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Modeling the implications of multiple hatching sites for larval dynamics in the resurgent Saginaw Bay walleye population

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ABSTRACT

The early life environment experienced by most larval fish is largely dependent on a combination of hatch site and water currents. Until larvae are able to swim fast enough to overcome currents, they are largely passively transported and have limited control over ambient environmental conditions, including temperature and prey availability. These factors strongly influence growth and survival of larvae, with direct consequences for subsequent recruitment. Early life survival of Saginaw Bay walleye was formerly limited by alewife predation on larvae; but following the collapse of Lake Huron alewives, the walleye population has rebounded and recruitment success may now be influenced by other factors including spawning habitat. We sought to assess the implications of successful hatching at multiple locations in Saginaw Bay, using a hydrodynamics model, particle transport model, and an individual-based bioenergetics model in series. Model results were compared to locations of young larvae collected in Saginaw Bay during 2009–2010. Results suggest that larval growth is strongly influenced by hatch date, driven by seasonal variation in temperature between sites. Larvae hatched at any location could be transported extensively within inner Saginaw Bay before reaching a sufficient size to swim independently of currents, and retention within the productive inner bay varied among years and sites. Our results indicate multiple larval walleye origins in the field, augmenting the continued production from the Saginaw River system. Successful hatching at more locations would serve to buffer walleye recruitment variation through portfolio effects, supporting arguments for more emphasis on diverse spawning habitat management and restoration.

Introduction

Variation in the environment experienced by larval fish strongly influences larval growth and survival (Roseman et al., 2005). Relatively fast growing and larger larvae generally experience higher survival (Legget and DeBlois, 1994; Miller et al., 1988) as increased size generally favors: increased swimming ability (e.g., Humphrey et al., 2012); improved predation on diverse prey through faster swimming and larger gape size (e.g., Bremigan and Stein, 1994); decreased risk of starvation through higher energy stores and lower mass-specific metabolic rates (e.g., Wieser, 1991); and better avoidance of gape- and mobility-limited predators (e.g., Legget and DeBlois, 1994). Thereby, factors affecting growth during early life can have a strong influence on survival and ultimate recruitment success. Within a system, spatio-temporal thermal heterogeneity leads to variability in hatch timing (Johnson, 1961) and may affect larval fish growth (Hoxmeier et al., 2006). In fact, temperature patterns have been linked to recruitment success of multiple fish species (e.g., Schupp, 2002) through thermal effects on growth. Similarly, prey availability is directly related to growth potential. Higher overall prey densities and spatio-temporal overlap between larval fish and their prey (Roseman et al., 2005) can lead to faster growth and greater subsequent recruitment (Dettmers et al., 2003). As most larval fish swim weakly upon hatching (Houde, 1969), their early-life environment is almost entirely dependent on hatch site and water currents (e.g., Höök et al., 2006). Larvae hatching from a low-quality location can be transported to a high-quality habitat, or alternatively may hatch in a prime location only to be transported to a poor habitat; such advection can ultimately influence survival and subsequent year class strength (e.g., Zhao et al., 2009).

Following a decades-long period of low recruitment, the walleye (*Sander vitreus*) population of Saginaw Bay, Lake Huron, has recently

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experienced a tremendous resurgence (Fielder and Thomas, 2006; Ivan et al., 2011). Previously, walleye reproduction was hindered by loss of suitable spawning sites through silt buildup on reefs and damming of spawning rivers (Fielder, 2002), and larvae that did hatch successfully were likely driven to low densities through voracious predation by invasive alewife (*Alosa pseudoharengus*) (Brooking et al., 1998). Following a recent collapse of the Lake Huron alewife population, the Saginaw Bay walleye population has rebounded to near target recovery levels (Fielder and Thomas, 2006; Fielder et al., 2007). With the removal of a main factor limiting walleye production (Fielder et al., 2007), it is appropriate to describe the new recruitment dynamics and elucidate additional factors that may influence the continued resurgence of this economically important fish population.

One such factor with the potential to strongly affect walleye production is spawning habitat. Historically many reefs within Saginaw Bay were important for walleye production (Schneider, 1977), but based on a survey by Fielder (2002), few of these reefs appeared to be used by walleye or were covered by sediment and unsuitable for spawning in the 1990s. Instead, during this time almost all natural walleye production was thought to emanate from larvae hatching in rivers (Fielder, 2002; Ivan et al., 2011). The Saginaw River and its tributaries, particularly the Tittabawassee River, produced the most larvae (Jude, 1992); and this reliance on production from limited habitats could lead to high inter-annual variability in recruitment as has been the recent trend (Ivan et al., 2011). However, the extent to which the current walleye population depends on input from the Saginaw River versus other spawning habitats is unknown. The most recent reef surveys and recruitment assessments occurred before the alewife collapse and subsequent walleye recovery, and increasing walleye densities suggest the possibility of increased production of recruits from alternative sites.

Consistently high, stable recruitment may result if walleye were to utilize a diverse collection of spawning grounds (portfolio effect: Figge, 2004; Yates et al., 2012). Recruitment based solely on a few geographically close sites would be strongly influenced by local conditions, but a return to contributions from a number of spawning grounds could take advantage of heterogeneous biotic and abiotic conditions to buffer inter-annual variability in system-wide recruitment (Beletsky et al., 2007). Utilizing diverse habitats is predicted to benefit recruitment in fish from alewives (Höök et al., 2008) to sharks (Yates et al., 2012). More stable system-wide recruitment would translate to a more stable population, decreasing some of the uncertainty in managing what was once the second-largest walleye fishery in the Great Lakes (Schneider and Leach, 1977).

Saginaw Bay is divided into inner and outer sections that likely represent high- and low-quality habitats, respectively, for larval walleye. The inner bay may serve as a nursery environment for newly-hatched walleye and is warmer and more productive than the outer bay (Beeton et al., 1967). Outer Saginaw Bay is relatively cold and unproductive, and is more similar to the main basin of Lake Huron than it is to the inner bay (Beeton et al., 1967). Larval walleye transported from the inner bay to the outer bay are likely to experience slow growth due to a combination of cool temperatures and low prey densities and may experience high size-dependent mortality. Water currents in Saginaw Bay are wind-dependent and highly volatile (Danek and Saylor, 1977), which, together with an estimated flushing time of 186 days (Keller et al., 1987), indicates a high risk of larvae being transported out of the inner bay. Currents typically vary spatially, and while one spawning site could be devastated by outward-flowing currents, the same conditions may serve to effectively trap larvae from another site within the favorable inner bay.

To assess the role of spatially disparate hatch locations on the Saginaw Bay walleye population, we modeled movement and growth of newly-hatched larvae for 2009 and 2010. Our simulations allowed us to investigate the variation in growth and fate of larvae from each of four potential spawning sites for Saginaw Bay walleye. Additionally, we collected larval walleye from Saginaw Bay in 2009 and 2010. Comparing distributions of these wild-caught larvae to patterns from simulations allows for elucidation of potential sources of walleye production in Saginaw Bay.

Materials and methods

Overview

We used a combination of modeling and field work to explore the interactive effects of spawning location and transport by water currents on larval walleye in Saginaw Bay. Larvae were collected for two years, and these specimens were used first to calibrate a growth model and then compared with model results to consider potential habitat sources of larvae. Our modeling strategy incorporated several methods: a hydrodynamics model, which drove a particle transport model, which in turn provided individual-level location and temperature input for an individual-based bioenergetics model. The series of models produced estimates of larval growth, dispersal, and fate in Saginaw Bay which compared favorably with patterns from field collections.

Observed field growth and distribution of larvae

We collected walleye larvae as part of general larval fish sampling in Saginaw Bay in 2009 and 2010, using a bongo sampler and a neuston net. The bongo sampler consisted of two 0.5 m diameter, ichthyoplankton nets, one with 333 μm mesh and one with 700 μm mesh, that were mounted on one frame. The neuston net frame was 2 m × 1 m, and the net mesh was 1000 μm. We conducted larval fish sampling approximately weekly from mid-April through early-July each year at sites described by Pothoven et al. (in this issue-a); sites used in our analyses were all located in the inner bay. Both nets were towed individually at approximately 2.5 knots for 5 min behind the research vessel. At each site, we towed the bongo sampler for two replicates; one just below the surface and one obliquely from near the bottom to the surface. For the oblique tow, we began sampling at approximately 1 m above the bottom and gradually decreased the tow depth during the tow to collect an integrated sample of the water column. Upon collection, all samples were preserved separately in 95% ethanol.

In the laboratory, we identified larvae using a dissecting microscope (Olympus SZ2-1 LST, 20× magnification) with a mounted Micrometrics camera and keys in Auer (1982), and measured total lengths (to 0.01 mm) with ImageJ open-source image analysis software. To estimate the age of larvae, we removed otoliths from each individual under a dissecting microscope and adhered otoliths to a slide with Crystalbond epoxy. Using a compound microscope (Leica DM1000, 40× magnification), we counted daily growth increments and estimated individual ages (in days) and hatch dates by assuming growth increments first appeared two days post-hatch. Timing of initial daily growth ring deposition is variable across species (Geffen, 1992), and so we assumed walleye would be similar to our estimates using yellow perch (i.e., initial daily growth ring deposition approximately 2 days post-hatch: C. Roswell, unpublished data). Growth increments were counted by at least two observers and the mean number of increments was used for calculations.

Hydrodynamics and particle transport models

We modeled the hydrodynamics of inner Saginaw Bay (and a portion of the outer bay) using the Environmental Fluid Dynamics Code (EFDC) (Hamrick, 1996). EFDC is an orthogonal, curvilinear grid, hydrodynamic model that provides solutions for salinity, temperature, and conservative tracers. We simulated water surface elevation, circulation, mass transport, and temperature in three dimensions using EFDC on a two by two kilometer computational grid (747 horizontal cells). Vertical layers were one meter of depth and the number varied up to a maximum of ten layers (at low water datum for Lake Huron)