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Diets and growth potential of early stage larval yellow perch and alewife in a nearshore region of southeastern Lake Michigan

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A B S T R A C T

Transition from endogenous to exogenous feeding is thought to be a critical period for many fish larvae, when prey availability (type, size, and density) and ambient physical conditions (e.g., temperature, water clarity) can strongly influence survival. In Lake Michigan, two important fish species, yellow perch (*Perca flavescens*) and alewife (*Alosa pseudoharengus*), hatch and, presumably, begin exogenously feeding in the nearshore zone, an area characterized by short-term variation in environmental conditions. During 2010-2011, we examined environmental conditions and spatial and temporal distributions of larval yellow perch, larval alewife, and their potential prey in a nearshore region of southeastern Lake Michigan. To consider implications of environmental conditions on larval fish habitat quality, we quantified diet contents of young larval yellow perch and alewife and modeled bioenergetic growth rate potential (an index of habitat quality) under observed and predicted prey consumption scenarios. As expected, in this dynamic nearshore zone temperatures, light levels, zooplankton prey availability, and resulting growth rate potential were highly variable. Many larval fish digestive tracts were empty, suggesting that starvation may affect cohort survival. Among early-feeding larval fish, relatively small diet items were common, with larval alewives consuming diatoms and larval yellow perch consuming veligers of invasive dreissenid mussels. Though the mechanisms underlying such prey consumption and the consequences of ingesting these prey items remain largely unexplored, our results suggest dreissenid mussel veligers present early-feeding larvae with a relatively abundant prey source that may partially offset the apparent low consumption of other prey sources within Lake Michigan's nearshore region.

Introduction

Annual recruitment success of many fish populations is set during early-life when abundance is high and survival is relatively low. The interaction of abiotic and biotic mechanisms structuring early-life survival and eventual recruitment to the adult population are often not fully understood and highly variable among systems and over time (Claramunt and Wahl, 2000; Hjort, 1914; Houde, 1996). While ultimate survival through early life involves surviving a series of ontogenetic stanzas with potentially differing controlling factors (Pepin and Myers, 1991), predation and starvation are two key processes that frequently affect survival of young fishes. Both these processes are strongly regulated by individual growth rates and size. As fish grow, they become less susceptible to starvation due to relatively high energy stores, have lower mass-specific metabolic rates, and have enhanced abilities to capture a diversity of prey. Similarly, risk of predation generally decreases as fish grow, as greater size and faster swimming speeds allow fish to escape gape-limited predators (e.g., Miller et al., 1988; Pepin, 1989). Feeding success and resulting growth rates, which regulate starvation and predation risk, are in turn affected by a suite of environmental factors including temperature, water clarity, and availability of prey (Houde, 1996; Letcher et al., 1996). In particular, for many fish larvae the transition from endogenous to exogenous feeding may represent a critical period for survival (Miller et al., 1988; Sifa and Mathias, 1987).

In Lake Michigan, USA, yellow perch (*Perca flavescens*) and alewife (*Alosa pseudoharengus*) are abundant components of the fish community and contribute either directly (yellow perch) or indirectly (alewife, as forage for piscivores) to economically important fisheries. Both species have experienced variable recruitment success in Lake Michigan over the past few decades (Clapp and Dettmers, 2004; Francis et al., 1996; Madenjian et al., 2005; Wells, 1977). Recruitment of yellow perch in Lake Michigan appears to be set during the first 60 days of life (Robillard et al., 1999), and recruitment success has been related to many factors, including fishing-induced changes in spawning stock

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composition (Headley and Lauer, 2008; Heyer et al., 2001; Wilberg et al., 2005), change in zooplankton assemblages (Dettmers et al., 2003; Redman et al., 2011; Weber et al., 2011), predation by alewives (Redman et al., 2011; Shroyer and McComish, 2000; Weber et al., 2011), and variable temperature regimes (Redman et al., 2011; Weber et al., 2011). Recruitment success of alewife across the Great Lakes is also highly variable and seemingly influenced by diverse factors (Jude and Tesar, 1985; Madenjian et al., 2005; O'Gorman et al., 2004). Madenjian et al. (2005) evaluated potential drivers of alewife recruitment in Lake Michigan from 1962 to 2002 and found that adult stock size, predation by salmonines, and spring–summer temperatures during the first year of life collectively affected alewife recruitment to age-3. Larval alewife appear to grow faster and survive better in a warm environment with dense small zooplankton (i.e., Muskegon Lake, a drowned river mouth lake), as compared to a cool environment with less small-bodied prey (i.e., nearshore Lake Michigan; Höök et al., 2007).

The majority of larval yellow perch and alewife in Lake Michigan hatch and presumably begin exogenous feeding in the nearshore zone (<20 m) (Höök et al., 2008; Jude et al., 1981; Perrone et al., 1983; Wells, 1973) where environmental conditions (e.g., temperature, water clarity, zooplankton densities) are relatively unstable and characterized by high spatial and temporal heterogeneity (Ayers et al., 1958; Mortimer, 2004; Troy et al., 2012). Past studies indicate that larval yellow perch and alewife growth and survival are responsive to ambient prey (Graeb et al., 2004; Heinrich, 1981), light, (Blaxter, 1986; Wellington et al., 2010) and temperature conditions (Edsall, 1970; Fry, 1971). First-feeding yellow perch expressed higher growth and survival when fed copepod nauplii, and did not survive when only provided adult copepods or cladocerans (Graeb et al., 2004). Not surprisingly, unfed larval alewife grow slower than fed larval alewife and may die between 2 and 7 days post-hatch, depending on ambient temperature (Edsall, 1970; Heinrich, 1981). Furthermore, water clarity has been shown to influence prey capture efficiency of larval yellow perch (Martin et al., 2012), and temperature is well established to affect various aspects of larval fish feeding and growth (Edsall, 1970; Fry, 1971).

Early stage larval yellow perch and alewife are relatively poor swimmers and their movement is essentially passive and strongly influenced by water currents (Höök et al., 2006; Houde, 1969; Klumb et al., 2003). Past studies have highlighted the potential importance of offshore advection of larval yellow perch in Lake Michigan, suggesting that in the past, lower predation pressure and availability of large-bodied zooplankton prey may have provided an advantage to individuals advected to offshore waters (e.g. Dettmers et al., 2003, 2005; Shroyer and McComish, 2000; Weber et al., 2011). However, depending on the timing of larval emergence, rapid changes in the nearshore environment may either expose larvae to warm temperatures, suitable water clarities and high densities of appropriate prey, facilitating a successful transition to exogenous feeding, high survival and adequate growth, or lead larval fish to experience less favorable conditions, leading to limited prey consumption, poor survival and slow growth.

Contemporary assessments of nearshore environmental conditions, prey consumption, and growth potential of larval yellow perch and alewife are important as the Lake Michigan ecosystem has fundamentally changed over the past 30 years. Earlier assessments of larval fish dynamics in the nearshore zone (e.g., Jude et al., 1981) may not be reflective of current dynamics, where reduced nutrient loading (Han and Allan, 2012; Lehman et al., 2013) and the proliferation of invasive species, most notably *Dreissena polymorpha* and *D. rostriformis bugensis* (hereafter dreissenids), have contributed to increased water clarity (Bunnell et al., 2014) and altered phytoplankton (Mida et al., 2010) and zooplankton (Pothoven and Fahnenstiel, 2015; Vanderploeg et al., 2012) assemblages. Moreover, differences in larval fish performance between nearshore and offshore hypothesized in the past (Dettmers et al., 2005) may not hold under this altered ecosystem. We assessed the effects of environmental conditions in a nearshore region of southeastern Lake Michigan on larval yellow perch and alewife by 1) characterizing water clarity, temperature, and zooplankton abundance, 2) evaluating diets of larval fishes as they transition from endogenous to exogenous feeding, and 3) evaluating the potential effects of temperature, light, and prey type on habitat quality using a bioenergetics approach. We expected that our results would provide insight as to mechanisms affecting growth and survival in this potentially important nursery area for first-feeding larval fish.

Methods

Field collections and laboratory processing

We sampled larval fish, zooplankton, temperature, and water clarity along a transect perpendicular to shore in Lake Michigan near Michigan City, IN, USA (Fig. 1). During daylight, we collected larval fish, zooplankton, and Secchi depth every 3–4 days from April to August of 2010 and once per week from April to August of 2011, and we deployed instruments to continuously monitor temperature and water clarity. We assessed variability in temperature by deploying three thermistor strings at depths of 15 m, 18 m, and 21 m. The 15 and 18 m string locations coincided with the center points of our ichthyoplankton sampling areas (see below; Fig. 1). Thermistor strings were deployed from day-of-year (DOY) 125–286 in 2010 and DOY 126–269 in 2011. Each thermistor string consisted of an anchored chain attached to a surface buoy, with temperature loggers attached every two meters from surface to bottom. Temperature loggers recorded temperature (°C) every 10 min while deployed. We measured water clarity continuously with a light meter that was attached at the bottom near the anchor of the thermistor string set at the 15 m depth contour. We used these measures to calculate mean daily transparency over 24 h intervals. We also used a Secchi disk to measure water clarity on each sampling day at three center points of our ichthyoplankton towing tracks (7 m, 15 m, and 18 m; see below and Fig. 1).

At the center point of the 15 m towing track (see below), potential zooplankton prey were collected via two replicate, vertical tows of a 0.5 m diameter, 2.0 m long, 64 μm mesh zooplankton net from ~0.5 m above the bottom to the surface at 0.2 m s^{-1}. Zooplankton samples were concentrated, then anesthetized with bicarbonate and preserved in 10% sugar-buffered formaldehyde (Haney and Hall, 1973). In the laboratory, zooplankton were counted and identified (see Table 1 for taxonomic groups; note rotifers were neither identified nor counted) using a subsample (1/32–1/16 of sample) of each vertical tow. Samples were split in order to expedite sorting time while still accounting for an accurate representation of the sample wherein subsamples contained at least 30 individuals from each designated taxon. We photographed and measured up to 20 individuals from each taxonomic group present in samples collected from the 15 m depth contour. We measured copepods from the tip of the head to the base of the caudal rami, nauplii from the tip of the head to the caudal base, cladocerans from the tip of the head to the base of the tail spine, and dreissenid mussel veligers from the anterior to posterior edge. We estimated dry weights of each zooplankter measured using published length–weight regressions adjusted for shrinkage in preservative (Table 1). We calculated mean daily biomass estimates for each zooplankton group by multiplying daily mean dry weights by densities.

To collect larval fish, we towed a bongo sampler (two 0.6 m diameter, 1.0 m long ichthyoplankton nets mounted on a single frame, 335 μm and 500 μm mesh, respectively) parallel to shore along three discrete depth contours (7 m, 15 m, and 18 m). Each tow lasted 10 min at 2–2.5 knots and ranged no further than 1500 m on either side of a pre-defined center point (Fig. 1). We performed replicate tows at each depth contour, targeting depths just below the surface of the water and every 5 m down in the water column (i.e., two tows at the 7 m depth, three tows at the 15 and 18 m depths). We attached a Sonotronics DTL sensor to the bongo sampler that recorded depth and temperature of each tow