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Early life history of alewife *Alosa pseudoharengus* in southwestern Lake Michigan

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ABSTRACT

Recruitment of fishes is difficult to predict due to inter-annual and system variation. For example, the early life history of fishes inhabiting expansive freshwater systems such as the Great Lakes differs from other freshwater environments but has received less attention. Alewife *Alosa pseudoharengus*, an anadromous species adapted to living exclusively in freshwater, provides an opportunity to evaluate processes regulating growth and survival of a fish with marine origins inhabiting a large freshwater system. We collected age-0 alewives at three distinct locations (nearshore Chicago, nearshore Waukegan, offshore) in southwestern Lake Michigan during 2005 and 2006 to estimate density, growth, and survival. Larval alewife densities were up to three times greater and hatching peaks occurred earlier in 2005 compared to 2006. Back-calculated alewife hatch dates indicated that peak hatch occurred two weeks prior to peak catch rates, with similar hatching distributions of larvae collected between nearshore and offshore environments. Alewives up to approximately 16 d of age were collected in both nearshore locations before appearing in the offshore environment. Alewife growth rates were influenced by zooplankton density, water temperature, and hatching date whereas survival from the nearshore to offshore environment was influenced by wind events and hatching date. Prey availability and passive larval transport driven by offshore wind events are more commonly identified as factors influencing marine rather than freshwater larvae. Thus, factors affecting recruitment dynamics of fishes in large complex inland systems may be more similar to marine than freshwater systems.

Introduction

Understanding processes governing recruitment of fishes presents one of the greatest challenges to ecologists, particularly in large, dynamic environments. Larval fish dynamics are influenced by a suite of biotic and abiotic factors (Houde, 1987), and survival during early life stages can be highly interdependent (Ludsin and DeVries, 1997) but spatially separated (Weber et al., 2011). Recruitment of freshwater fishes is primarily regulated by predation during juvenile stages whereas prey availability and abiotic conditions during larval stages affects recruitment more strongly in marine systems (Houde, 1994). However, recent evidence indicates that factors affecting growth and survival of larval fishes in large freshwater environments may be more similar to marine than freshwater environments (Dettmers et al., 2005; Weber et al., 2011; Janssen et al., 2014; Pritt et al., 2014).

Large freshwater systems present challenging environments within which the ability of larval fishes to survive determines year-class strength. For instance, yellow perch *Perca flavescens* in Lake Michigan experience prolonged pelagic larval durations due to hydrodynamic processes where a suite of biotic and abiotic factors affect growth and survival across multiple locations to produce highly variable year-class strength across years (Beletsky et al., 2007; Miehls and Dettmers, 2011; Redman et al., 2011; Weber et al., 2011). While early life history dynamics of yellow perch have been studied in some detail in the Laurentian Great Lakes, less is known about the early life history of other fishes in these large systems. Alewife *Alosa pseudoharengus* provides an interesting evaluation of early life history strategies within Great Lakes fishes because, like yellow perch, alewife experiences a prolonged pelagic larval phase (Nash and Geffen, 1991), suggesting that biotic and abiotic pelagic conditions are likely important to recruitment dynamics in a manner similar to yellow perch. However, alewives originated in the marine environment and may be better adapted to large-scale hydrodynamic processes that are common in marine environments compared to other freshwater fishes. Further, although both species have long pelagic phases, yellow perch appear offshore about a month earlier than alewife. As such, alternative factors may regulate

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alewife growth and survival during early life stages or differences in timing of appearance, availability of plankton nearshore, or behavioral differences may differentially affect growth and survival of alewife and yellow perch.

Alewives were first documented in the Great Lakes during 1873, became established in Lake Michigan in 1950, were a dominant portion of the lakewide biomass in the 1960s, and remain an important component of the dynamic ecosystem as both a predator and prey (Taylor and Ferreri, 1999; Madenjian et al., 2002). Alewife abundance has been sufficiently high at times to exert strong ecosystem consequences (Madenjian et al., 2002). Abundant alewife populations have been linked to dramatic declines in zooplankton and native fishes through predation and competition (Madenjian et al., 2002; Creque and Czesny, 2012). Additionally, alewives are the primary prey for economically valuable salmonids *Oncorhynchus* spp. (Madenjian et al., 2002) and yellow perch (Weber et al., 2010). However, alewife recruitment is highly variable (O'Gorman et al., 2004; Madenjian et al., 2005), which can influence adult abundance and subsequent food web interactions. Thus, variation in alewife recruitment has implications for ecosystem and sport fish management.

Little is known about processes regulating alewife growth and survival during early life stages. A few studies have focused on larval alewife dynamics at nearshore locations in the Great Lakes (Klumb et al., 2003; Höök et al., 2007) but because of the hydrodynamics of Lake Michigan (Beletsky et al., 2007), larval alewife likely spend a significant portion of their first months of life offshore (Nash and Geffen, 1991). Processes occurring in the offshore environment help shape yellow perch recruitment (Dettmers et al., 2005; Weber et al., 2011) and may also have important implications for alewife recruitment. However, the early life history of alewife in the offshore environment has received limited attention. Additionally, environmental processes that regulate lake physics are changing in the Great Lakes (ice cover: Wang et al., 2012, temperature: Austin and Colman, 2007, wind: Desai et al., 2009), potentially influencing larval transport from the nearshore to offshore environment and growth and survival processes. Because the early life history of fishes is characterized by high mortality (>99%; Houde, 1987), understanding how biotic and abiotic factors regulate growth and survival of larval alewife can lead to increased understanding of recruitment dynamics of alewife and other fishes inhabiting large freshwater environments. To evaluate alewife recruitment in Lake Michigan, we first compared alewife density, hatching and age distributions, and growth and survival rates in three areas in southwestern Lake Michigan. Second, we examined the influence of biotic (zooplankton density) and abiotic (water temperature, offshore wind) factors and larval processes (hatching date, growth rate) on alewife growth and survival. We hypothesized that 1) alewife hatching distributions and peak densities would be earlier south near Chicago compared to further north near Waukegan, 2) alewife growth and survival would be lower for early compared to later hatching cohorts and 3) alewife growth and survival would be positively related to prey availability, water temperature, and offshore wind events that would transport larvae from nearshore to offshore locations. Finally, we qualitatively compared factors regulating alewife and yellow perch growth and survival to gain a better perspective on processes influencing larval fishes during important transition bottlenecks in large freshwater ecosystems. Combined, these results provide new insights into specific factors regulating alewife recruitment and general information about recruitment dynamics of fishes in large lake ecosystems.

Methods

Ichthyoplankton collection and processing

Sampling encompassed a large spatial area in southwestern Lake Michigan. Field sampling methods have been described in Miehls and Dettmers (2011) and Weber et al. (2011) and thus are described in brevity here. Larval fishes were collected at two nearshore locations, one 1.5 km offshore of Waukegan, IL, and another 1.5 km offshore of Chicago, IL, with two replicate samples collected at two sampling stations between 0.5 and 2.0 km from shore over water depths of 5–10 m (Fig. 1). The offshore location encompassed three sampling stations at 5, 16, and 27 km offshore of Waukegan, IL at water depths of 0, 30, 70, and 100 meters, respectively (Fig. 1).

Epilimnetic larval fish were captured at nearshore locations with a 1.0-m × 2.0-m fixed-frame neuston net with 500-μm mesh netting towed at the water's surface (0-2 m) for 10 min at 4-5 m/s. Sampling was conducted at night on a weekly basis from 6 June to 24 August 2005 (23 samples total) and 23 May to 21 August 2006 (22 samples total) at Waukegan and from 25 May to 28 July 2005 (18 samples total) and 23 May to 27 July 2006 (20 samples total) at Chicago. Sampling was conducted in the offshore pelagia from 7 July and 24 August 2005 (72 samples total) and 13 July to 21 August 2006 (36 samples total). Larval fish were collected at the surface with the same fixed-frame neuston net used for nearshore sampling, but equipped with a 1000-μm nitex mesh to effectively capture larger larvae (O'Gorman, 1984; Fulford et al., 2006). A multi-net opening/closing 1.0-m × 1.4-m mid-water Tucker trawl with 1000-μm nitex was also used to sample larval fish offshore within the epilimnion (2005 and 2006) and metalimnion (2005 only). Metalimnion sampling was discontinued in 2006 due to low abundance of larval fishes inhabiting this habitat (Martin et al., 2011). Nets were towed for 30 min at a speed of 3–6 m/s. The contents of all nearshore and offshore pelagic samples were immediately preserved and stored in 95% ethanol.

In the lab, larvae were sorted by species, enumerated, and measured to the nearest 0.1 mm using a digital imaging system. Larval alewife density was determined by dividing the number of fish caught by the volume of water sampled as determined by flow meter readings taken for each tow (number/100 m^3). Alewives collected from sampling stations near Chicago, Waukegan, and offshore were grouped into a single data set for each location to increase the number of larvae available per location and sampling date for analysis. Thus, mean weekly age-0 alewife density was calculated for three main sampling locations: nearshore Chicago, neashore Waukegan, and offshore.

Up to 40 alewives from each date and location were randomly subsampled for aging. When fewer than 40 alewives were collected, all alewives from that date and location were used. Sagittal otoliths were removed and mounted on glass slides using super glue. Daily increments were counted by two independent readers using a compound microscope (200x magnification) and estimates of daily increments were averaged for the final estimated age of each fish. Age estimates differing by >10% were re-examined and a consensus was made by both readers. Larval alewives do not develop daily otolith rings until 2 days after hatch (Essig and Cole, 1986). Therefore, age-0 alewife ages were determined by adding two days to the number of increments counted.

Each alewife was assigned to a 7-day hatching cohort based on daily hatching age (Pine and Allen, 2001; Santucci and Wahl, 2003; Weber et al., 2011). A corrected hatching distribution was used to account for all alewives sampled on each sampling date and within each location as

$$H_i = (N_i/T) * A$$

where H_i represents the corrected hatching distribution, i represents the weekly cohort, N represents the total number of alewife aged in a cohort, T represents the total number of alewife aged, and A represents the total number of alewife captured. Number of fish collected per cohort was then summed across dates by location and year to determine annual corrected hatching distributions.

Zooplankton collection and processing

Zooplankton was collected at the location of each ichthyoplankton tow using a 0.5 m diameter conical zooplankton net with 64-μm

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