nearshore waters in 2001 more closely resembled the growth rate distribution of larvae exposed to 2000 conditions in the model.

Larval diet predicted by the model changed as a function of larval size, year and the timing of transport from nearshore to offshore waters (Figure 5.11). Yellow perch larvae less than 7 mm TL were predicted to feed predominantly on rotifers and copepods. Rotifers disappeared from the diet of larvae greater than 10 mm TL and diet shifted to dominance by calanoid copepods at this larval size. These findings agree well with my field data for diet of yellow perch larvae greater than 10 mm TL in Lake Michigan.

Diet predicted in the model for larvae in 2000 did not change as a function of the timing of transport into offshore waters. In contrast, diet of larvae in 2001 was predicted to change as a function of the timing of offshore transport. When transport into offshore waters occurred on either day 10 or day 20, diet of larvae less than 7 mm TL contained a lower proportion of rotifers (< 10% by mass) and a higher proportion of copepods (80-90% by mass). Diet of larvae that remained nearshore for the entire model run in 2001 and all larvae in 2000 contained a higher proportion of rotifers (30-45% by mass) when larvae were less than 7 mm TL. These data suggest that timing of transport relative to the larval period primarily affected the composition of available prey for early-stage larvae.
Discussion

*Larval advection* - Larval yellow perch are present in the offshore pelagic habitat of Lake Michigan in some years. Larvae were collected all the way to the middle of the lake in 2001. Moreover, all larvae captured farther than 20 km from shore had food in their guts and appeared in good condition, which suggests that the offshore pelagic habitat is capable of supporting larval yellow perch. In 2000, larvae were collected for only a brief period in the nearshore zone and were not captured at all in the offshore zone. However absence from the offshore zone may be an indicator of low survival for this year class overall rather than evidence for reduced larval use of offshore habitat.

Timing of transport from nearshore to offshore pelagic habitat may be correlated with the strength and frequency of wind-driven episodic water movement. If larval transport from nearshore hatching areas into the offshore zone is dependent primarily on episodic wind-driven current events such as upwelling, then the rate of movement into the offshore zone should show some correlation with the timing and strength of these events. No detectable upwelling events occurred in waters near Milwaukee, WI in 2000. Two upwelling events were detected during the larval period in 2001. The first was fairly short and early in the larval period, so it is not likely to have affected much of the 2001 cohort. The second upwelling event occurred after peak hatch, so most of the cohort was present, but it was a weak upwelling event based on the small temperature shift in surface waters and the mean wind speed during the event. These data suggest that if larval transport is dependent on episodic current events, then offshore transport would have been minimal in 2000 and it would have occurred slowly in 2001.
Evidence from larval sampling in 2001 suggests that larvae were transported offshore slowly. Yellow perch larvae appeared at the site 12 km from shore two weeks after peak hatch and did not appear at the site farthest from shore (32 km) until a month after peak hatch. Moreover, the significant relationship between larval total length and distance from shore indicates that larvae took time to reach offshore sites and were growing as they moved offshore in 2001. These data plus the fact that larval yellow perch were not found offshore in 2000 support the hypothesis that episodic current events are an important transport mechanism for larval yellow perch in Lake Michigan.

Another indication of the importance of wind-driven current events for larval transport is the vertical distribution of larval yellow perch. Larvae smaller than 15 mm TL were evenly distributed throughout the epilimnion during the day. This pattern of vertical distribution is appropriate for maximizing wind-driven offshore dispersal (Lazzari et al. 1993, Neilson and Perry 2000) as larvae in different depth layers of the epilimnion would be moving in slightly different directions due to Ekman transport (Garrison 1993). Larvae near the water surface would be pushed in a direction close to the direction of the wind. Since alongshore winds are associated with upwelling events, larvae near the surface would be pushed more along shore than in an offshore direction. As larvae move deeper in the water column, the direction of advection would become increasingly perpendicular to shore. Current velocity will also decrease with depth, but there is likely to be a depth zone where offshore movement is maximized. The larvae of blue crabs are known to manipulate their vertical distribution in order to exploit this phenomenon to move from coastal hatching zones through inlets and into sheltered nursery areas along the Atlantic coast of the US (Roman and Boicourt 1999). In the case of larval yellow perch in Lake Michigan, an increase in the depth
distribution of larval yellow perch combined with Ekman transport would be more likely to push larvae away from shore rather than retain them nearshore. Therefore, even if larvae are not actively choosing to leave the nearshore zone of Lake Michigan, passive transport is likely to push larvae offshore in years when wind-driven current events are frequent.

One significant question unanswered at present is how larval yellow perch are able to return to the nearshore littoral zone at the time of juvenile transition. The specific biological cue used by yellow perch to navigate 20-30 km back to shore at the end of the larval period is not clear. However, physical modeling conducted at the Great Lakes Environmental Research Center suggests that even without any assumptions regarding swimming ability, the 30-40 day pelagic period is sufficient for larval yellow perch to be passively transported by episodic current events to the middle of the lake and back to the nearshore littoral zone prior to the juvenile transition (E. Rutherford University of Michigan in prep). Further, my data suggest that larvae larger than 15 mm TL disappear from the surface waters altogether while still offshore. These larger, older larvae are displaying both ability and pattern in their vertical distribution, which may act together with passive transport for the journey back to the littoral zone during juvenile transition.

Consequences of advection – Potential consequences of offshore advection in the model were an increase or decrease in individual probability of survival through starvation, or an indirect effect through increased or decreased growth rate, which would alter individual vulnerability to size-dependent predation. Differences between the nearshore and offshore habitat likely to affect larvae were differences in prey community composition and density and differences in daily mean water temperature. Seasonal changes in both prey density and daily mean water
temperature did not differ substantially between the nearshore and offshore zone in either year. Two episodic wind events (an upwelling and a downwelling) in 2001 caused offshore waters to be 5-10°C warmer during these periods; this difference should result in slightly higher growth rates for larvae that were offshore at these times in 2001. The main difference between the nearshore and offshore habitat likely to result in consequences for larvae was differences in prey community composition.

Offshore advection early in the larval period was beneficial to larval survival in both years examined, although this result was more dramatic in 2001. The model predicted increased larval survival and individual growth rate for larvae advected offshore early. Early transport from nearshore to offshore habitat would expose the majority of individual larvae to offshore conditions. In both years, the offshore prey community was comprised of more copepods and fewer rotifers when compared to the nearshore prey community. First-feeding larvae have been observed to feed on both rotifers and cyclopoid copepods, however model analysis suggests that larval growth rates will be noticeably higher if larvae choose to eat copepods. Based on my empirical foraging rules (Chapter 3), yellow perch larvae are predicted to change their diet to included more copepods in the offshore zone resulting in a measurable growth advantage for larvae advected offshore early compared to larvae that remain nearshore for a longer period. Increased survival of yellow perch larvae advected offshore early in the larval period was correlated with a shift in diet composition predicted for these larvae.

Model simulations predict that larvae advected into offshore habitat will change their diet in response to changes in the relative abundance of prey between the nearshore prey community and the offshore prey community. These predictions agree with observed diet
data for larval yellow perch in the offshore habitat of Lake Michigan. Larval yellow perch less than 7 mm TL are predicted to select positively for rotifers and only neutrally for copepods based on the results of selectivity experiments (Figure 3.2). However, the observed change in copepod abundance between zones, particularly in 2001 (6/L nearshore and 22/L offshore) is important to larval foraging because larvae in the offshore habitat encounter more copepods and this is predicted to increased individual choice to attack. As a result, early transport from a rotifer-dominated community (i.e., nearshore) to a more balanced prey community (i.e., offshore) in 2001 resulted in an earlier shift to copepods in larval diet and higher growth rates for individual larvae. This earlier transition to copepods in larval diets translated into increased growth and decreased likelihood of starvation in the model. These positive consequences of offshore advection would not be predicted based on a more traditional optimal foraging approach in which changes in diet are primarily dependent on changes in larval size.

Model results suggest that timing of transport was not likely to improve growth or survival in 2000 as both the nearshore and offshore prey communities were dominated by rotifers. Year classes that encounter these conditions are highly unlikely to be strong. However, model results also suggest that in 2001 the probability of a good year class would have been greatly increased by early advection for a large part of the larval cohort. If passive water movement is the most likely vector for advection, a significant upwelling event 5-10 days after peak hatch was predicted to result in increased offshore movement and increased larval survival in 2001.

There was potential for a good year class for larval yellow perch in 2001, but the transport events may not have been adequate to move larvae into optimal habitat quickly
enough to exploit it. An interaction of prey resources and physical transport may be difficult to detect in long-term recruitment data, but there are some clues to its importance. A comparison of the number and intensity of upwelling events based on Advanced Very High Resolution Radiometer (AVHRR) satellite imagery between 1998 (i.e., good recruitment year) and 2000 revealed that upwelling events lake-wide were both more numerous and lasted longer in 1998 than in 2000 (D. Mason personal communication), which supports the notion that upwelling activity in Lake Michigan is correlated with a good perch year class.

One potentially important difference between habitats in Lake Michigan that I did not consider is predator density. Variation in predator density between the nearshore and offshore zones is likely to interact with variation in larval size to affect larval survival. Previous work has indicated that larvae with a higher mean growth rate are more likely to survive predation. Higher individual growth rates were correlated with higher survival in my model analysis, but this advantage could be reversed by differences in predator encounter rates between habitats. Alewife, *Alosa pseudoharengus*, is the only predator known to consume yellow perch larvae (See Chapter 2) that is common in Lake Michigan, and thought to limit recruitment of yellow perch by limiting larval survival (Crowder 1980, Eck and Wells 1987). The available information regarding temporal and spatial variation in predator density in Lake Michigan is limited to large-scale annual patterns and biomass estimates based on only a few samples in any one location (Hatch et al. 1981, Fabrizio et al. 1997). A detailed analysis of differences in alewife density between nearshore and offshore habitat during the larval period for yellow perch has yet to be done, and these data may be an important piece of the recruitment puzzle.
However, experimental and model analyses indicate the period of high vulnerability for larval yellow perch to alewife predation as a function of predator and prey size is short; predation by alewives on larval yellow perch is maximized for only a brief portion of the larval period (Chapter 2). Further, alewife feeding rate on larval yellow perch is positively associated with larval density (Chapter 2). There is evidence from natural systems that even when alewife encounter larval yellow perch at optimal prey densities, alewife feeding rate on larvae drops to near zero at low larval densities (11 m$^3$, Brandt et al. 1987). Data from larval sampling in Lake Michigan from 1998 – 2001 indicate current densities of larval yellow perch in Lake Michigan are low (< 1/m$^3$) and alewife would not be predicted to seek out larval prey at these low densities. Moreover, if larval advection into offshore pelagic habitat is common, as my data suggest, then even in years of high larval abundance larval density is likely to be high for only a brief period around the timing of peak hatch and prior to significant larval dispersal. These data suggest that at present predation is not a pivotal component of recruitment variability for larval perch in Lake Michigan. Therefore, while it is important to consider all differences between nearshore and offshore habitat, it seems unlikely at present that changes in predator abundance would alter my results.

A confluence of biological factors (prey community composition) and the physical factors (timing and rates of advection) is important to the development of a good year class for larval perch in Lake Michigan. In a large, open system like Lake Michigan, it seems that variance in prey quality and quantity is more important than variation in predation pressure to good larval survival. In fact, a lower importance for predation in controlling recruitment is a direct dichotomy between Lake Michigan and smaller systems such as Oneida Lake, NY and
Lake Mendota, WI where the prey community is more stable and variation in predation pressure seems very important to a year class strength of yellow perch (Mayer et al. 2000).

Predation by alewife on larval yellow perch has been cited historically as an important determinant of larval survival in Lake Michigan (Crowder 1980, Eck and Wells 1987) and this has been re-affirmed recently in Indiana waters of Lake Michigan (Shroyer and McComish 2000). However, the current evidence for the importance of alewife predation to larval survival is largely indirect and based on correlation between increases in alewife abundance and decreases in yellow perch abundance, as well as a high level of spatial interaction between alewife and yellow perch larvae in the pelagic zone. This evidence may need to be reevaluated in connection with current conditions in the Lake and evidence for offshore advection of larval yellow perch.

Spatial overlap of alewife and larval yellow perch suggests that alewife can affect larval survival, but the hypothesized importance of interactions between alewife and larval yellow perch to yellow perch recruitment has been based on whether other factors that may impact recruitment can be ruled out. Eck and Wells (1987) pointed out food limitation may not limit larval survival because a strong yellow perch year class was produced in 1983 and food abundance in the nearshore zone of Lake Michigan had declined 90% between 1970 and 1983 (Evans 1986). However, zooplankton abundance in the offshore zone of Lake Michigan showed no trend between 1975 and 1992 (Madenjian et al. 2002). If larval yellow perch were transported offshore in 1983, then low prey density in the nearshore zone would not have been an issue for larval survival.

There is strong evidence that the population size of yellow perch in Lake Michigan in the 1970s was depressed by the invasion of alewife. However, differences also exist between
conditions at the time of alewife establishment in Lake Michigan and current conditions (Table 5.1). Alewife abundance was reduced dramatically in the early 1980s and has remained fairly constant over the last two decades (Madenjian et al. 2002). Juvenile yellow perch abundance was about seven times higher in the late 1980s compared to juvenile abundance data from 1998 – 2001 (Clapp and Makauskas 2002). Assuming larvae were seven times more abundant in these years as well and taking into account the distribution of larval yellow perch throughout the pelagic zone of Lake Michigan, mean density of larval yellow perch during the peak of abundance in 1983 would have been about 0.24/m³. Therefore, if larval yellow perch were distributed throughout the pelagic zone, it is questionable whether densities of larval yellow perch would have been sufficient to make density-dependent factors like predation by alewife important to year class strength even in the late 1980s when the yellow perch population was large. It is more likely that density dependence would be detectable after the juvenile transition when yellow perch are concentrated in the nearshore zone. If year class strength is largely dependent on larval survival, which is affected more by density-independent factors such as prey community composition, then these density-dependent factors affecting the juvenile stage may be only loosely correlated with adult abundance. Density-independent factors are often cited as important to larval survival and year class strength for marine fish larvae (Leggett et al. 1984, Bjorkstedt et al. 2002).

Viewing Lake Michigan as a small ocean rather than a big lake may be a productive approach for analysis of larval recruitment in Lake Michigan. Primarily, this approach would involve efforts similar to this project to further analyze distributions of larvae throughout the pelagic zone to understand the influence of the offshore zone on year class
strength and how that influence may vary over a longer period. Additionally, it would be valuable to apply some of the transport and upwelling models applied to marine coastal species such as rockfish (Bjorkstedt et al. 2002) to understand how episodic events may affect larval movement in the lake. Finally, it is important to view fish populations in Lake Michigan that experience mixing during the pelagic larval phase as a larger body of ecologically interconnected units. This meta-population approach to research and management predicts populations will be relatively isolated as adults, but will mix during the larval phase. Under these conditions, it would be important to adopt a lake-wide viewpoint to management that crosses state boundaries, and that takes into account the high level of variability in annual recruitment that results from larval exposure to density-independent mortality during the pelagic larval period. From this perspective, Lake Michigan resembles a more open marine environment for larval fishes.

The primary criticisms of this approach in marine systems are that it is not supported by genetic data and that larval duration is not long enough for significant transport across the long distances between populations (Warner and Cowen 2002). Neither of these criticisms are supported for larval advection in Lake Michigan. Population mixing in the offshore habitat in Lake Michigan is supported by genetic data that suggest perch in Lake Michigan comprise two regional meta-populations (i.e., northern and southern, Miller 2003). Further, recent analysis of the movement of passive particles around Lake Michigan during the larval period has shown that it is highly probable that larvae could be passively moved into the offshore zone and return to shore within the 30-40 day larval period (Ed Rutherford, Great Lakes Environmental Research Lab Ann Arbor, MI personal communication).
Offshore movement of larval yellow perch appears to be a natural part of their life cycle. The large amount of offshore habitat in Lake Michigan complicates my ability to observe or predict this movement in comparison to a smaller system where such movement would be trivial. By applying lessons learned in lakes and lessons learned in marine systems where appropriate, we can maximize our use of prior knowledge in a way that accounts for both biological and environmental factors. In this case, incorporation of the small ocean approach to analysis of variation in larval survival will be an invaluable tool for the appropriate management of yellow perch and other similar fishes in Lake Michigan. Ultimately, it will be important to ask similar questions about any fishes that reside in a meso-oceanic freshwater system and make use of offshore pelagic habitat.

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Table 5.1 Summary of evidence for a significant impact of alewife predation on survival of larval yellow perch in Lake Michigan and implications of current conditions in Lake Michigan and evidence for offshore advection of larval yellow perch for re-evaluation of this hypothesis.

<table>
<thead>
<tr>
<th>Evidence for predation by alewife on yellow perch larvae</th>
<th>Source</th>
<th>Implications of current conditions and larval advection</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spatial overlap of alewife with larval yellow perch in the pelagic zone of Lake Michigan</td>
<td>Crowder 1980</td>
<td>Overlap remains high during the larval period for yellow perch</td>
</tr>
<tr>
<td>Alewife observed to feed on larval yellow perch in laboratory experiments and in other systems</td>
<td>Mason and Brandt 1996, Chapter 2</td>
<td>Alewife feeding rate on larval yellow perch positively correlated with larval density.</td>
</tr>
<tr>
<td>Changes in alewife abundance only correlated with a decline in large zooplankton unavailable to larval yellow perch</td>
<td>Crowder 1980, Eck and wells 1987</td>
<td>Decline in zooplankton abundance in 1990s over a broader size range possibly due to predation by invasive cladocerans such as <em>Bythotrephes cederstromii</em> (Lehman 1991)</td>
</tr>
<tr>
<td>Changes in yellow perch recruitment not correlated with changes in prey density in nearshore zone</td>
<td>Eck and Wells 1987, Evans 1986</td>
<td>Did not include the potential effect of offshore zooplankton densities, which showed no change between 1975 and 1992 (Mandenjian et al. 2002)</td>
</tr>
</tbody>
</table>
Figure 5.1 Map of Lake Michigan showing sampling area near Milwaukee, WI. Vertical bars are nearshore transects oriented north-south and horizontal bars are offshore transects oriented east-west. Large dot is Milwaukee, WI and small dot is the location of the offshore weather buoy 45007 (NOAA National Data Buoy Center). Based on map figure obtained from David Schwab, Great Lakes Environmental Research Center Ann Arbor, MI.
Figure 5.2  Flow chart describing the foraging-growth-predation IBM used to investigate consequences of offshore movement for larval yellow perch. Nearshore and offshore conditions in the model were based on field data for water temperature, zooplankton community composition and predator density.
Figure 5.3  Mean abundance by date of larval yellow perch collected from all sites in Lake Michigan in 2000 (▲) and 2001(●). Note the difference in scale between left and right y-axes.
Figure 5.4  Mean total length (mm) as a function of capture distance from shore and depth of capture for yellow perch larvae captured at all sites between June 15 and July 30, 2001. Depth of capture was set to the median depth for the depth zone of capture (surface, upper epilimnion, lower epilimnion). Symbol type denotes the depth zone of capture and symbol marked ‘Epilimnion’ is for larvae captured by sampling the entire epilimnion with one net. Hatched line indicates the depth (2 m) separating surface samples from epilimnion samples. Depth of the thermocline, and the size of the upper and lower epilimnion, varied as a function of both site and sample date and therefore are not labeled on the figure.

\[
y = 0.59x + 4.01 \\
R^2 = 0.87 \\
N=735
\]
Figure 5.5 Mean zooplankton density and community composition at nearshore and offshore sites sampled every four days from June 15 to July 17, 2000.
Figure 5.6 Mean zooplankton density and community composition at nearshore and offshore sites sampled every four days from June 18 to July 30, 2001.
Figure 5.7 Six-hour mean surface water temperatures collected from June 15 to July 30 in 2000 and 2001 at a site 1 km (25 m) southeast of Milwaukee harbor and from NOAA weather buoy 45007 located 47 km southeast of Milwaukee harbor (100 m). Data at the 1-km site in 2000 ended on July 17 due to an equipment failure.
Figure 5.8  Six-hour mean water temperature collected at the water surface and lake bottom at sites 1 km (depth 10 m) and 2 km (depth 25 m) from shore from June 15 to July 30, 2001. Black bars indicate probable upwelling events and gray bars indicate probable downwelling events based on changes in water temperatures, wind speed and wind direction. Upwelling events are labeled 1 and 2. Wind direction (deg) for the 24-hr period preceding the two upwelling events is summarized in the lower pie charts as proportion of 24-hour period that wind direction was in a given quadrant. Maximum wind speeds for the preceding 24-hr periods are also given. Horizontal line near date axis indicates hatching period for yellow perch and black arrow indicates date of peak hatch.
2001

Sample Date

Temperature °C

- Offshore surface
- Offshore bottom
- Onshore surface

Upwelling #1

Maximum
Wind Speed = 10.7 m/s

0-90
91-180
181-270
270-360

Upwelling #2

Maximum
Wind Speed = 4.5 m/s

0-90
91-180
181-270
271-360
Figure 5.9  Proportion of larvae that survived to the end of the model run. Model runs differed in the timing of offshore advection. Offshore advection occurred on day 0, 10, 20, 30 or never. Data are given for model runs under both 2000 (●) or 2001(▲) conditions. Day of peak hatch in the model is indicated by a black arrow under the x axis.
Figure 5.10  Growth rate distribution (mm/day) for larval survivors from model runs in which larvae were advected offshore on day 0, 10, 20, 30 or they remained nearshore (Never) for the entire model run. Data are given for both 2000 and 2001 conditions. Mean growth rate (mm/day) is given for each chart respectively.
Figure 5.11 Predicted larval diet as a function of growth for all larvae in the model expressed as a proportion from each of six prey groups. Data are grouped for four larval size groups and a larva may grow through all size groups depending on its growth rate and length at mortality. Size groups are 5-7 mm, 7.1-10 mm, 10.1 – 20 mm, 20.1 – 30 mm and 30.1 – 40 mm. The top chart gives data for larvae exposed to 2000 conditions and advected offshore on model day 10. The middle chart gives data for larvae exposed to 2001 conditions and advected offshore on model day 10, and the bottom chart gives data for larvae exposed to 2001 conditions and which remained nearshore for the entire model run.
General Conclusions

Studying the larval stage of fishes is more complicated than analyses of later life-stages because larvae are small, live for a relatively short period and have a significantly higher mortality rate. However these complications do not diminish the importance of understanding what affects larval survival. Indirect analytical tools such as individual-based modeling are well suited to the ephemeral nature of the larval stage. This project has addressed four hypotheses concerning factors currently limiting survival of larval yellow perch in southern Lake Michigan. I have used an individual-based modeling approach and the analysis of characteristics of larval survivors to address these hypotheses. These techniques have been applied in the past to understand the recruitment processes of other larval fishes both in Lake Michigan (Rice et al. 1987, Letcher et al. 1996) and in other systems (Crecco and Savoy 1985, Cowan et al. 1996). My work has been an extension of these previous analyses, but it is also unique in several respects.

First, I have used the individual-based modeling approach to address the current management problems of yellow perch in Lake Michigan. The yellow perch population decline in Lake Michigan during the 1990s has resulted in a high degree of interest among fishery managers in larval survival. The Yellow Perch Task Group has identified these hypotheses as critical to understanding and correcting the current recruitment failure of larval yellow perch in southern Lake Michigan. Moreover, field sampling was unlikely to generate clear data to identify what factors are important to larval yellow perch survival. My combination of field sampling with model analysis has allowed me to address particular hypotheses in a more comprehensive way than would be possible based on field data alone.
The second unique aspect of this study was that variation in individual hatchdate was included in the individual-based model. Individual hatchdate was included in the model as a source of size variability. The inclusion of hatchdate variation in the model allowed for more similarity between a natural larval year class and the simulated larval yearclasses. Moreover, my results suggest that hatchdate distributions of survivors can be an important characteristic of survivors for gauging the intensity of size-dependence in larval mortality. Size-dependent mortality is affected by variation in growth rate and variation in hatchdate. However, for the youngest larvae, differences in hatchdate among individuals are much more important to size variability than differences in growth rate. Further, I demonstrated in chapter two that patterns of change in the hatchdate distribution over the larval period are sensitive to the presence of size-dependence in larval mortality; these patterns can be valuable for interpreting patterns in larval hatchdate distributions observed in field data. This approach has already proven effective for assessing the importance of the timing and intensity of predation to survival of larval yellow perch in Green Bay (Chapter 4).

Another unique contribution of this study was the empirical approach for predicting the diet composition of larval yellow perch presented in chapter three. My approach predicts that individual larvae will make foraging decisions based on preference, capture efficiency and prey availability. This approach also allows for a common set of foraging rules that are not dependent on assumptions regarding optimal diet and that are consistent even when larvae are exposed to different prey communities. These foraging rules performed well in two very different systems, which indicates that this approach is effective for predicting diet choice of larval yellow perch in different environments. The value of this study is not
limited to the points summarized here. However, many of the conclusions of my work would not be possible without the inclusion of these elements in my analysis.

Factors affecting larval survival in Lake Michigan

Growth and survival of larval yellow perch in southern Lake Michigan are primarily affected by variation in overlap between yellow perch larvae and adequate prey resources. A comparison of the Lake Michigan zooplankton assemblage to the zooplankton assemblage of Green Bay revealed that differences in prey community composition were sufficient to predict lower growth rates and higher starvation rates in southern Lake Michigan, even at comparable prey densities. Predicted differences in larval growth are largely dependent on the relative proportion of rotifers and small copepods in the prey assemblage. The high rotifer density in Lake Michigan results in a dependence on rotifers for first-feeding larvae. However, larval growth rates are predicted to be low when rotifers are a big portion of the diet during the early-larval period. Temporal variation in zooplankton density combined with the lower quality zooplankton assemblage in Lake Michigan results in higher variability in the quality of conditions experienced by individual larvae. These results suggest that variation in larval survival in southern Lake Michigan is strongly dependent on variation in prey density and community composition.

Variation in larval survival in southern Lake Michigan can also be strongly affected by larval advection from the nearshore hatching zone to the offshore pelagic zone. Field data document that larvae are transported offshore. Larval survival in model simulations was maximized by advection from nearshore to offshore pelagic habitat near of just after peak hatch. Advection at this time resulted in a maximum number of larvae encountering
cyclopoid copepods near first feeding, which resulted in a large growth advantage for these larvae. However, this advantage was dependent on conditions in the offshore zone as the optimal prey community was present in one year but not in another. This interaction between timing of advection and prey community composition suggests a synergistic effect of these two factors. Prey quality for larval yellow perch is low in nearshore Lake Michigan at present due to the high abundance of rotifers. Therefore good larval survival, and consequently a good year class for yellow perch, would require high copepod abundance offshore and advection of larvae timed so they could exploit the superior offshore prey assemblage early during ontogeny. Understanding the dynamics of Lake Michigan, and predicting when these two conditions are most likely to occur, seems a key research question for understanding larval yellow perch survival in Lake Michigan.

Variation in larval survival in southern Lake Michigan does not appear to be correlated with variation in the intensity of size-selective predation. Alewife are the only predator that is abundant in the pelagic zone of Lake Michigan and known to feed on yellow perch. Strong indirect evidence points to a negative relationship between alewife abundance and larval survival (Crowder 1980, Shroyer and McComish 2000). However, my results suggest that alewife feeding rate on larval yellow perch will be low due to rapid larval dispersal from nearshore habitat and the current low larval densities in the open lake.

Predation does appear to be an important factor limiting larval yellow perch survival in Green Bay. Unlike the main body of Lake Michigan, Green Bay contains several predator species that are known to feed on yellow perch larvae. Alewife and white perch are the most likely candidates based on gill net sampling and both have been found with significant numbers of larval yellow perch in their guts. The increased importance of the timing of
predation and the decreased importance of low growth rate to larval survival is not unexpected in a system like Green Bay where optimal prey resources are abundant and most larvae are predicted to grow at an optimal rate. Larval survival is then more dependent on whether larval encounter rate with predators is high or low. In general, the increased importance of predation to variability in larval survival in smaller systems like Green Bay may be a key difference between yellow perch dynamics in smaller systems and yellow perch dynamics in Lake Michigan.

Lake Michigan more closely resembles an oceanic environment than a lake environment with regards to larval recruitment. Larval yellow perch are advected offshore either by episodic or seasonal current events. Movement into offshore habitat appears to be a natural part of yellow perch life history. However, offshore movement would not be an important event in a smaller system where nearshore and offshore pelagic habitats are more similar such as Green Bay or Oneida Lake, NY. In Lake Michigan, there are important differences between nearshore and offshore pelagic habitat; these differences are important to growth and survival of larval yellow perch.

A significant result of offshore advection for larval yellow perch is that offspring of relatively isolated sub-populations of adult yellow perch in Lake Michigan may be intermixed in the offshore habitat during the larval stage; this has two implications. First, conditions in the offshore habitat have the potential to impact perch recruitment lakewide as larvae from many different hatching locations experience the same conditions offshore. Second, the yellow perch population of Lake Michigan is likely made up of several large meta-populations rather than many smaller isolated populations as previously thought. This conclusion is supported by genetic data for adult yellow perch in Lake Michigan (Miller
2003). These two conditions are more often encountered in marine fish communities and lessons learned regarding the dynamics of these marine fish communities may be valuable for management of yellow perch in Lake Michigan.

My results suggest that Lake Michigan should be treated as a small ocean rather than a large lake with respect to larval yellow perch recruitment. This conclusion applies to any pelagic larval fish, however it is most significant at present for yellow perch. Annual variability in year-class strength is highly correlated with survival during the larval stage. Variation in survival for yellow perch larvae is most effected by a synergism of prey community composition in the offshore pelagic zone and the timing of larval advection. Our ability to understand and maximize larval survival between years is highly dependent on our understanding of dynamics in the offshore pelagic habitat of Lake Michigan.

Unfortunately, these data are lacking at present. Future research should focus on improving our knowledge of offshore habitat for larval yellow perch and how strongly adult populations are linked by larval mixing. More importantly, management of the yellow perch population in Lake Michigan must account for linkages between adult populations and the dependence of a strong year class on larval survival lakewide. Yellow perch should be managed cooperatively on a lakewide basis rather than within state boundaries. The formation of the Yellow Perch Task Group was an important first step towards cooperative management. In the future, my findings can be combined with other Task Group research to further facilitate this process. As with any such analysis, this one produced as many new questions as answers. However, I hope that this work will aid in focusing future research and in the development of a conceptual model for how growth and survival is determined for larval yellow perch in Lake Michigan. In this way, I have contributed to the advancement of
our understanding of a valuable fishery resource in one of the most dynamic freshwater systems on earth.

Literature Cited


Appendices
Appendix 1 – Estimation of larval age and the calculation of hatchdate distributions based on ring counts from otoliths of larval yellow perch.

Hatchdate distributions for larval yellow perch collected in southern Lake Michigan and Green Bay were calculated separately for each year class from 1998 – 2001 in southern Lake Michigan and 1998-1999 in Green Bay. These hatchdate distributions were used for comparisons among years and as a framework for introducing larvae into model simulations. Hatchdate distributions were based on individual hatchdates estimated from otolith ring counts and date of capture. Otolith ring count is correlated with larval age in days for yellow perch (Post and Prankevicius 1987). Individual age estimates were acquired from otolith ring counts made by a series of readers over four years.

However, there is uncertainty in age estimates derived from ring counts. Two sources of variance are accounted for in the process of developing a hatchdate distribution from otoliths examined by multiple readers. First, otolith ring deposition may not begin on the day of hatch and I must adjust individual ring counts to account for any discrepancy. Further, the relationship between ring count and actual age may not be 1:1 and is likely to include some variation due to otolith clarity and reader perceptions (Rice 1987). In order to account for these factors, I used a known-age otolith set and an inverse regression method to establish a relationship between ring count and true age in days.

Ring counts for larval yellow perch collected from Lake Michigan were made by four different readers over four years. Each reader received 4-6 hours of training in counting rings on otoliths from larval and juvenile yellow perch. Each individual otolith used for analysis was examined by at least two readers. Further, a proportion (10%) of all otoliths
examined by these readers were also reexamined by an experienced reader (R. Fulford; D. Jude University of Michigan). In order to estimate variation in ring count, each reader conducted a blind ring count for a set of known-age otoliths. These blind counts were made prior to reading otoliths from field-collected larvae, but after receiving training reading yellow perch otoliths.

This known-age otolith set was assembled from laboratory-reared yellow perch larvae collected every two days between 0 and 10 dph and every five days between 10 and 25 dph. The otoliths were removed by dissection and mounted on clear glass slides in Cytoseal (Fisher Corp.). Larger otoliths were polished with fine grit sandpaper for clarity. Each otolith was assigned an individual random number identification, which allowed a reader to examine the otolith without knowing the larva’s size or age. These otoliths were also randomly ordered for examination. Each reader examined the entire validation otolith set three times and the reader’s ring count for an individual otolith was the mean value of the three readings for that otolith.

I performed a linear regression of ring count on true age for the known-age dataset and determined the 95% confidence interval for individual ring counts. The regression was fit to data for each reader separately and for data from all readers combined. The relationship for combined data was not significantly different from the individual reader data, so reader data were pooled for analysis (pooled data slope 0.82, SE=0.02; individual data slope 0.79-0.84, SE=0.02).

An inverse regression analysis was used to estimate age (days) from individual ring count (Figure A.1, Draper and Smith 1966, Rice et al. 1987); the 95% confidence interval for
individual estimates of age was ± 4 days over the entire range of observed known age (0 – 25 days; Table A.1).

Ring counts from field-collected larvae were converted to an estimate of larval age based on the ring count - age regression relationship (\( \text{AGE} = (\text{COUNT} - 0.83) / 0.82 \)). Within-otolith variance in ring counts for field-collected larvae was similar to observed within-otolith variance in ring count for the known-age otolith set. Because observed variance in within-otolith ring counts was comparable between laboratory-reared and field-collected larvae, it is reasonable to use variance estimates from laboratory-reared larvae to develop a hatchdate distribution from field data. Further, variance estimates in ring count for laboratory-reared larvae showed no trend with larval age, so these variance estimates were also applied to ring counts for field-collected larvae older than 25 dph (maximum larval age 50 dph).

Estimates of true age were subtracted from the date of capture to estimate hatchdate. Individual hatchdate estimates were combined within each larval fish sample to form a hatchdate distribution. In the formation of the hatchdate distribution, individual hatchdate estimates were not assigned discretely to a single date. Instead, the confidence interval of individual age estimates was used to partition individual hatchdate estimates to the range of dates around the estimated date of hatch based on a normal distribution. These ‘mini distributions’ for each larva were then combined to form a sample hatchdate distribution (Figure A.2). Finally, these estimates of hatch date were converted to a hatchdate distribution for each sample date and the distributions for all sample dates within a given year were combined to form a hatchdate distribution for the entire yearclass.
Literature Cited


Table A.1 Cumulative proportions and daily proportions for allocating individual larvae to a hatchdate distribution based on a 95% confidence interval for estimates of larval age as a function of ring count. The hatchdate probability for a given larva was divided among dates according to the increment percentages in column three. Rather than 1 individual being added discretely to the date of estimated hatch, 0.4060 of that fish was added to the hatchdate, then 0.1538 of that fish was added to $\pm$ 1 day and $-$ 1 day and so on out to $\pm$ 4 days.

<table>
<thead>
<tr>
<th>Daily Increment</th>
<th>Cumulative%</th>
<th>Increment %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Estimated Hatchdate</td>
<td>0.4060</td>
<td>0.4060</td>
</tr>
<tr>
<td>$\pm$ 1 day</td>
<td>0.7136</td>
<td>0.1538</td>
</tr>
<tr>
<td>$\pm$ 2 days</td>
<td>0.8902</td>
<td>0.0883</td>
</tr>
<tr>
<td>$\pm$ 3 days</td>
<td>0.9670</td>
<td>0.0384</td>
</tr>
<tr>
<td>$\pm$ 4 days</td>
<td>0.9923</td>
<td>0.0126</td>
</tr>
</tbody>
</table>
Figure A.1 Demonstration of inverse regression method for estimating larval age as a function of ring count as described by Rice (1987). Broad solid line is the regression of ring count on true age and thin solid lines are the upper and lower 95% confidence interval for the individual estimates of ring count. Arrow indicates an example conversion of ring count to an estimate of larval age for a ring count of ten. Center vertical line gives the point estimate and the right and left vertical lines are an estimate of the upper and lower 95% confidence limits of the estimate. Formula used to convert ring counts to individual age estimates is presented.

Age = (Count-0.83)/0.82
Figure A.2 An example hatchdate distribution calculated based on ring count variance estimates for a sample collected on 5/10/98 from Green Bay (N=1769) and compared to the count distribution for a sub-sample (N=50) of these larvae that were aged.
Appendix 2 – Digestion time and the identification of larval yellow perch in the guts of alewife and adult yellow perch

A serial sacrifice experiment was conducted to establish how long larval yellow perch are identifiable after they have been eaten by a predator. Alewife (180 mm TL) and yellow perch (100 mm TL) were used as predators. 20 alewives and 20 yellow perch were placed separately into two 589-L round tanks and held at 18-20°C at a flow rate of 42 L/min. The predators were allowed to acclimate to the tanks for eight days. During the first five days, predators were fed larval yellow perch once per day to re-acclimate them to a live food source. Predators were starved for the remaining three days to insure they would feed during the experimental period and to assure that previously eaten larvae had passed through their system.

On day nine, 250-300 yellow perch larvae (10 mm TL) were introduced into each tank and the predators were allowed to feed for 10 minutes. After 10 minutes, all remaining larvae were removed from both tanks. Three predators from each tank were removed at 0, 15, 30, 60, 120 and 240 minutes after the feeding period ended. Predators were euthanized with MS-222 and placed on ice. Predator stomachs and intestines were immediately removed by dissection and preserved in 95% ethanol for analysis. The number and condition of each larvae found in predator guts was later determined.

Results

No differences in digestion rates were detected between the two predator species. Larval yellow perch were identifiable to species up to an hour after consumption by a
predator under experimental conditions. Twenty percent of larvae consumed were still identifiable as yellow perch after two hours; all larvae were identifiable as fish larvae two hours after consumption. Digestion time was also affected by the number of larvae consumed by a predator. Larvae taken from predator guts that contained more than ten larvae were always identifiable as yellow perch two hours after consumption. In contrast larvae from guts that contained less than 10 larvae (usually 1-2 larvae/gut) were never identifiable as yellow perch after two hours. These results suggest that yellow perch should be identifiable in predator guts up to one hour after consumption independent of predator feeding rate. Temperatures used in this experiment were generally warmer than observed in the pelagic zone of Lake Michigan: 10 – 22° C over the larval period. Digestion time is likely to be longer for predators in Lake Michigan, where they experience cooler temperatures.