EXPLORING PHYSICAL, BIOLOGICAL, AND BEHAVIORAL PROCESSES THAT AFFECT LARVAL FISH DISTRIBUTION IN THE PELAGIC ZONE OF LAKE MICHIGAN

BY

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THESIS

Submitted in partial fulfillment of the requirements
for the degree of Master of Science in Natural Resources and Environmental Sciences
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2010

Urbana, Illinois

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ABSTRACT

The growth and survival of larval fish are influenced by a suite of biotic and abiotic factors. Because aquatic systems are characterized by strong heterogeneity in biotic and abiotic conditions along a vertical gradient, the vertical distribution of larval fish can profoundly affect their growth and survival. In large systems such as the Great Lakes, vertical distribution patterns can also influence dispersal and ultimately settlement events. Despite its importance during early life stages, little is known about vertical distribution patterns of larval fish in Lake Michigan. My objective was to describe the vertical distribution of the larval fish community in pelagic waters of Lake Michigan and determine which biotic and abiotic factors most strongly influence their vertical distribution. Additionally with controlled laboratory experiments I sought to determine how two of these factors (light intensity and prey density) influence the foraging success of a fish species with a pelagic larval stage, yellow perch (*Perca flavescens*).

To determine vertical distribution, the upper 27 meters of the water column was divided into six discrete depth bins where larval fish and zooplankton were collected, in addition to recording light intensity, and temperature. Larval fish from 5 species were collected during the study: alewife (*Alosa pseudoharengus*), bloater (*Coregonus hoyi*), burbot (*Lota lota*), deepwater sculpin (*Myoxocephalus thompsonii*), and yellow perch (*Perca flavecens*). Among the five species, I observed three general patterns of larval distribution. Alewife and yellow perch larvae were restricted to the epilimnion, deepwater sculpin were restricted to the hypolimnion, and bloater and burbot were collected throughout the upper 27 m of the water column, and exhibited diel differences in distribution patterns. My analysis elucidates the importance of abiotic over biotic factors in the structuring of larval fish vertical distribution in Lake Michigan, as temperature was shown to influence the distribution of most species, while density of crustacean zooplankton did not. The inter-specific differences of vertical distribution observed among the 5 species collected have important consequences for dispersal, settlement, and recruitment variability.

In the laboratory I examined the influence of light intensity on foraging success and prey selection of larval yellow perch at both high (150 zooplankton/L) and low (25 zooplankton/L) prey densities, with a mixture of zooplankton taxa common to lakes containing yellow perch. In addition to light intensity and prey density, the effect of ontogeny of yellow perch larvae was examined by using fish ranging from 9 to 15 mm. The results of my study indicated that larval yellow perch are well adapted to feed at a wide range of light intensities, as there was no difference in foraging success between light intensities ranging from 0.1 to 60 μmol s^{-1} m^{-2} PAR. Increasing prey density from 25 to 150 (zooplankton/L) significantly improved the foraging success of larval yellow perch. However, the influence of prey density on foraging success of larval yellow perch was dependent on fish length, with improved foraging success with increased prey density occurring only for larger larvae. Overall, prey selection by larval fish was influenced by light intensity, prey density, and fish length, but the set factors which influenced selection for specific prey types differed. The results of this study combined with evidence from other field and laboratory work, highlight the need for a better understanding of the influence of prey density on foraging success throughout ontogeny.

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CHAPTER 1: VERTICAL DISTRIBUTION OF LARVAL FISH IN PELAGIC WATERS OF LAKE MICHIGAN: IMPLICATIONS FOR GROWTH, SURVIVAL, AND DISPERSAL

ABSTRACT

Due to variability in biotic and abiotic conditions along a vertical gradient within aquatic systems, the vertical distribution of larval fish can profoundly affect their growth and survival. In large systems such as the Great Lakes, vertical distribution patterns can also influence dispersal and ultimately settlement events. Despite its importance during early life stages, little is known about vertical distribution patterns of larval fish in Lake Michigan. My objective was to describe the diel vertical distribution of the larval fish community in the pelagic waters of Lake Michigan and determine which biotic and abiotic factors most strongly influence their vertical distribution. To determine vertical distribution, the upper 27 meters of the water column was divided into six discrete depth bins. Larval fish sampling was conducted within each of these depth bins on seven occasions during both day and night. Temperature, light intensity and prey density were also recorded at depths corresponding to larval fish sampling. Larval fish from 5 species were collected during the study: alewife (*Alosa pseudoharengus*), bloater (*Coregonus hoyi*), burbot (*Lota lota*), deepwater sculpin (*Myoxocephalus thompsonii*), and yellow perch (*Perca flavecens*). Among the five species collected, three general patterns of depth distribution were observed. Alewife and yellow perch were restricted to the upper strata, while the opposite trend was observed for deepwater sculpin. Bloater and burbot larvae were more evenly distributed throughout the upper 27 meters, and their pattern of vertical distribution changed between diel periods. My analysis suggests abiotic factors were more important than biotic factors in structuring the vertical distribution of larval fish in Lake Michigan. Of the abiotic factors investigated, temperature had the largest influence on distribution of larval fish. In addition to influencing the biotic and abiotic conditions larvae experience, the inter-specific differences in vertical distribution observed among the five species will have important consequences for dispersal and recruitment variability.

INTRODUCTION

The general life history strategy of most fish species is characterized by a partitioning of reproductive output among many small offspring (Duarte and Alcaraz 1989; Elgar 1990; Winemiller and Rose 1993). Due to the sheer magnitude of progeny produced and their high probability of dying, small variations in growth or survival during the early life history stages of fish can have dramatic effects on recruitment strength within a year (Houde 1989). Variation in growth and survival of larval fish is driven by complex interactions among biological, physical, and behavioral processes in a dynamic environment (Sale 1990; Claramunt and Wahl 2000; Fiksen et al. 2007). Within the Lake Michigan fishery, considerable effort has been directed toward the understanding of how natural variation in biotic and abiotic conditions affects larval growth and mortality. However, little consideration has been given to how the behavior of larval fish may influence population level recruitment dynamics.

A fundamental behavior exhibited by nearly all animal taxa is habitat selection (Morris 2003). When dispersal capabilities of individuals exceed the scale of spatial heterogeneity, dispersal behavior can have large effects on the environmental conditions experienced by individuals (Ranta et al. 1999; Tyler and Hargrove 1997). For pelagic fish larvae, horizontal dispersal is likely limited, as water current speed often far exceeds larval swimming capabilities and abiotic conditions change gradually over vast spatial extent (Höök et al. 2006). Conversely, along a vertical gradient, aquatic systems are typified by large variation in abiotic conditions at a small spatial scale. Furthermore, both predators and prey of larval fish often exhibit non-random patterns of depth distribution in response to biotic and abiotic influences (Lampert 1989). As most larval fish and their predators are visual feeders, foraging both by and on larval fish can be influenced by interactions between the biotic and abiotic conditions at a depth (Clark and Levy 1988). Consequently, even relatively small vertical movements can directly influence what temperatures, illumination levels, turbulence, prey density, and predator density that larval fish experience.

In marine systems and large freshwater lakes such as Lake Michigan, the vertical distribution of larval fish will not only influence instantaneous growth potential and mortality risk, but will also have long-term consequences for survival (Fiksen et al. 2007; Vikebø et al. 2007). Current velocity decreases with depth, and in large aquatic systems the direction of advection rotates with decreasing depth due to vertical sheer. Thus the vertical distribution of larval fish will influence horizontal dispersal, and consequently the environmental conditions encountered along a drift trajectory. Ultimately the interaction between larval behavior and water circulation patterns within a system will influence the encounter probability of suitable habitats for settlement (Hinckley et al. 1996; Werner et al. 1996; 2001; Hinrichsen et al. 2001). Moreover, swimming capabilities much weaker than exhibited by most larval fish can potentially have a larger influence on settlement location than inter-annual variation in circulation patterns (North et al. 2008). For many species, recruitment is not set immediately after settlement. The conditions experienced by fish during the pelagic larval stage can influence not only the size and condition upon settlement, but also growth trajectories experienced post-settlement (Hamilton et al. 2008). Thus the vertical distribution of larval fish influences growth and survival on multiple temporal scales, and the consequences realized at each scale are not independent.

Despite the potential influence of vertical distribution behavior on recruitment dynamics, information on vertical distribution patterns of larval fish in Lake Michigan is scarce. Previous studies examining vertical distribution of larval fish species in Lake Michigan were primarily aimed at describing the lake wide spatial and temporal distribution and overlap of larval fish species during the early larval stage (Mansfield et al. 1983; Perrone et al. 1981; Nash and Geffen 1991). Sampling effort and consequently resolution on a vertical gradient in these studies was generally low and comparisons made between depths, qualitative. In this study I attempt to achieve a more quantitative understanding of larval distribution with respect to depth. Additionally I seek to determine which biotic and abiotic factors most strongly influence larval distribution. To achieve these objectives I concentrated vertical sampling at fixed locations where larvae of several fish species are known to occur in Lake Michigan.

METHODS

Sampling was conducted at fixed stations approximately 15 km offshore Waukengan, IL, in southwest Lake Michigan. A total of seven diel vertical distribution surveys were conducted between June 24th and July 30th, sampling consisted of six depth strata in the upper 27 meters of the water column during both day (1000 -1600 hours) and night (2200-0400 hours). Sampling the upper 27 meters of the water column encompassed the epilimnion, metalimnion, and hypolimnion. The bottom depth at this location was approximately 80 m; however sampling effort was concentrated in the upper 27 meter to achieve higher resolution in depth distribution where variation in abiotic conditions is known to be greatest.

The six depth strata sampled during each survey consisted of 4 meter depth bins of: 3-7, 7-11, 11-15, 15-19, 19-23, and 23-27m. The upper three meters were not sampled as catches in this stratum could be influenced by boat wake. Each depth strata was sampled with a dual net tucker trawl with an opening /closing mechanism (Kelso and Rutherford 1996). Sampling was initiated by lowering the net to the top or bottom of a depth bin and then sampling each meter within the 4 meter depth bin for 6 minutes (24 minutes total). After each meter in a depth bin had been sampled the first net was closed and the second opened by sending a mechanical messenger down the cable as the net was lowered or raised to the adjacent depth bin. Upon the conclusion of sampling with the net, a second messenger was released to close the second net and the tucker trawl was retrieved. The cod ends were removed from the nets and larval fish were preserved in ethanol. These procedures were repeated for the remaining four depth bins, and the order at which depths were sampled was randomized. Both nets on the tucker trawl had a mesh size of 1000 µm. The effective sampling area of the tucker trawl was one square meter and nets were towed at an average of 1.5 knots. Larval fish density was determined by dividing the fish caught by the volume of water sampled as determined by a flow meter.

Zooplankton density, light intensity, and temperature were all determined at the depths corresponding with larval fish sampling. Zooplankton samples were collected for each strata preceding the larval fish tow. Each zooplankton sample was collected by a vertical haul of a 0.5 diameter circular net with an opening/closing mechanism. Zooplankton samples were preserved in 10% sugar formalin. Temperature profiles were constructed from a temperature logger attached to the tucker trawl during sampling. Light intensity (μmol $s^{-1}m^{-2}$ PAR) was determined by three replicate light profiles taken immediately before each tucker trawl deployment using a BIC radiometer (Biospherical Instruments). The mean light intensity and temperature for each depth bin was determined as the average temperature and light intensity of each meter within each depth bin.

All larval fish samples were sorted and identified to species, and subsequently measured to the nearest 0.1 mm using a dissecting microscope (6 x magnification) equipped with a drawing tube and electromagnetic digitizing tablet (Welker et al. 1994). Zooplankton densities were estimated from counting three, 5 ml subsamples. For analysis zooplankton were divided into main groups of copepod nauplii, adult calanoid copepods, adult cyclopoid copepods, and cladocerans.

Data analysis

Analysis was conducted using a generalized linear model for count data. This approach allows the use of non-normal probability distributions which more accurately account for low mean to variance relationships characteristic of net catch data (Power and Moser 1999). The natural probability distribution for count data is the Poisson distribution which assumes that variance is equal to the mean. However a common characteristic of biological data is overdispersion, thus the negative binomial probability distribution, which includes an extra parameter to account for additional variation relative to the mean, k, typically provides a better fit (White and Bennetts 1996). A Poisson distribution was used for each species and switched to a negative binomial probability distribution when there was evidence of overdispersion as revealed (deviance [similar to variance in general linear models] to degrees of freedom

ratios greater than 1) (Littell et al. 2002). Generalized linear models used a "link" function to provide a relationship between the linear predictors and the mean of the distribution function. For both Poisson and negative binomial distributions the canonical link is the natural log (Littell et al. 2002).

To describe the diel vertical distribution each species, density was modeled as a function of depth and diel period. If the diel period by depth interaction was not significant with an alpha of 0.05, the term was dropped and larval density (N m^{-3}) was measured solely as a function of depth. Data were excluded from analysis if no larvae of a fish species were caught in any of the sampled depths for a diel period.

To determine which biotic or abiotic factors most strongly influenced the distribution of larval fish, a set of multiple linear regression models for larval density was evaluated (N m^{-3}). The relative contribution of independent variables was evaluated via an information-theoretic approach using Akaike's information criterion analysis with a second order correction for small sample sizes (AIC_C) (Burnham and Anderson 2002). The independent variables used for model selection included depth, temperature, light intensity, and crustacean zooplankton density (zooplankton/L). The candidate set of models consisted of the null model with no independent variables, all univariate models, their interactions with diel period (day or night), and specific interactions which represent a suite of hypotheses thought to influence the vertical distribution of larval fish. For example, larval fish may distribute themselves at depths with high prey concentrations during the day to feed and then migrate to depths with preferred temperatures at night. Alternatively, because larvae are visual feeders their daytime distribution may be a function of prey density and light intensity (Munk et al. 1989). A complete list of each of the 12 candidate models is given in Table 1. Quadratic effects were included when a visual inspection of residuals indicated they may exist, and were kept in the model when they were significant at an alpha of 0.05. Candidate models with $\Delta AIC_C < 2$ were considered to be competing with the model with the lowest AIC_C as "parsimonious models".

To compare depth distribution patterns and the influence of biotic and abiotic variables among species, I jointly analyzed all species together, using species as an independent variable. Because not all species exhibited similar levels of overdispersion, unique probability distributions for each species were constructed.

RESULTS

Physical factors and zooplankton

The water column was stratified throughout the survey. Thermocline depth decreased from 6 m on June 26th to 13 m on July 30th. There was considerable variation in surface light intensity between sampling dates due to varying levels of cloud cover. Mean daily surface light intensities ranged from 300–1500 µmol $s^{-1}m^{-2}$ PAR. The mean attenuation coefficient of PAR during the study was 0.13.

Crustacean zooplankton densities were low throughout the study (3.65 zooplankton/L std ± 4.28). Calanoid copepods and copepod nauplii represented the majority of zooplankton captured and made up 59% and 34% of the crustacean zooplankton. The next most common zooplankton group was cyclopoid copepods (5%). Few cladocerans were found throughout the study (< 2%) and this group was composed mainly of *Bosmina*, *Daphnia*, and *Ceriodaphnia*. Generally, the daytime distribution of crustacean zooplankton was heterogeneously distributed among depths. Peak density was not related to a specific depth and no significant variation could be explained by light or temperature (Figure 1.1). At night, crustacean zooplankton density exhibited a dome shape relationship with temperature, with highest densities occurring at intermediate temperatures.

Larval fish

A total of 1,099 larval fish of 5 species were collected throughout the study. The most common species was bloater (*Coregonus hoyi*), followed by alewife (*Alosa pseudoharengus*), burbot (*Lota lota*), yellow perch (*Perca flavecens*), and deepwater sculpin (*Myoxocephalus thompsonii*). Analysis of depth distribution for larvae of each species with the Poisson distribution indicated that alewife (deviance to df ratio = 16.57), bloater (9.79), burbot (4.74), and yellow perch (2.73) were overdispersed. For deepwater sculpin, the deviance to df ratio (0.44) indicated underdispersion, with variance lower than the mean. Thus for all further analysis a negative binomial distribution was assumed for alewife, bloater, burbot, and yellow perch, and a quasi-Poisson distribution was used for deepwater sculpin with an extra parameter to account for underdispersion. Because deepwater sculpin were modeled with a different probability distribution, I was unable to model this species jointly with the other species and thus I could not directly compare parameter estimates.

Larval densities were not significantly different between day and night for alewife, burbot, deepwater sculpin, or yellow perch (Table 1.2a). Density of larval bloater was approximately 8 times greater at night than during the day. There were also no significant differences in mean length of larvae caught between day and night sampling periods for alewife, bloater, burbot, and yellow perch (Table 1.2b). Deepwater sculpin collected at night were significantly longer than those collected during daytime sampling.

Three distinct patterns of depth distribution were exhibited among the larvae of the 5 species (Figure 1.2). Alewife and yellow perch densities decreased sharply with depth, and this pattern did not differ between diel periods. These two species were almost always found in the upper strata of the water column. The daytime depth distribution of bloater and burbot larvae was generally similar to that of alewife and yellow perch in that it decreased with depth, however, unlike yellow perch and alewife which were only found in the upper strata, bloater and burbot were more evenly distributed among depths during the day. The nighttime distributions of bloater and burbot exhibited a quadratic relationship with depth, with peak densities occurring at intermediate depths. A third pattern of vertical distribution was exhibited

by deepwater sculpin, which showed an increase in density with depth, and were never collected in waters shallower than 11 meters.

Factors influencing larval fish distribution

For most species considered, temperature was found to be the most influential variable on the distribution of larval fish species (Table 1.3). However, not all species were distributed similarly in response to temperature. For both alewife and yellow perch, the candidate model with the lowest AIC_C score included temperature (Figure 1.3). The effect of temperature on larval distribution was not significantly different between larval alewife and yellow perch ($P = .81$). For alewife, no other candidate models had ΔAIC_C scores > 2, thus they were not considered to be competing models. For yellow perch, the model where larval fish density was a linear function of depth was also a robust model (Table 1.3).

The model with the lowest AIC_C score indicated that different factors were influencing distribution during each diel period for bloater and burbot. During the day, density of bloater and burbot larvae was positively related to light intensity. At night density of both species was related quadraticly to temperature (Figure 1.4). The distribution of bloater and burbot in relation to these abiotic factors was similar as there were no significant differences between the effects of the daytime light intensity ($P = 0.95$), the linear effect of night temperature ($P = 0.31$), or the quadratic effect of night temperature ($P = 0.21$) on the distribution of larval bloater and burbot. The next best models for bloater and burbot had ΔAIC_C scores > 2, thus they were not considered to be competing models.

For deepwater sculpin the model with the lowest AIC_C included depth, where the log of density increased linearly with depth. None of the other candidate models had ΔAIC_C scores > 2. The next best model which did not include depth was the univariate model including temperature. No deepwater sculpin larvae were collected in or above the thermocline, however because their density increased with depth in

the hypolimnion where temperature was relatively homogenous, the model with only depth provided a better fit.

Zooplankton density was not included in a robust model for any of the 5 species collected, and the models including prey as a predictive variable were generally low ranking models (Table 1.3). Total crustacean density (zooplankton/L) was used for the AIC_C model selection; however results for all species were similar when analyzed as proportion of zooplankton at a depth. Additionally, no larval fish species exhibited significantly better fits when density of either one of the two main zooplankton groups, calanoid copepods and copepod nauplii, were used as the independent variable.

DISCUSSION

My analysis suggests abiotic factors were more important than biotic factors in structuring the vertical distribution of larval fish in Lake Michigan. Of the abiotic factors investigated, temperature had the largest influence on distribution of larval fish, and was included in the best models for alewife, bloater, burbot, and yellow perch. The importance of temperature in structuring the vertical distribution of larvae in Lake Michigan is consistent with the findings from many marine studies (Ahlstrom 1959; Moser and Boehlert 1991; Sakuma et al. 1999; Sassa and Konishi 2006; Garrido et al. 2009). Like most poikilotherms, fish occur within species specific temperatures ranges, and exhibit temperature dependent metabolic rates (Magnuson et al. 1979). Within the water column of Lake Michigan a wide range of temperatures were available to larval fish. Alewife and yellow perch appeared to be limited to the warmer waters in the epilimnion. The fact that density of both species increased with temperature indicates that their thermal optima may exceed the temperatures available in the water column in Lake Michigan. Previous work supports this conclusion demonstrating that alewife and yellow perch preferred temperatures of 23-28 C° (McCauley and Read 1973; Otto et al. 1976; McCormick 1976). Though the univariate model of depth was the best model describing deepwater sculpin distribution, temperature also

may be important as they were not found in or above the thermocline. Additionally deepwater sculpin have been found in the surface strata in March and April before thermal stratification occurs, but were never found at temperatures above 11 C° (Mansfield et al. 1983). Bloater and burbot exhibited tolerance for a wide range of temperatures, however at night they occurred at highest densities at intermediate temperatures.

Density of zooplankton did not appear to influence the daytime distribution of any fish species. The lack of a positive relationship between the distribution of larval fish and their prey could be a result of abiotic conditions more strongly influencing distribution, fish not feeding throughout the diel period, a lack of an ability of larvae to track prey density and adjust their distribution, or a combination of these factors. The strong thermal preferences of larval fish species such as alewife, yellow perch, and deepwater sculpin likely prevent them from tracking maximum prey densities, as peak prey densities were found within, below, and above the thermocline on different sampling dates. However neither the distribution of bloater nor burbot, which exhibited thermal flexibility, were correlated with prey density. Burbot, like most species in the cod family, have larvae that feed primarily at dusk (Probst and Eckmann 2009), thus the lack of a correlation with prey density may be a result of larvae not feeding during daytime sampling. Bloater larvae on the other hand, feed throughout the day and foraging periodicity cannot explain the lack of a relationship with prey density.

Many studies which examine the vertical distribution of larval fish in relation to prey density have found positive correlations between larval density and either prey density or prey availability (prey density adjusted for light intensity) (Munk et al. 1989; Dominique and Louis 1992; Grønkjær and Weiland 1997). However, in these studies peak prey availability consistently occurred above either the pynocline or thermocline and whether abiotic conditions better explained larval distribution was not explicitly tested. When the vertical distribution of zooplankton is more variable a lack of a positive relationship between the distribution of larval fish and their prey has been found (Gray and Kingsford 2003). Additionally when models of larval vertical distribution have tested abiotic and biotic conditions

simultaneously, the effects of abiotic conditions were consistently stronger among all species tested, while relationships with prey density were often non-significant and species specific (Garrido et al. 2009).

Zooplankton density can be distributed heterogeneously on small vertical scales (Alldredge et al. 2002; McManus et al. 2003; Young et al. 2009). In this study I applied a finer resolution of sampling depths compared to most previous research on the vertical distribution of larval fish, which have sampled a much broader range of depths, but with depth bins of 10-20 m. In these previous studies positive correlations between larval fish and zooplankton availability may be driven by the general presence of both larvae and zooplankton in the epilimnion or photic zone and absence from the deepest depths sampled. At the fine scale examined in this study (4 m), no positive relationships between larval fish density and their prey were detected. The extent to which larval fish can track changes in prey density remains unclear. Due to their poor swimming and visual capability larval fish larval fish "sample" relatively low volumes of water. Because encounters between larval fish and their prey are stochastic, it may be difficult for larval fish to distinguish between depths of differing prey density. This task is made more difficult as zooplankton may continually alter their vertical distribution to optimize their own temperature-prey availability tradeoff (Lampert et al. 2003; Kessler and Lampert 2004). For a better understanding of how the vertical distribution fish larvae is influenced by prey density, finer spatial and temporal resolution may be required. The use of hydro-acoustics to simultaneously monitor the distribution of both larval fish and their prey may prove to be a promising method to achieve this resolution.

The sampling in this study was restricted to the upper portion of the water column (surface to 27 m deep) with narrow depth bins. Although this allowed me to increase the "resolution" in detecting distribution patterns of fish larvae in the upper water column where abiotic heterogeneity is the greatest, it also prevented me, because of time constraints, from sampling the entire range of depths. As a result a complete description of the vertical distribution of larvae that may occupy deeper waters (below 27m) cannot be provided. Deepwater sculpin occurred in greatest concentration in the deepest sampled strata

and it is likely they occur over a wide range of depths in the hypolimnion. Likewise the lower range of bloater and burbot larvae distribution may have been missed. For both species this seems more likely during the day than at night as only 3 out of 380 bloater and none of the 176 bloater caught at night were found at the lowest strata sampled. The significantly higher densities of bloater recorded at night could be interpreted as either migration upward in the water column by some bloater larvae occupying waters deeper than 27 meters during the day, better visual net avoidance during the day, or a combination of these two factors. However, there were no significant differences in mean length between day and night samples for bloater or burbot larvae, hence potential net avoidance by larger individuals with better visual acuity and swimming skills is unlikely. Additionally, among alewife and yellow perch larvae of similar sizes which were restricted to the upper strata, there were no diel differences in density. As such, it seems probable that some burbot and a substantial proportion of bloater larvae occupy waters deeper than 27 meters during the day and migrate up to warmer waters at night. For a more complete description of bloater and burbot larvae daytime distribution, future studies should include a wider range of depths (below 27 m).

Vertical distribution patterns exhibited by larvae of fish species in Lake Michigan will likely influence dispersal. During the summer stratification period in Lake Michigan, currents in the warmer, less dense epilimnion are greater and more variable than in the deeper, less dynamic hypolimnion (Beletsky at al. 2006). The trajectory and ultimately terminal settlement of larvae distributed in the epilimnion will be dependent on the temperature and wind conditions during their pelagic life stage. Surface currents in Lake Michigan would cause larvae originating from the southwest portion of the lake to be advected either to the eastern or southern shore depending on whether yearly circulation patterns were anti-cyclonic or cyclonic (Beletsky et al. 2007). In some strongly anti-cyclonic years, larvae could be advected into the northern basin. The magnitude and yearly variation in surface currents, in conjunction with the near surface distribution of larval yellow perch could explain the genetic homogeneity of yellow perch in the main basin of Lake Michigan (Miller 2003). Because alewife

exhibited similar vertical distribution patterns, they may be subjected to similar advective forces as yellow perch. In the denser, cold waters of the hypolimnion where deepwater sculpin occur, current velocities are much lower (Beletsky et al. 2006; Beletsky and Schwab 2008). Additionally, during upwelling events the deeper waters have an onshore movement component. Thus the deep distribution of deepwater sculpin may facilitate their retention in waters proximate to where they hatched. Bloater and burbot larvae were distributed throughout the epilimnion, metalimnion, and hypolimnion during the day, and these environments are characterized by very different circulation patterns Therefore predictions of population dispersal patterns will largely depend on what mechanisms drive intra-specific variation in the vertical distribution of these species. For example, the observed differences in depth distribution could be due to stochastic dispersion, individual variation in recent foraging success (Pearre 2003), their condition (Neilson et al. 1986), ontogeny (Davis and Olla 1994), or behavioral strategy (Vikebø et al. 2007). Future work is needed to identify the mechanisms driving intra-specific variation of larval fish in Lake Michigan.

Large aquatic systems like Lake Michigan are not only characterized by heterogeneity in abiotic conditions along a vertical gradient, but additionally vary in their degree of sensitivity to inter-annual variation in climatological conditions. For example surface temperatures fluctuate annually and can vary from year to year by 4-5 C°, while at deeper depths, temperature remains relatively constant between and within years (Beletsky et al. 2006; Beletsky and Schwab 2008). Thus species which exhibit different patterns in depth distribution will not only differ in the conditions experienced during a year, but will also differ in the range of conditions they may encounter between years. Alewife and yellow perch larvae were restricted to the upper strata of the water column in Lake Michigan. As a result, the abiotic conditions to which these larvae are exposed will vary from year to year. In the Great Lakes, recruitment strength for both alewife and yellow perch exhibit wide year to year fluctuations, and is positively correlated with temperature (Wilberg et al. 2005; O'Gormen et al. 2004; Madenjian et al. 2005; Redman et al. in prep). Conversely the much deeper distribution of deepwater sculpin larvae may buffer the effects of inter-annual variation in environmental conditions. Thus their recruitment may be more strongly influenced by

population dynamics and biotic factors (i.e. predation). Unfortunately, no data is currently available to test these hypotheses. Predictions of how recruitment of bloater and burbot will be influenced by inter-annual climatological variation will depend on which underlying mechanisms are driving intra-specific variation in vertical distribution.

This study represents one step toward the inclusion of larval behavior in the understanding of recruitment dynamics, however far more information on the vertical distribution behavior of larval fish in Lake Michigan is needed. I have highlighted three different areas of research important for a better understanding of how larval behavior can influence recruitment in Lake Michigan. One promising approach is the use of hydroacoustics to determine fine scale spatial and temporal relationships between larval fish distribution and environmental conditions. In addition multi-year studies may elucidate how inter-annual variation in lake thermal structure influences the overlap between larval fish and conditions favorable for growth on a vertical gradient. Finally, investigations of whether intra-specific variation in depth distribution is random, or caused by some ontogenetic, phenotypic, or behavioral variation among individuals are needed. As insights on larval behavior are obtained it is important to consider not only the direct influence of the abiotic and biotic conditions on growth and survival, but also the longer term consequences of trajectory and settlement (Fiksen et al. 2007). The complexity and variability of circulation patterns, necessitates the integration of mechanistic individual-based models of behavior and growth with general circulation models.

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TABLES AND FIGURES

Table 1.1. Set of 12 candidate models tested in the AIC_C. "Day:" and "Night:" indicate that different variables are modeled for each diel period.

Candidate Models
Null
Depth
Temp
Prey
Depth*Diel period
Temp*Diel period
Day: Light / Night: Depth
Day: Light / Night: Temp
Day: Prey / Night: Depth
Day: Prey / Night: Temp
Day: Prey*Light / Night: Depth
Day: Prey*Light / Night: Temp

Table 1.2. Mean species specific density during day and night of larval fish in Lake Michigan and a chi square test for statistical difference between diel periods using a generalized linear model with a negative binomial distribution for alewife, bloater, burbot, and yellow perch, and a Poisson distribution for deepwater sculpin. Additionally mean total lengths of larvae collected at each diel period and ANOVA results for a test a differences in lengths between diel periods are shown.

	Time of day		Statistical test	
species	Day	Night	df	*P* value
	Density (N m^{-3})			
Alewife	0.54	0.70	39	0.79
Bloater	0.11	0.80	81	<.0001
Burbot	0.29	0.43	63	0.29
Deepwater Sculpin	0.03	0.04	45	0.83
Yellow perch	0.08	0.06	51	0.78
	Total length (mm)			
Alewife	13.70	14.40	10	0.30
Bloater	12.50	13.40	54	0.12
Burbot	8.34	8.62	39	0.61
Deepwater Sculpin	12.60	16.60	10	0.01
Yellow perch	11.90	11.70	7	0.85

Table 1.3. Results of AIC_C analysis, for factors explaining the vertical distribution of larval fish species in Lake Michigan. For each model the number of parameters (k), the AIC_C score, the difference between in AIC_C score between the model and the model with the lowest AIC_C score (Δ AIC_C), and the Akaike weight (w_i) are shown.

Model	k	AIC_C	Δ AIC_C	w_i
		Alewife		
Temp	4	144.69	0	0.87
Temp*Diel period	6	148.48	3.79	0.13
Depth	4	156.09	11.4	0
Depth*Diel period	6	160.74	16.05	0
null	3	175.06	30.37	0
Day: light / Night: Temp	5	175.48	30.79	0
Day: Prey*Light / Night: Depth	7	175.49	30.8	0
Day: Prey/ Night: Temp	5	175.84	31.15	0
Prey	4	177.48	32.79	0
Day: Light/ Night: Depth	5	177.73	33.04	0
Day: Prey / Night: Depth	5	177.84	33.15	0
Day: Prey*light / Night: Temp	7	179.29	34.6	0
		Bloater		
Day: Light / Night: Temp	7	324.04	0	0.79
Day: Prey*Light / Night: Temp	9	327.31	3.27	0.15
Temp*Diel period	7	329.89	5.85	0.04
Day: Prey / Night: Temp	7	333.93	9.89	0.01
Temp	6	334.79	10.75	0
Day: Light / Night: Depth	7	336.2	12.16	0
Day: Prey*Light / Night: Depth	9	339.95	15.91	0
Depth*Diel period	7	342.16	18.12	0
Day: Prey / Night: Depth	7	344.45	20.41	0
Depth	6	347.55	23.51	0
Prey	5	358.44	34.4	0
null	4	359.35	35.31	0
		Burbot		
Day: Light/ Night: Temp	7	289.98	0	0.58
Day: Prey*light / Night: Temp	9	292.12	2.14	0.2
Temp*Diel period	7	292.25	2.27	0.19
Day: Light / Night: Depth	7	296.89	6.91	0.02
Day: Prey / Night :Temp	7	299.2	9.22	0.01
Day: Prey*Light / Night: Depth	9	299.41	9.43	0.01
Temp	5	302.75	12.77	0
Depth*Diel period	7	302.95	12.97	0
Day: Prey / Night: Depth	7	304.95	14.97	0
Depth	5	310.75	20.77	0
null	3	327.88	37.08	0
Prey	4	329.06	39.08	0

Table 1.3. continued

Model	k	AIC_C	ΔAIC_C	w_i
		Deepwater Sculpin		
Depth	4	34.27	0	0.69
Depth* Diel period	6	36.61	2.34	0.21
Temp	4	39.16	4.89	0.06
Temp*Diel period	6	41.06	6.79	0.02
Day: Light / Night: Depth	5	43.72	9.45	0.01
Day: Prey / Night: Depth	5	44.25	9.98	0
Day: Prey / Night: Temp	5	44.52	10.25	0
Day: Light / Night: Temp	5	45.03	10.76	0
Day: Prey*Light / Night: Depth	7	47.36	13.09	0
Day: Prey*Light / Night: Temp	7	48.16	13.89	0
Prey	4	54.47	20.2	0
null	3	55.32	21.05	0
		Yellow perch		
Temp	4	82.61	0	0.44
Depth	4	82.73	0.12	0.42
Depth*Diel_period	6	86.22	3.61	0.07
Temp*Diel_period	6	86.52	3.91	0.06
Day: Light / Night: Temp	5	93.6	10.99	0
Day: Prey*Light / Night: Depth	7	97.11	14.5	0
Day: Prey*Light / Night: Temp	7	97.88	15.27	0
Day: Prey / Night: Temp	5	102.38	19.77	0
Day: Light / Night: Depth	5	103.66	21.05	0
Prey	4	104.99	22.38	0
null	3	105.2	22.59	0
Day: Prey / Night: Depth	5	105.23	22.62	0

Figure 1.1. Diel density of crustacean zooplankton at each of the 6, 4m depth bins during each sampling date. Bar colors represent the composition of each zooplankton group: calanoid copepods (black), cyclopoid copepods (grey), copepod nauplii (white, diagonal stripes), cladocerans (dark grey, cross-hatched).

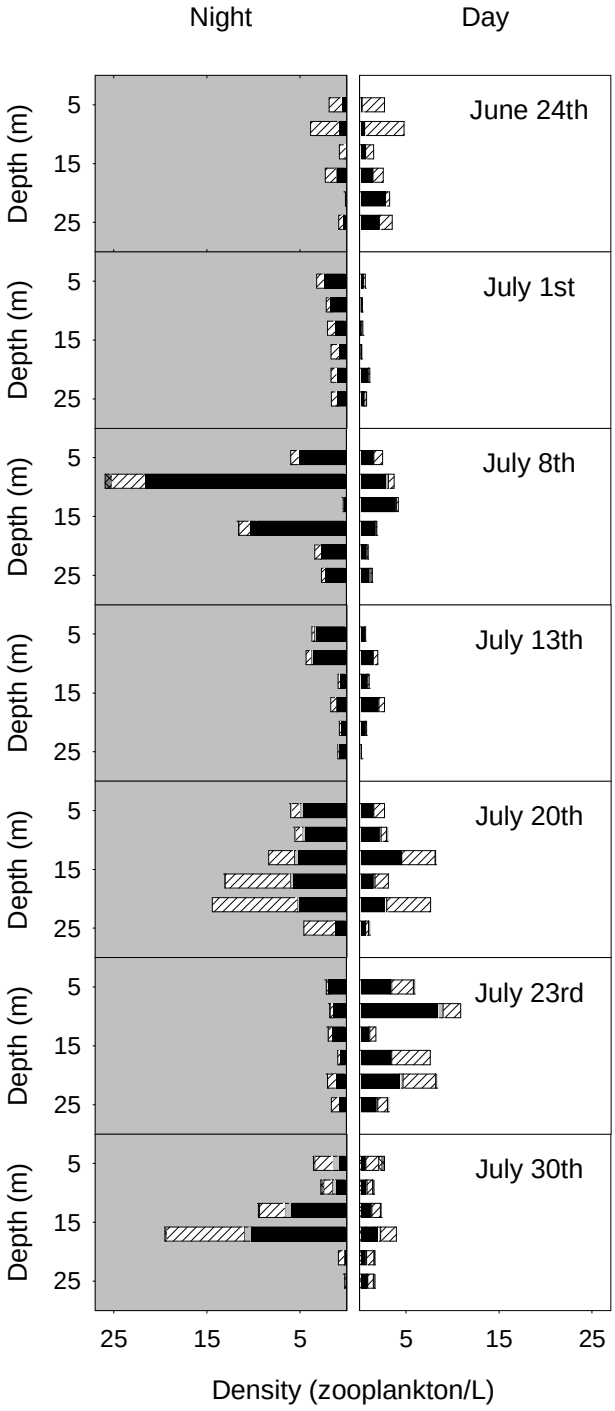


Figure 1.2. Diel vertical distribution of alewife, bloater, burbot, deepwater sculpin, and yellow perch larvae collected at the 6, 4 m depth bins between June 24th and July 30th.

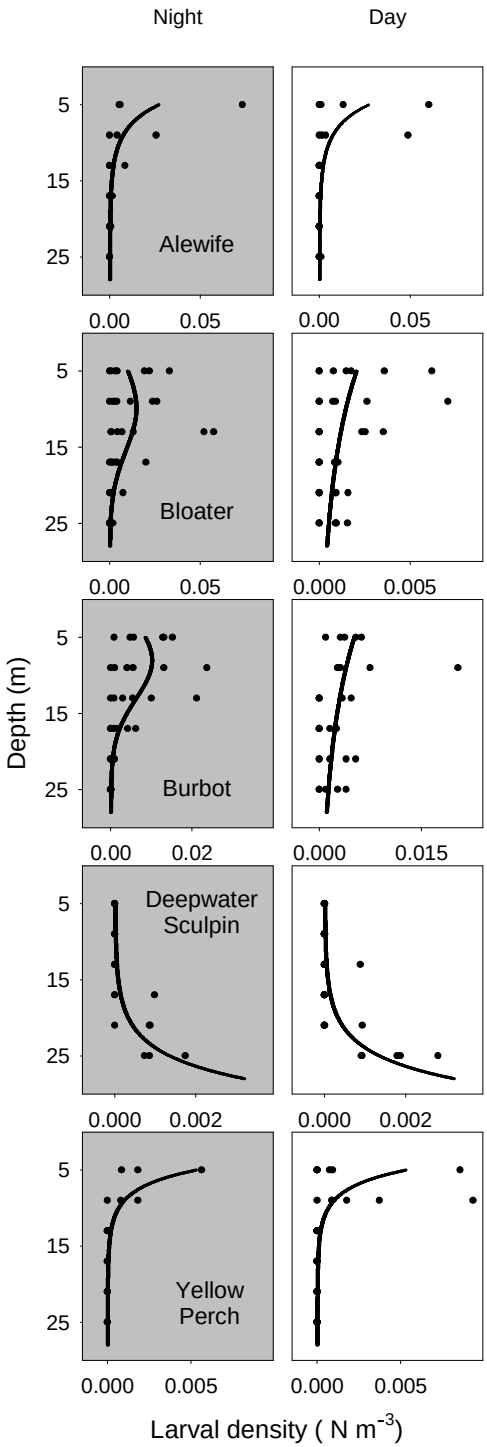


Figure 1.3. Density of alewife and yellow perch larvae collected in 6, 4 m depth bins between 3 and 27 m in relation to temperature.

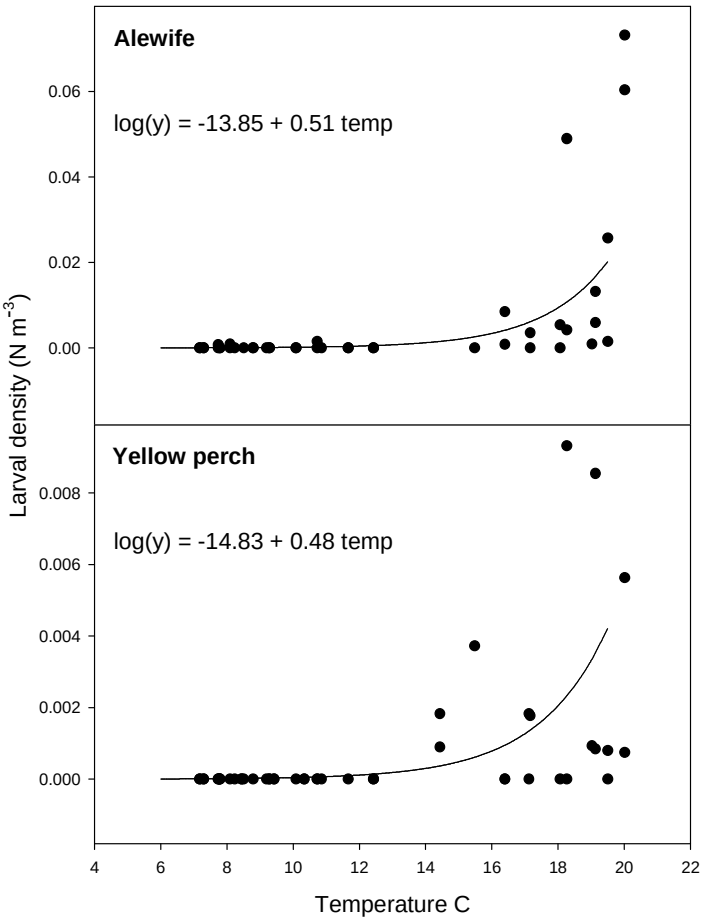
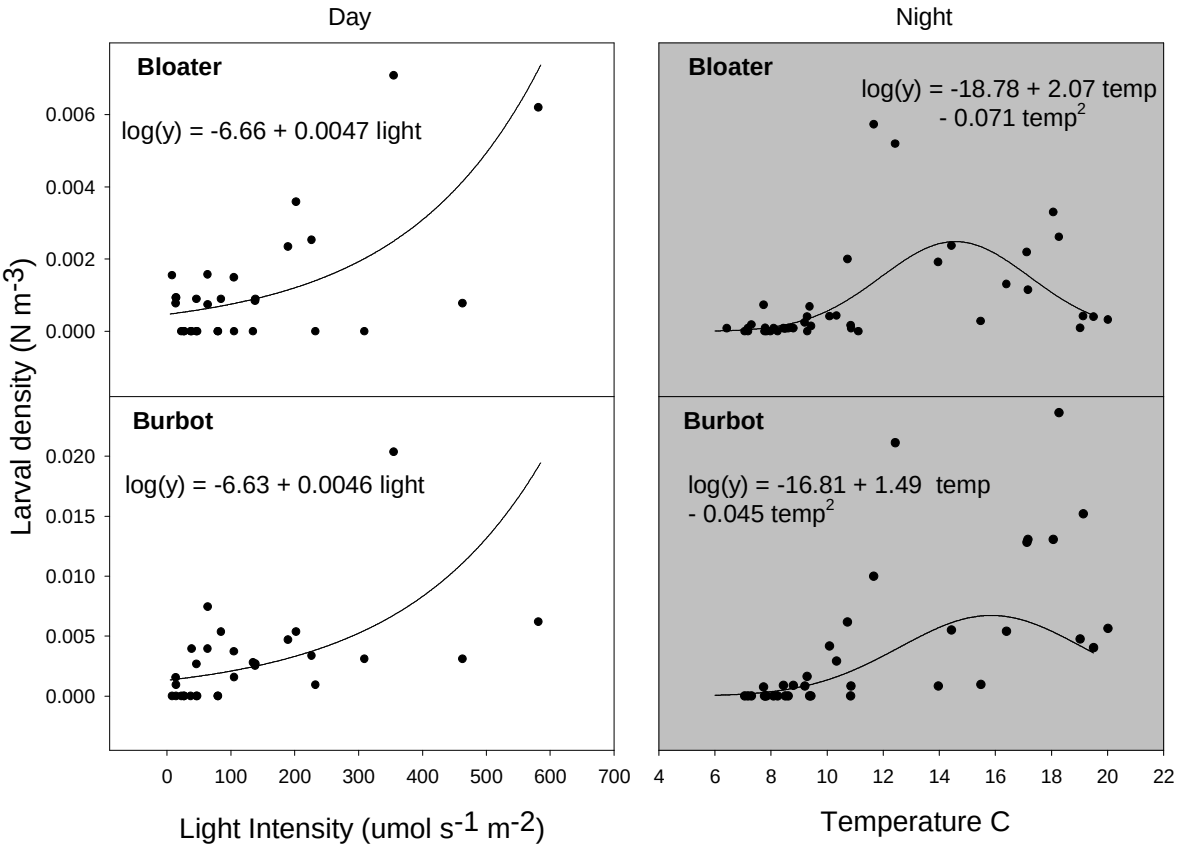


Figure 1.4. Density of bloater and burbot collected in 6, 4 m depth bins between 3 and 27 m in relation light intensity during the day (left), and temperature at night (right).



CHAPTER 2: EFFECT OF LIGHT INTENSITY, PREY DENSITY, AND ONTOGENY ON FORAGING SUCCESS AND PREY SELECTION OF LARVAL YELLOW PERCH (*PERCA FLAVESCENS*)

ABSTRACT

Light intensity has been shown to influence the foraging success of larval fish. However, the effect of light intensity on larval foraging is likely influenced by both the density and characteristics of their prey. In this study I examine the influence of light intensity on foraging of larval yellow perch at both high (150 zooplankton/L) and low (25 zooplankton/L) prey densities, with a mixture of zooplankton taxa common to lakes containing yellow perch. In addition to light intensity and prey density, the effect of ontogeny of larval yellow perch was examined by using fish ranging from 9 to 15 mm. The results of my study indicated that larval yellow perch are well adapted to feed at a wide range of light intensities, as there was no difference in foraging success between light intensities ranging from 0.1 to 60 $\mu mol\ s^{-1}\ m^{-2}$ PAR. Increasing prey density from 25 to 150 (zooplankton/L) significantly improved the foraging success of larval yellow perch. However, the influence of prey density on foraging success of larval yellow perch was dependent on fish length, with improved foraging success at increased prey densities occurring only for larger larvae. Overall, prey selection by larval fish was influenced by light intensity, prey density, and fish length, but the set factors which influenced selection for specific prey types differed. The results of this study combined with evidence from other field and laboratory work, highlight the need for a better understanding of the influence of prey density and prey type on foraging success throughout ontogeny.

INTRODUCTION

The foraging success of fish larvae is influenced by the availability of appropriate prey as well as physical conditions of the environment (Claramunt and Wahl 2000). Among environmental conditions, light intensity has been shown to strongly influence the foraging success of fish larvae (Batty 1987). Larval fish are generally visual feeders, and thus a reduction in light intensity below a certain threshold results in a decreased visual range, affecting encounter rate with prey. Much work has been aimed at determining the light intensity threshold below which the foraging success of fish larvae is reduced (Batty 1987; Job and Bellwood 2000). Light intensity diminishes exponentially with depth, thus laboratory derived estimates of visual acuity as a function of light intensity can be used to predict foraging success based on vertical distribution of fish larvae in the water column.

The general approach of previous laboratory studies has been to quantify the effect of light intensity on foraging by examining larval fish feeding success under a range of light intensities with a constant prey density. Seldom considered is how the influence of light intensity is affected by variable prey availability. As prey density increases foragers should gradually switch from being search time limited to being handling time limited (Sornes and Aksnes 2004). Because light intensity reduces the search capacity of fish via a reduction in visual range (Aksnes and Giske 1993), one could expect that the degree to which reduced light intensity effects foraging success should be greater when larvae are search time limited. Thus the magnitude of the effect of light intensity on foraging success may increase with decreasing prey density. In addition to prey density, the morphological and behavioral characteristics of prey may alter the effect of light intensity on foraging success (Aksnes and Giske 1993). Reaction distance to prey increases with its size and contrast, thus a reduction in light intensity may have a stronger impact for foragers feeding on less conspicuous prey types. Prey selection by juvenile yellow perch has been shown to be influenced by light intensity (Mills et al. 1986), with perch selecting larger prey items at low light intensities. Despite the potential of prey types and densities to alter the effect of light intensity on foraging success of larval fish, the vast majority of previous studies have been conducted with

relatively homogenous prey conditions, using either rotifers or *Artemia* nauplii at prey densities between 2000 and 7000 zooplankton/L (Pankhurst 1998; Cobcroft 2001; Downing and Litvak 2001; Carton 2005). Because the prey conditions under which estimates of light sensitivity were derived are not characteristic of those encountered by larval fish in the wild, the influence of light intensity may not be accurately portrayed and estimated by past laboratory studies.

Yellow perch are a species with a pelagic larval stage, where a broad range of light intensities may be encountered depending on depth distribution. To understand the influence of light intensity on the foraging success of yellow perch larvae, foraging experiments were conducted under a range of light intensities (0.1 - 60 µmol s^{-1} m^{-2}). The influence of light intensity was investigated at both a high (150 zooplankton/L) and low (25 zooplankton/L) prey density with a mixture of zooplankton taxa common to lakes inhabited by yellow perch. Because the visual acuity of larval fish has been shown to improve throughout ontogeny (Job and Bellwood 2000), we will examine the its affect and potential interaction with light intensity and prey density, by using fish ranging from 9 to 15 mm. These sizes include the pelagic phase of larval yellow perch life history, where a wider range of depths and subsequently, light conditions are encountered.

METHODS

Yellow perch egg skeins were collected from ripe females caught in gillnets in Southwest Lake Michigan, 2 nautical miles from Waukegan harbor, IL. Each skein was fertilized with pooled sperm from 5-7 males and washed with lake water. Fertilized eggs skeins were brought back to the Lake Michigan Biological Station where they were incubated in ambient Lake Michigan water. After hatching, yellow perch larvae were reared in 8, 38 liter tanks with a photoperiod of 14 h light: 10 h dark. Larvae were initially fed *ad libitum* with *Artemia* nauplii for the first week and then switched to a diet of crustacean

zooplankton collected from nearby, Sand Pond, IL. Foraging experiments began between 15 and 20 days after hatching and included only larvae that had been successfully feeding to this point.

The effect of two prey densities and three light intensities were examined in a two-way complete randomized block design with fish length as a covariate. Twenty four hours before each block of trials, approximately 60 yellow perch larvae were randomly removed from the eight holding tanks and divided into 6, 38 liter experimental tanks. The experimental tanks were each filled with 25 liters of filtered (0.44 µm mash screen) Lake Michigan water prior to the transfer of larvae. To remove zooplankton potentially transferred to the experimental tanks along with larval fish, approximately 90% of the water in each tank was suctioned out of the tank and through a .44 µm filter and back into the tank. This process was repeated twice. Larvae were then starved for a minimum of 18 hours before the foraging experiments.

Zooplankton density

On the morning of the experiment bulk zooplankton was collected from Sand Pond and stored in an aerated container. Three 5 ml subsamples of the zooplankton stock were analyzed to estimate density and composition. The goal was to create two prey densities: high (150 zooplankton/L) and low (25 zooplankton/L). Estimated densities were used to determine how much of the zooplankton solution to add to each experimental tank to create target densities. To account for any variation in day to day zooplankton composition over the course of the experiments a blocked design was implemented. All treatment combinations were run each day of the experiment using the same zooplankton stock. Each day, a subsample of the zooplankton stock was set aside and preserved in formalin to determine the density, composition, and size distribution of zooplankton used for each block.

Light intensity

Light was provided by overhead fluorescent bulbs. To diminish light intensity without altering the light spectrum I used white linen sheets stretched over wooden frames that completely covered the top of the experimental tanks (Utne-Palm and Stiansen 2002). All other sides of the tanks were covered with black construction paper. The desired light intensities of 0.1, 2.0, and 60 µmol s^{-1} m^{-2} were created by varying the number of overhead lights and number of linen sheets covering the tanks. Light intensity was measured with a submersible BIC radiometer (Biospherical Instruments) at the beginning and end of the experiment and was within 5% of the desired intensity for all experiments. The order of the six treatments (3 light intensities by two prey densities) was randomized for each block. To begin each experiment, the desired volume of zooplankton stock was added to achieve either the high or low prey density. Larval fish were allowed to forage for 15 minutes. After this time, MS -222 was added to the tanks and tanks were covered with an opaque board to cease the trial. Once euthanized, yellow perch larvae were removed from the tanks and stored in ethanol.

Sample analysis

Larval fish from all experiments were measured to the nearest 0.1 mm using a dissecting microscope (6x magnification) equipped with a drawing tube and electromagnetic digitizing tablet (Welker et al. 1994). The digestive tract of each larvae was dissected to determine their foraging success. Prey items found in the gut were enumerated and identified into main groups: adult calanoid copepods, adult cyclopoid copepods, copepod nauplii, and cladocerans. All intact prey items were measured under 25x magnification to the nearest 0.01 mm. Prey selectivity was determined by calculating Chesson's (1983) coefficient of selectivity (α). Actual densities and composition used in the experiments were determined by analyzing three, 5 ml subsamples of the preserved zooplankton stock solution used in each of the 9 blocks.

Statistical analysis

Data were analyzed using an ANCOVA to test the effects of light, prey density and fish length on total prey consumed, prey selection, and mean length of prey consumed. I first tested if all the slopes of a dependent variable and the covariate were equal to zero. If the slope was zero the data was analyzed as an ANOVA (Littell et al. 2006). If the slopes were not equal to zero and a common slope was adequate to describe the data, I compared differences of the intercepts between treatments. If a common slope was inadequate, or there was a significant treatment by covariate interaction, I fit a separate slope for each level of the treatment which interacted with the covariate.

RESULTS

Total prey consumed

Actual zooplankton density means for the high and low prey treatments were 153.6 (SD ± 25.6) and 25.6 zooplankton/L (± 4.1). Neither zooplankton composition nor size distribution used for each block varied significantly with time (Figure 2.1a). Zooplankton consisted of equal proportions of cladoceran and copepod prey (Figure 2.1b), copepod groups included cyclopoid and calanoid adults, and copepod nauplii. The gape size of the smallest larvae used in our experiments (9 mm) is approximately 0.83 mm (Schael et al 1991), and 95% of the zooplankton used in our experiments had lengths less than the gape size of the smallest larvae used in our experiments.

Neither light intensity nor it's interaction with fish length or prey density significantly affected the number of prey consumed by yellow perch larvae (Table 2.1 Figure 2.2). However, total prey consumed by larval fish during the experiments was influenced by the interaction of fish length and prey density. The number of prey items consumed by larval fish increased with fish length; however, the slope was influenced by prey density (Figure 2.3). At high prey densities, foraging success increased more

rapidly with fish length than with low prey densities. Foraging success at high and low prey densities did not differ for the smallest yellow perch larvae.

Prey selection

Overall, prey selection by yellow perch larvae was influenced by light intensity, prey density, and fish length, however, the set factors which influenced selection for specific prey types differed (Table 2.2). Selection for cladocerans was positive for all combinations of light intensity and prey density throughout the range of larval sizes. The strength of selection for cladocerans, however, was only significantly affected by prey density (Figure 2.4). At low prey densities, selection for cladocerans was greater than at high prey densities. Neither light intensity nor prey density influenced selection for adult calanoid copepods. However, selection for calanoid copepods was significantly influenced by fish length. As fish length increased, selection for calanoid copepods increased (Figure 2.5a). A similar trend was found for cyclopoid copepods; however, the slope was affected by light intensity. At higher light intensities, selection for cyclopoid copepods increased more rapidly with fish length (Figure 2.5b). Selection for cyclopoid copepods was not significantly affected by prey density. Selection for copepod nauplii was negative at all light intensities and prey densities across all fish lengths (Figure 2.5c). At low prey densities, copepod nauplii were more strongly selected for than at high prey densities. The mean length of prey consumed by larval fish increased with fish length. Neither prey density nor light intensity had any additional effect on the mean size of consumed zooplankton (Figure 2.6).

DISCUSSION

In this experiment, foraging abilities of yellow perch larvae were compared at light intensities ranging from 0.1 - 60 μmol s^{-1} m^{-2}. In nature, the light conditions encountered by fish larvae are a

function of surface light intensity, the light absorption properties of the water, and their depth. The amount of light penetrating the surface of any aquatic system is determined by latitude, season, cloud cover, and time of day (Jerlov 1976). Light extinction coefficients for PAR in aquatic systems are largely influenced by the concentration of dissolved organic carbon (Fee et al. 1996). In Lake Michigan, depending on cloud conditions, daytime (1000-1700 hours) surface light intensities ranged from 1500 – 300 µmol s^{-1} m^{-2} between June 24 and July 30th (Chapter 1). Lake Michigan is an oligiotrophic lake with a relatively low light extinction coefficient of 0.13 m^{-1} (Chapter 1), thus the 0.1 µmol s^{-1} m^{-2} isolume would occur between 61 and 73 m depending on cloud conditions. In more eutrophic lakes with a light extinction coefficient of 2.0 m^{-1}, the 0.1 µmol s^{-1} m^{-2} isolume would be between 3.3 and 4 m deep. Due to the deep penetration of light in oligiotrophic systems, and the strong thermal preference of yellow perch (McCormick 1976; McCauley and Read 1973), temperature will likely limit their distribution to depths well above the lowest light intensity tested in this study. In more turbid aquatic systems low light intensities will occur much closer to the surface, however lake productivity, and subsequently dissolved organic carbon, are often inversely related mean bottom depth of lakes (Rawson 1952; Hayes and Anthony 1964). Because highly eutrophic lakes are often very shallow, conditions where light intensity is below the lowest level tested in this experiment during the day may be rare. Yellow perch larvae foraged equally well within the range of light intensities examined, thus I would not expect their foraging abilities to be reduced by light intensity under most circumstances.

Although zooplankton compositions used in this study were representative of a typical lake inhabited by yellow perch, there is considerable variability in zooplankton composition among lakes which was not accounted for in this study. For example, if foraging success for a specific prey type was negatively influenced by low light levels, and that prey type was dominant, low light intensities may reduce foraging success more severely than was found in this experiment where larvae could compensate by consuming alternative prey types. In this study, selectivity for cladocerans, calanoid copepods, and copepod nauplii did not decrease with light intensity. Because neither overall foraging success nor

selection for cladocerans, calanoid copepods, and copepod nauplii were reduced at low light intensities, I would not expect foraging success for these three prey types to be reduced with light intensity.

The case is more complex for cyclopoid copepods. Selection for cyclopoid copepods increased throughout ontogeny, however, the rate of increase was influenced by light intensity, with selection increasing more rapidly with fish size at higher light intensities. Prey selectivity indices like Chesson's α inherently group several mechanistic processes of foraging. It is not possible to determine if observed differences in selectivity are due to actual preference for a specific prey type or a function of encounter rate and capture success. There are two plausible ways in which increased light intensity could increase observed selection for cyclopoid copepods. First, an increase in light intensity should increase the reaction distance of fish larvae, increasing its encounter rate with all prey types. Optimal foraging theory suggests that as encounter rate increases selectivity for the preferred prey type should increase. Thus if fish larvae have an inherent preference for cyclopoid copepods then increased encounter rates, brought about by increased light intensity, should increase observed selectivity. Alternatively, the higher selectivity observed at increased light intensities may result from enhanced capture success of cyclopoid copepods compared to that at lower light intensities. Cyclopoid copepods exhibit a characteristic hop and sink swimming behavior with hops occurring approximately once per second (Williamson 1986). This type of motion differs from the constantly swimming cladocerans and calanoid copepods. At low light intensities, the swimming behavior of cyclopoids may propel them out of the reduced visual range of yellow perch larvae. An increase in both larval yellow perch visual range and prey density should increase encounter rates with prey items. Thus either increased light intensity or prey density should both cause increased selectivity for cyclopoids if increased selectivity was due to an increase encounter rate with prey items. However, this was not the case, as yellow perch larvae did not feed more selectively on cyclopoid copepods at increased prey densities. Therefore it seems more likely that the decrease in selectivity for cyclopoids was caused by a decrease in ability to capture cyclopoids at reduced light intensities. In

systems dominated by cyclopoid copepods, larval fish foraging success may be more sensitive to light intensity than in systems where cladocerans and calanoid copepods are more common.

The aim of this study was to determine the effect of light intensity and its interaction with prey density on foraging success. However, the effect of light intensity on foraging success may also be influenced by other abiotic conditions such as turbidity, turbulence, etc. Larval yellow perch may not forage successfully at lower light intensities if turbidity or turbulence affects foraging disproportionally in these light conditions. Turbidity can negatively influence foraging abilities via a reduction in visual range (Vinyard and O'Brian 1976), or improve foraging success through an increase in contrast between a prey item and background (Utne-Palm 2002). The net influence of turbidity on foraging success is likely determined by the relative importance of each of these mechanisms. The negative influence of turbidity on foraging success is more severe for fish with larger reaction distance (Fisken et al 2002; De Robertis et al 2003). For larval fish with relatively small reaction distance the effect of turbidity on foraging success is generally neutral or positive (Chesney 1989; Bristow et al. 1996; Cobcroft at al. 2001). The interaction of light intensity and turbidity has been less studied. Miner and Stein (1993) found an interacting effect between surface light intensity and turbidity on foraging success of bluegill larvae in experimental mesocosms. At high surface light intensities, consumption by bluegill larvae increased with higher turbidity, while at low surface light intensities, increased turbidity decreased. However, because increased turbidity increases light attenuation and decreases ambient light intensity, the effects of turbidity are confounded with light intensity. Therefore it remains undetermined whether bluegill larvae consumed less prey because of the interaction between light intensity and turbidity or because increased turbidity reduced light intensity. In contrast, first feeding incidence and foraging success for yellowtail kingfish, *Seriola lalandi,* was similar under clear and greenwater conditions at light intensities ranging from 0.1 to 17 μmol s^{-1} m^{-2} (Carton 2005). Like turbidity, the effect of turbulence on foraging abilities of fish larvae has been described by a dome shaped relationship, with optimal foraging success occurring at some intermediate level of turbulence (MacKenzie at al. 1994). Additionally, exposure to intermediate levels of

turbidity at both high and low light intensities resulted in greater foraging success in herring larvae (Utne and Stiansen 2002). While other abiotic conditions clearly affect foraging success, there is currently little evidence suggesting that these factors interact with light intensity in a way which would disproportionally decrease foraging success at low light intensities.

Overall, foraging success of yellow perch larvae was higher at high prey densities (~150 zooplankton/L); however, this pattern interacted with fish length. For small larvae, an increase in prey density did not result in increased foraging success. However, as the size of yellow perch larvae increased, differences in total consumption at the two experimental prey densities were noted, suggesting that the functional response of larvae changed throughout their ontogeny. For fish larvae following a Holling type II functional response, these differences imply a disproportionate improvement in handing time over search efficiency. A similar pattern of a change in functional response has been found in a closely related percid, walleye (*Sander vitreus*). Walleye larvae of 9.9 mm required 20-30 zooplankton/L to achieve maximum consumption, while consumption by larvae 19-30 mm peaked at 100 zooplankton/L Mathias and Li 1982; Hoximeir et al. 2004). In another study, 9 mm walleye larvae were found to require lower prey densities to achieve maximum consumption than larvae 10- 13 mm in length (Johnson and Mathias 1994). Thus, for percids, there is significant support that smaller larvae may require lower prey densities to forage at maximum rates.

Laboratory experiments do not provide unequivocal support for a shift in the functional response of fish larvae. In fact, regardless of ontogeny studies on the functional response of fish larvae have produced widely variant estimates of prey densities required to reach maximum consumption. Whether this variation is representative of true differences among different fish species, or is an artifact of experimental conditions such as the prey type, remains unclear. In studies where rotifers or *Artemia* nauplii were used, prey densities required to reach maximum consumption ranged of 1000-10000 zooplankton/L (Werner and Blaxter 1981; Theilacker 1987; Tucker 1989; Miller et al. 1992; Dou et al. 2000; Parra and Yufara 2000; Laural et al 2001; Rabe et al. 2001). Whereas in studies where copepods or

cladocerans were used, generally much lower prey densities (10-200 zooplankton/L) were required to reach maximum attack or consumption rates (Mathais and Li 1982; Munk and Kirobe 1985; Kirobe and Munk 1986; Bregiman and Stein 1997; Johnston and Mathais 1994; Hoximeir et al. 2004). The inclusion of studies which used rotifers and *Artemia* nauplii in a critical review by MacKenzie at al. (1990) likely influenced their conclusion that laboratory derived functional response's should not be extrapolated to the wild. Due to the large differences in results among studies which use different prey types, few general conclusions can be drawn on the ontogeny of functional response in larval fish. Further research on the functional response of larval fish with natural zooplankton assemblages is needed to generate more realistic patterns.

The general consensus that food limitation is most severe at the earliest larval stage can be traced back to the "critical period" hypothesis (Hjort 1914). Field studies indicating that the number of prey items in the gut of fish larvae increases with fish length have provided additional evidence and strengthened this notion (eg. Dickman et al. 2007). However, often only a small proportion of larvae caught in the wild show evidence of starvation, and starvation alone has failed to explain variation in recruitment (Buckley 1984; McGurk 1985; Bodchasky at al. 2008). Predation during the vulnerable larval stage is likely an additional source of great mortality among fish larvae (Bailey and Houde 1989). Because predation is size-dependent, fast growth out of vulnerable sizes should strongly influence survival (Folkvord and Hunter 1986). Although the foraging capabilities of fish larvae increase with size, the scope of feeding potential also increases (Bodchansky et al. 2008). Thus the question of importance is not the absolute foraging rates, but rather how well are larvae feeding relative to their maximum feeding potential. Bodchansky et al. (2008) compared the foraging success of field caught radiated shanny, *Ulvaria subbifurcata* to laboratory reared larvae feeding at maximal rates, and determined that while a smaller proportion of large larvae were starving compared to small larvae, a much lower proportion were feeding at maximum rates. In an additional laboratory experiment, larvae of Atlantic cod (*Gadus morhua*) were exposed to food conditions which were either consistently high, consistently low, or switched from

low to high or high to low midway throughout the experiments (Gotceitas at al. 1996). At the end of the experiments, fish which were exposed to the low then high prey concentrations had significantly greater length, body depths, and weights than fish exposed to the low and high to low treatments, and were not significantly different on any of those measures than fish exposed to consistently high food concentrations. The results of these studies highlight the need for a better understanding of food limitation and abiotic factors which may influence food limitation for intermediate and late larval stages.

In summary, yellow perch larvae appear to be well adapted to forage at a wide range of light intensities. However, light intensity may be more limiting in systems where cyclopoid copepods constitute a high proportion of the zooplankton assemblage. The influence of prey density on foraging success of yellow perch larvae was dependent on fish length, with improved foraging success at increased prey densities occurring only for larger larvae. The results of this study combined with evidence from other field and laboratory work, highlight the need for a better understanding of the influence of prey density on foraging success throughout ontogeny. Because all aspects of foraging are influenced by the characteristics of the prey type, I stress the importance of using relevant prey items for studies examining the effects of biotic or abiotic conditions on foraging success.

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TABLES AND FIGURES

Table 2.1: Results from ANCOVA for the effects of light intensity (light), prey density (prey), and the covariate fish length on foraging success, measured by total number of prey consumed.

Type 3 Tests of Fixed Effects				
Effect	Num DF	Den DF	F value	Pr > F
Light	2	39.3	1.6	0.22
Prey	1	39.5	19.92	< .0001
Light*prey	2	39.9	0.19	0.83
Fish length*prey	2	22.5	70.41	<.0001

Table 2.2. Results from ANCOVA for the effects of light intensity (light), prey density (prey), and the covariate fish length on Chesson's selectivity index for cladocerans, copepod nauplii, calanoid copepods, cyclopoid copepods. When the covariate (fish length) was not significant, it was deleted and data was reanalyzed with an ANOVA

Type 3 Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
		Cladocerans		
Prey	1	40	7.26	0.010
Light	2	40	2.53	0.092
Light*Prey	2	40	0.98	0.39
		Copepod nauplii		
Prey	1	40	7.05	0.01
Light	2	40	1.67	0.20
Light*Prey	2	40	1.6	0.21
		Calanoid copepods		
Fish length	1	8.93	14.38	0.0041
Light	2	40	0.0	0.99
Prey	1	39.8	0.02	0.90
Light*Prey	2	40.4	0.4	0.68
		Cyclopoid copepods		
Fish length	1	11.6	9.41	0.010
Light	2	38.5	3.71	0.03
Prey	1	37.9	0.79	0.38
Light*Prey	2	38.9	0.4	0.69
Fish length*Light	2	38.4	4.77	0.014

Figure 2.1. Zooplankton compositions used for each block of the experiment by prey type (a) and prey length in mm (b).

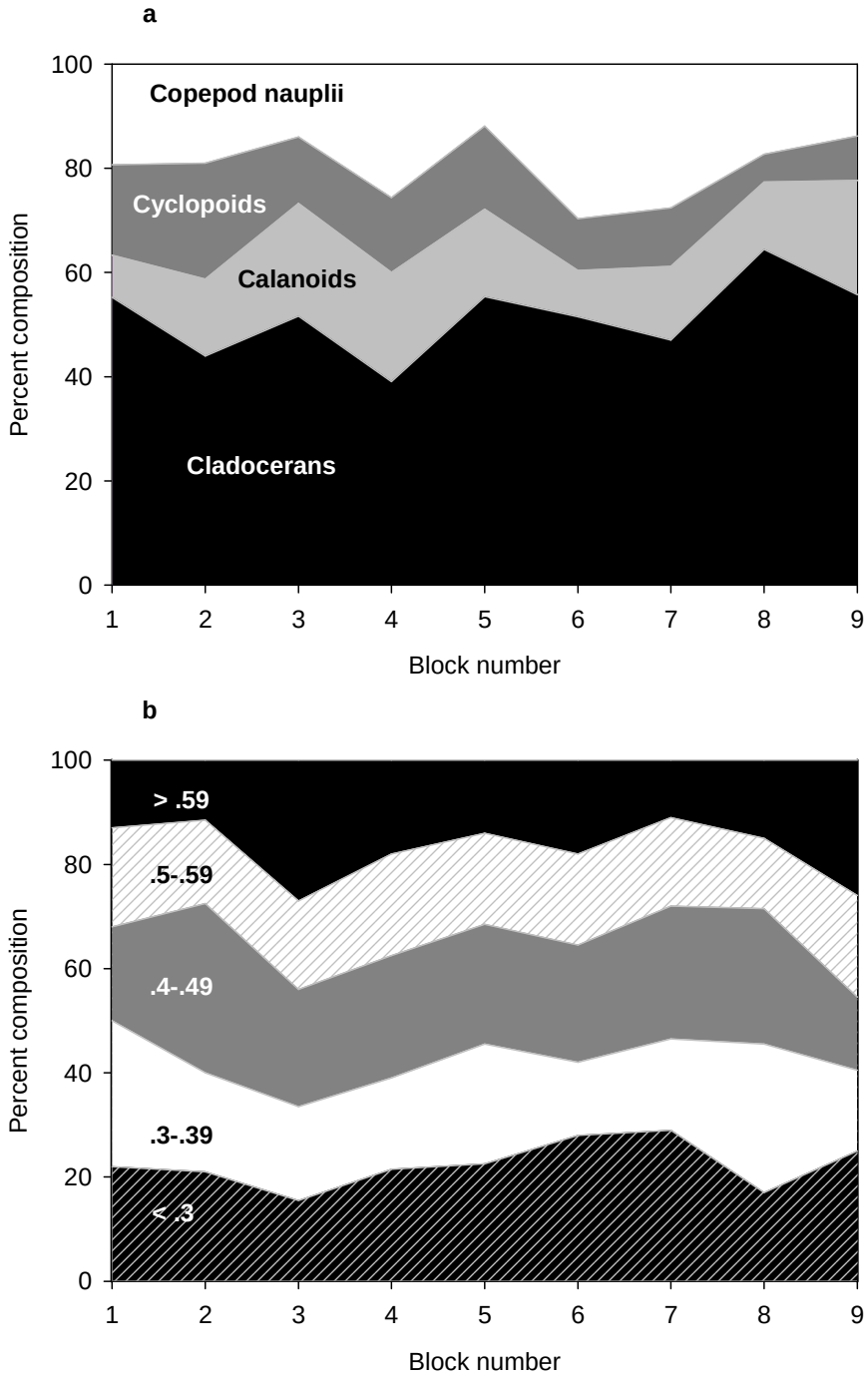


Figure 2.2. Total prey consumed by larval yellow perch in 15 minutes adjusted by the covariate, fish length, at each light intensity (µmol s^{-1} m^{-2}) for high and low prey densities, error bars represent 1 SE.

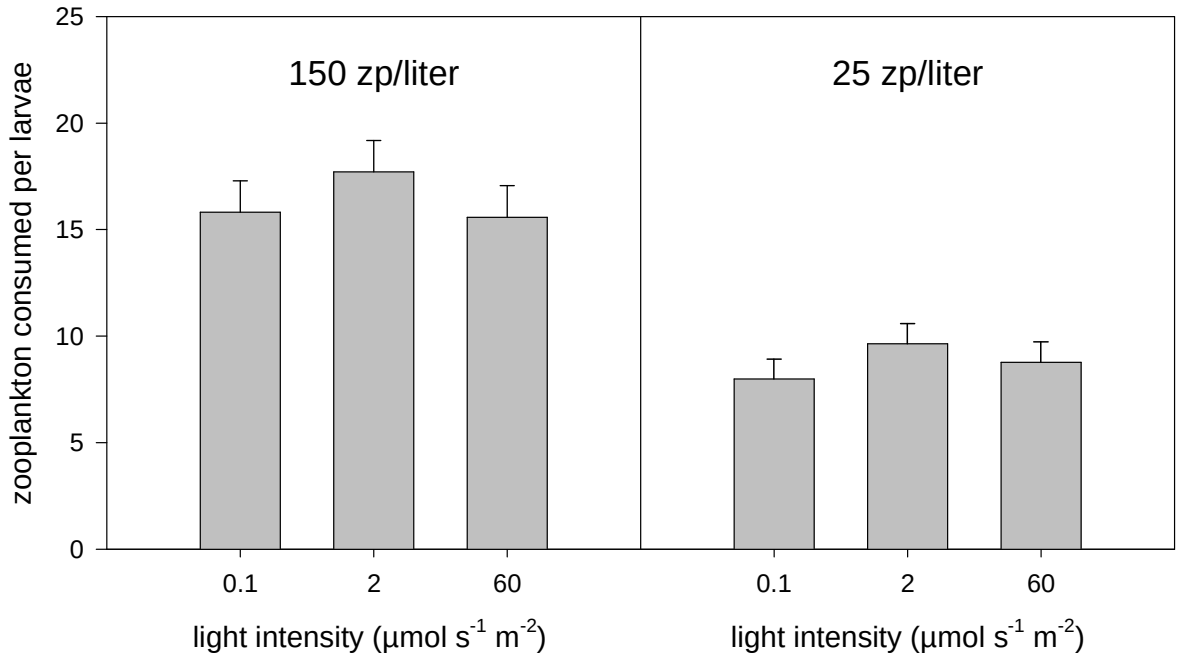


Figure 2.3. Total prey consumed by fish length for high (closed circles, solid line), and low (open triangles, dotted line) prey densities by larval yellow perch foraging for 15 min. in 38 liter aquaria.

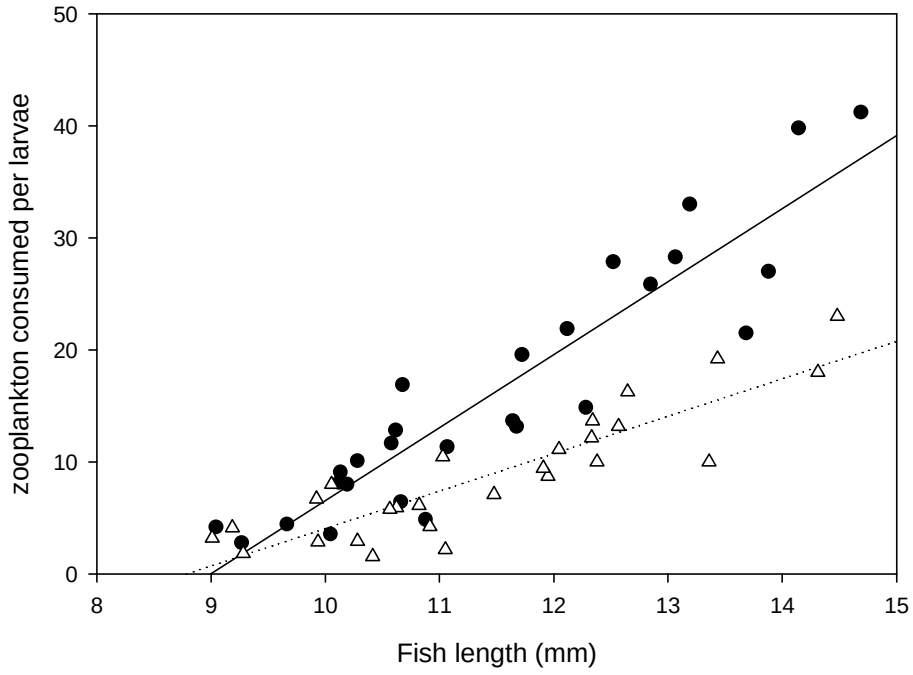


Figure 2.4. Chesson's α of yellow perch larvae for cladocerans foraging in 38 liter aquaria on a mixed zooplankton composition at two prey densities: high (150 zooplankton/L) closed circles, solid line, and low (25 zooplankton/L) open triangles, dotted line.

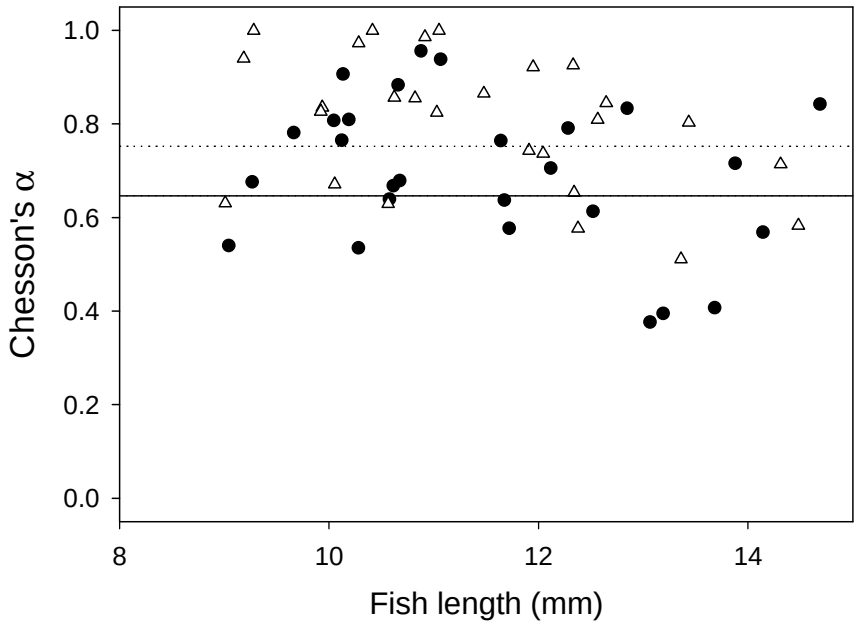


Figure 2.5. Chesson's α by length of yellow perch larvae for copepod nauplii at high (closed circles, solid line) and low (open triangles, dotted line) (a), and at three light intensities : 0.1 (open squares, dotted line), 2.0 (grey circle, dashed line), and 60 (closed triangles, solid line) µmol s^{-1} m^{-2} PAR for adult calanoid copepods (b), and cyclopoid copepods (c)

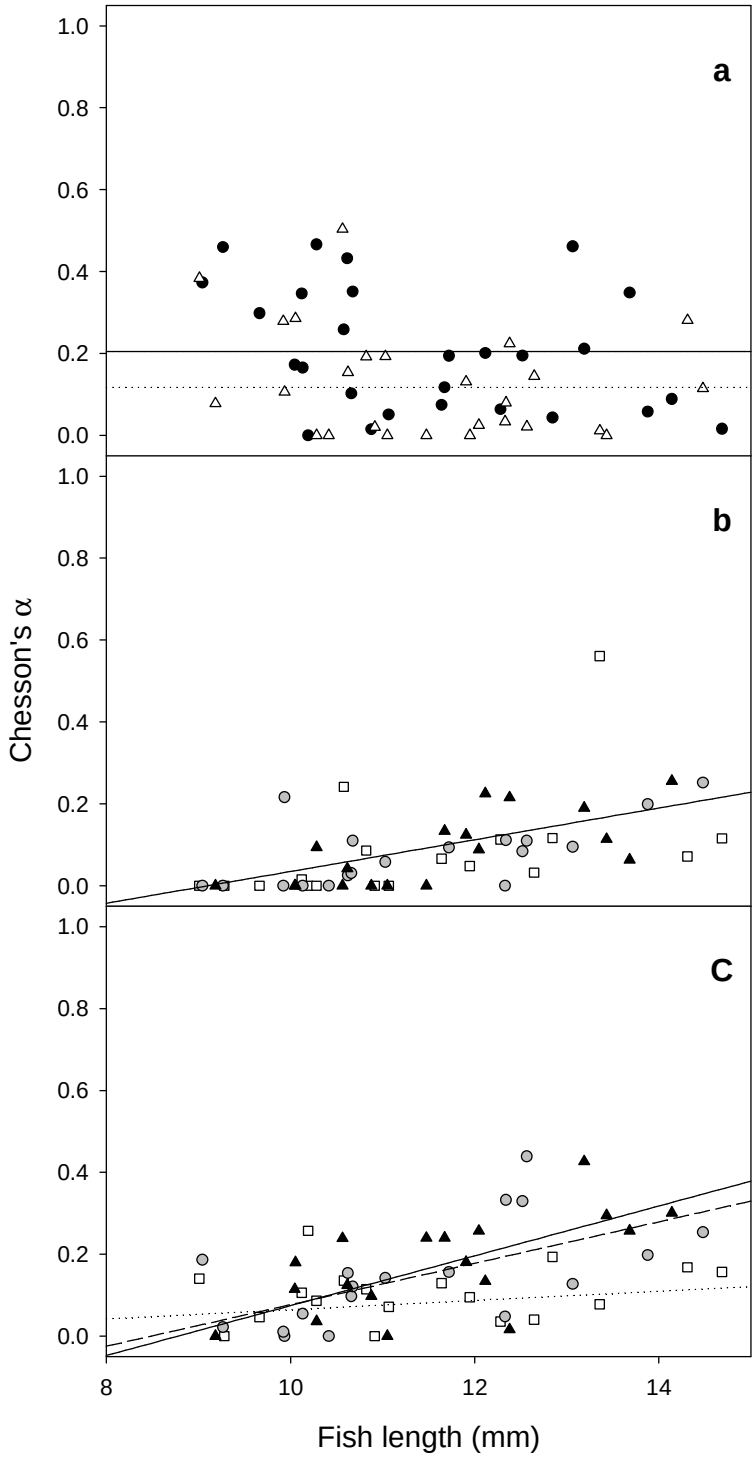
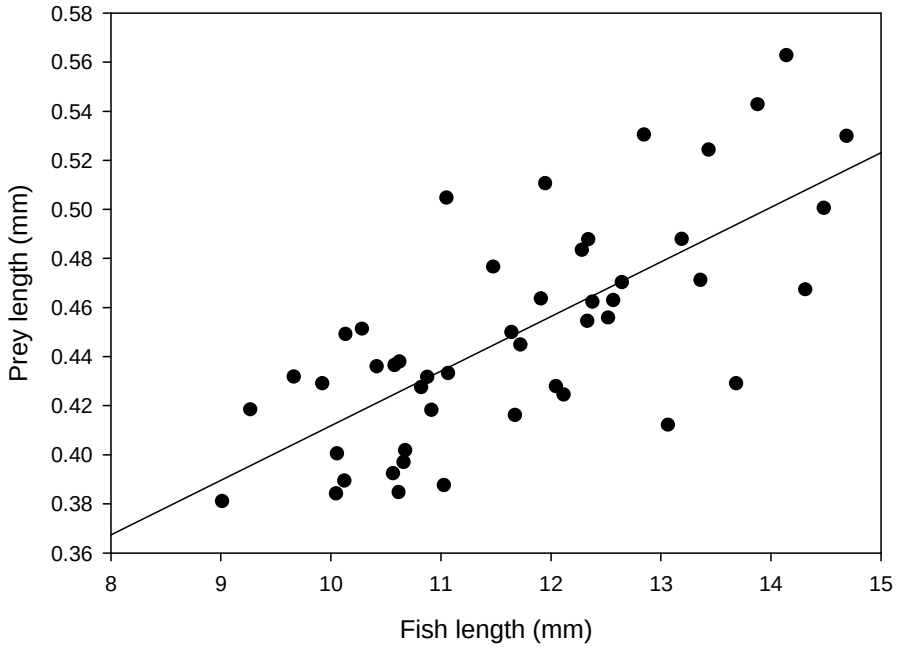


Figure 2.6. Mean length (mm) of prey consumed by larval yellow perch during 15 minute foraging experiments in 38 liter aquaria as a function larval length.



CONCLUSION

Of the five species collected in this field study, three distinct patterns of vertical distribution were observed. Alewife and yellow perch larvae were restricted to the epilimnion, whereas deepwater sculpin were restricted to the hypolimnion. In contrast, bloater and burbot were collected throughout the upper 27 m of the water column, and exhibited diel differences in distribution patterns. My analysis elucidates the importance of abiotic over biotic factors in the structuring of larval fish vertical distribution in Lake Michigan, as temperature was shown to influence the distribution of most species. Conversely, the vertical distribution of the 5 species collected was not related to crustacean zooplankton density. Alewife and yellow perch larvae were distributed in the upper strata where currents are stronger and highly variable between years. As such, larvae originating from the southeastern portion of Lake Michigan may be dispersed throughout the basin depending on the lake circulation patterns of a year. These findings support the continued use of a "basin wide" approach to management of these species. Conversely the deeper distribution of deepwater sculpin may facilitate their retention in waters proximate to where they hatched. As a result, deepwater sculpin populations may be more "closed" and require management on a more local level. Bloater and burbot larvae were distributed throughout the epilimnion, metalimnion, and hypolimnion during the day, and these environments are characterized by very different circulation patterns Therefore predictions of population dispersal patterns will largely depend on what mechanisms drive intra-specific variation in the vertical distribution of these species. Results from my laboratory study suggest that foraging success of yellow perch larvae was not influenced by light intensity between 0.1 to 60 µmol s^{-1} m^{-2} PAR. In oligiotrophic Lake Michigan the 0.1 µmol s^{-1} m^{-2} isolume corresponds with depths between 61-73 m depending on cloud conditions. Because larval fish yellow perch were restricted to the epilimnion, their foraging success in Lake Michigan may not be strongly influenced by light intensity. The influence of prey density on foraging success of yellow perch larvae was dependent on fish length, with improved foraging success with increased prey density occurring only for larger larvae. The

results of this study combined with evidence from other field and laboratory work, highlight the need for a better understanding of the influence of prey density on foraging success throughout ontogeny.