



Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Stock-specific advection of larval walleye (*Sander vitreus*) in western Lake Erie: Implications for larval growth, mixing, and stock discrimination

Michael E. Fraker^{a,*}, Eric J. Anderson^b, Cassandra J. May^a, Kuan-Yu Chen^a, Jeremiah J. Davis^c, Kristen M. DeVanna^a, Mark R. DuFour^d, Elizabeth A. Marschall^a, Christine M. Mayer^d, Jeffrey G. Miner^c, Kevin L. Pangle^e, Jeremy J. Pritt^d, Edward F. Roseman^f, Jeffrey T. Tyson^g, Yingming Zhao^{h,i}, Stuart A. Ludsin^a

^a Aquatic Ecology Laboratory, Department of Evolution, Ecology and Organismal Biology, The Ohio State University, Columbus, OH 43212, USA

^b NOAA Great Lakes Environmental Research Laboratory, Ann Arbor, MI 48108-9719, USA

^c Department of Biological Sciences, Bowling Green State University, Bowling Green, OH 43403, USA

^d Department of Biological Sciences, University of Toledo, Toledo, OH 43606, USA

^e Department of Biology, Central Michigan University, Mt. Pleasant, MI 48859, USA

^f USGS Great Lakes Science Center, Ann Arbor, MI 48105, USA

^g Ohio Department of Natural Resources—Division of Wildlife, Sandusky Fish Research Unit, Sandusky, OH 44870, USA

^h Department of Biological Sciences, University of Windsor, Windsor, ON N9B 3P4, Canada

ⁱ Aquatic Research and Development Section, Ontario Ministry of Natural Resources, Wheatley, ON N0P 2P0, Canada

ARTICLE INFO

Article history:

Received 25 July 2014

Accepted 29 March 2015

Available online xxxx

Communicated by: Dr. Ram Yerubandi

Index words:

Connectivity

Ecosystem-based fisheries management

ICPBM

Physical–biological model

Portfolio effect

Stock structure

ABSTRACT

Physical processes can generate spatiotemporal heterogeneity in habitat quality for fish and also influence the overlap of pre-recruit individuals (e.g., larvae) with high-quality habitat through hydrodynamic advection. In turn, individuals from different stocks that are produced in different spawning locations or at different times may experience dissimilar habitat conditions, which can underlie within- and among-stock variability in larval growth and survival. While such physically-mediated variation has been shown to be important in driving intra- and inter-annual patterns in recruitment in marine ecosystems, its role in governing larval advection, growth, survival, and recruitment has received less attention in large lake ecosystems such as the Laurentian Great Lakes. Herein, we used a hydrodynamic model linked to a larval walleye (*Sander vitreus*) individual-based model to explore how the timing and location of larval walleye emergence from several spawning sites in western Lake Erie (Maumee, Sandusky, and Detroit rivers; Ohio reef complex) can influence advection pathways and mixing among these local spawning populations (stocks), and how spatiotemporal variation in thermal habitat can influence stock-specific larval growth. While basin-wide advection patterns were fairly similar during 2011 and 2012, smaller scale advection patterns and the degree of stock mixing varied both within and between years. Additionally, differences in larval growth were evident among stocks and among cohorts within stocks which were attributed to spatiotemporal differences in water temperature. Using these findings, we discuss the value of linked physical–biological models for understanding the recruitment process and addressing fisheries management problems in the world's Great Lakes.

© 2015 International Association for Great Lakes Research. Published by Elsevier B.V. All rights reserved.

Introduction

Physical processes can strongly influence the growth, development, and recruitment of larval fish through a variety of direct and indirect pathways (Houde, 1987, 1989, 2008, 2009; Ludsin et al., 2014). Multiple physical processes, including heating and cooling, precipitation-driven river discharge, and wind-driven water circulation and upwelling, can generate spatial and temporal heterogeneity in habitat quality through effects on the thermal environment, planktonic prey availability, and predation risk (Houde, 1989; Grimes and Kingsford, 1996; Myers,

1997; Steinhart et al., 2005; Allain et al., 2007; Reichert et al., 2010). Concurrently, the initial dispersal of pelagic larvae of many species has been shown to be strongly influenced by hydrodynamic advection (James et al., 2002; Hilborn et al., 2003; Hook et al., 2006; Beletsky et al., 2007; Pineda et al., 2007; Cowen and Sponaugle, 2009; North et al., 2009; Zhao et al., 2009). Thus, whether and for how long larvae respectively encounter and occupy high-quality habitat depend on the interplay of multiple physical processes (Roseman et al., 2005; Beletsky et al., 2007; Zhao et al., 2009; Doyle and Mier, 2012). Because even small differences in larval growth and survival rates can propagate into large differences in year-class strength (Houde, 1987, 1989), ability to identify recurring patterns in physical processes and how they impact larval growth and survival by affecting the overlap between larvae and

* Corresponding author. Tel.: +1 614 292 1613.

E-mail address: fraker.24@osu.edu (M.E. Fraker).

high-quality habitat should improve our understanding of intra- and inter-annual recruitment variations (Cushing, 1990; Durant et al., 2007).

Individual-based, coupled physical–biological models (ICPBMs) offer a useful approach to studying the biophysical drivers of larval fish recruitment (Miller, 2007; Werner et al., 2007; North et al., 2009; Hinrichsen et al., 2011). Such ICPBMs typically consist of a hydrodynamic model that simulates the physical conditions of the aquatic environment (e.g., water circulation, temperature). These conditions, in turn, serve as inputs into a lower food web model and (or) an individual-based model (IBM) of fish larvae. The lower food web model can take many forms, from a simple statistical model to a complex mechanistic model (North et al., 2009) that describe physicochemical conditions of the environment (e.g., nutrient concentrations, water clarity), as well as the distribution and abundance of planktonic and benthic organisms, some of which act as prey for the larval fish. The larval fish IBM often describes larval foraging, development, growth, and survival, the rates of which are influenced by state- (or stage-) dependent processes such as starvation and predation (Miller, 2007). Because individual larvae are unlikely to experience precisely the same environment, studying larvae as populations of discrete individuals, rather than as a mean, can be more informative (i.e., variation within a population and differences among traits of survivors relative to the rest of the individuals can be important and informative; DeAngelis and Gross, 1992; Grimm and Railsback, 2005; Miller, 2007).

Given that many processes simultaneously operate to influence habitat conditions important to larvae, one should expect to find that many of these processes have only small and (or) conflicting effects on recruitment, which may lead to emergent or interactive effects. By using empirically-based model parameters (e.g., field- or laboratory-collected environmental data) or hypothetical conditions (e.g., estimates of future habitat conditions) to simulate the integrative effects of these multiple biophysical drivers, ICPBMs can be used to identify their collective role in driving recruitment variation or in a hypothesis-testing framework to assess the importance of individual drivers of the recruitment process (Miller, 2007). Through such modeling, one can address questions such as: How consistent are patterns in larval dispersal/advection from particular spawning locations across the production season and across years? Which stocks are mixing as larvae, when are they mixing within a season, and how consistent are mixing patterns both within and across years? Do repeated spatiotemporal patterns in relevant physical processes exist? Do particular areas have consistently lower or higher habitat quality for larvae, and at what temporal or spatial scale do these patterns occur? Answering these questions is likely to be informative to several issues in fisheries ecology, including understanding recruitment variation and identifying stock structure.

In marine ecosystems, ICPBMs have successfully been used for several decades to help understand the role of biophysical processes in larval fish transport, growth, development, mortality, and recruitment (Werner et al., 2007; Miller, 2007; Cowen and Sponaugle, 2009). However, while many economically and ecologically important species in large freshwater lakes have similar life-history characteristics (e.g., a long, pelagic larval stage, Ludsin et al., 2014; Pritt et al., 2014) and are likely influenced by similar biophysical processes (e.g., large- and small-scale currents, seasonal warming, upwelling, river discharge rates; see review by Ludsin et al., 2014), ICPBMs have been used much less frequently. From their use of an ICPBM in Lake Michigan, Beletsky et al. (2007) found that large-scale circulation patterns may advect yellow perch (*Perca flavescens*) larvae away from their southwestern spawning and nursery areas to potential settlement areas throughout Lake Michigan. Zhao et al. (2009) and Smith and Zhao (2011) used an ICPBM to simulate walleye (*Sander vitreus*) transport in western Lake Erie, finding that pelagic larvae could be advected by lake currents into and out of regions of high food (zooplankton) availability, which in turn may have influenced walleye recruitment variation. Sesterhenn

et al. (2014) similarly used an ICPBM to study transport and growth of walleye larvae in Saginaw Bay. Although a larger number of models of lake and plankton dynamics have been developed (e.g., Leon et al., 2005; Bruce et al., 2006; Leon et al., 2011; Michalak et al., 2013), the above examples are the only ones of which we are aware that have used an ICPBM to address fish recruitment in a large lake ecosystem.

Using walleye produced in Lake Erie's western basin as our focal population, we illustrate how ICPBMs can be used to address recruitment questions in large lake ecosystems such as the Laurentian Great Lakes. Specifically, we explore how larval advection can interact with heterogeneity in habitat quality to influence variation in growth rate among larvae produced at four major spawning locations within the western basin: Maumee, Sandusky, and Detroit rivers and the Ohio reef complex (Fig. 1). Toward this end, we use a physical model to investigate the consistency of advection patterns within and between years (2011–2012), including how much mixing occurs among local spawning populations (i.e., stocks). Afterwards, we use output from the physical model as input into a larval walleye IBM to quantify how larval advection and spatiotemporal heterogeneity in thermal habitat interact to drive growth rate variation during the first month of larval life within and among cohorts produced by these four western basin stocks. A focus on growth during the larval stage is justified as walleye recruitment to the fishery at age-2 is set during the larval or early juvenile stage (Ludsin, 2000; Walleye Task Group, 2013) with research from both marine and freshwater ecosystems demonstrating that rapid developmental and larval growth rates can benefit recruitment by reducing the risk of mortality to both abiotic (e.g., storms) and biotic (e.g., predation, starvation) factors (Houde, 1987, 1989, 2008, 2009; Miller et al., 1988; Bailey and Houde, 1989; Rice et al., 1993; Ludsin and Devries, 1997). We hypothesized that the degree of mixing among stocks during the larval stage would vary considerably within and between years because wind is a major driver of water circulation patterns in the Lake Erie (Beletsky et al., 2013; Ludsin et al., 2014), and that this variable mixing would lead to intra- and inter-annual variations in stock-specific larval growth trajectories.

Methods

Study system and species

Lake Erie (USA–Canada) is a part of the Laurentian Great Lakes ecosystem, and is warmer, shallower (mean depth of the western basin = 7.4 m, mean depth of entire lake = 19 m), and is more productive than the other Great Lakes (Fuller et al., 1995). Large-scale water circulation patterns in western Lake Erie are driven by both wind forcing and inflows from the Detroit and Maumee Rivers (Beletsky et al., 2013). In turn, water circulation and inputs of sediments, nutrients, and water from these rivers can drive spatiotemporal variability in habitat features important to larval walleye residing in the western basin during the spring, including temperature, zooplankton prey availability, and water transparency (Frost and Culver, 2001; Jones et al., 2003; Roseman et al., 2005). Most prominently, the inputs of warm water, sediments, and nutrients from the Maumee River, which drains into the western basin along its southern shore (Fig. 1), can be a particularly important driver of habitat quality during the spring through formation of a warm, productive, and turbid river plume (Reichert et al., 2010; Ludsin et al., 2010) that has been hypothesized to benefit recruitment of larval walleye to the juvenile stage (Roseman et al., 2005; Ludsin et al., 2010).

Lake Erie's walleye population is both ecologically and economically important. In addition to being Lake Erie's most abundant native top predator, walleye support Lake Erie's largest recreational fishery and second largest commercial fishery (Hatch et al., 1987; Walleye Task Group, 2013). Lake Erie's walleye population historically has exhibited wide fluctuations in size, which has been largely driven by inter-annual variability in recruitment of individuals through the egg and

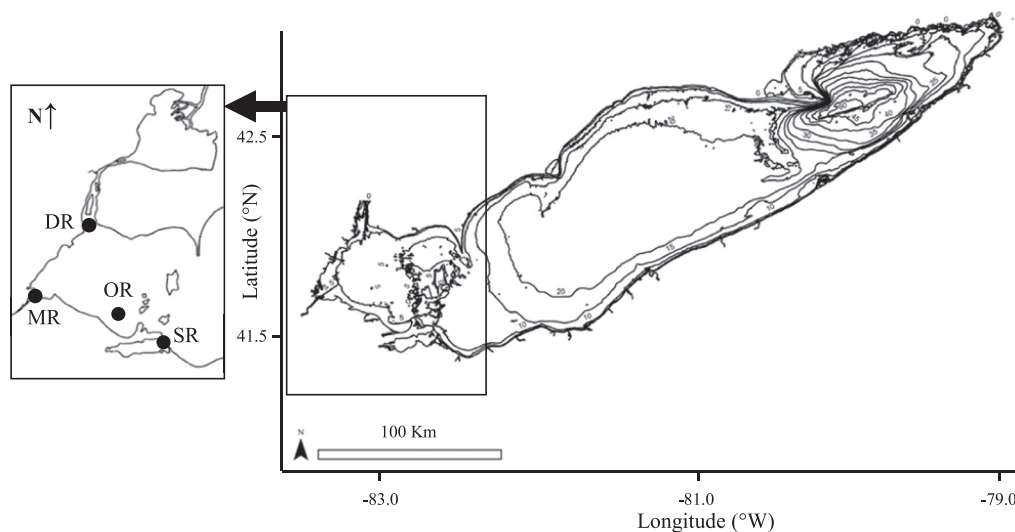


Fig. 1. Map of Lake Erie with an inset of western Lake Erie. Bathymetric contour lines are at 5 m intervals. Relevant walleye spawning sites (release sites in model) are marked on the inset (Detroit River, DR; Maumee River, MR; Ohio reef complex, OR; and Sandusky River and Bay, SR) with filled circles.

larval stage (Busch et al., 1975; Mion et al., 1998; Roseman et al., 2005). Since 2003, however, recruitment has predominantly been below average for reasons that remain unknown, thus leading to a reduction in lakewide population size (Walleye Task Group, 2013).

The western basin supports Lake Erie's largest spawning populations, with larval production emanating from both riverine (Maumee, Sandusky, and Detroit) and open-lake reef populations (e.g., Ohio reef complex; Fig. 1). All western basin stocks spawn during early spring (Goodyear et al., 1982) although the timing and duration of spawning typically vary among both stocks and years (Mion et al., 1998; Roseman et al., 2005). Walleye hatch at 6–8 mm in total length (TL, Roseman 1997), have weak swimming abilities until ~21 mm TL (Humphrey et al., 2012), and spend ~20–30 d as pelagic larvae that feed on zooplankton before becoming demersal as juveniles at ~30 mm TL (McElman and Balon, 1979; Gopalan et al., 1998).

Many gaps exist in our understanding of the larval walleye recruitment environment, as well as the degree to which stocks mix. Previous field and modeling studies have suggested that the southern, nearshore area of the western basin, which typically receives outflows from the Maumee River, tends to act as high-quality nursery habitat for walleye larvae (Jones et al., 2003; Roseman et al., 2005) and that offshore advection of larvae away from this area has negative consequences for year-class strength (Zhao et al., 2009). However, because no previous study has quantified larval walleye habitat and growth in offshore regions of western Lake Erie (e.g., in non-US waters), their potential as nursery habitat remains highly speculative. Similarly, while previous investigations have suggested that walleye stocks in western Lake Erie are mixed at both the juvenile (Hedges, 2002; Bartnik, 2005) and adult (Bigrigg, 2006) life stages and exhibit a complicated population structure (e.g., Merker and Woodruff, 1996; Gatt et al., 2003; Strange and Stepien, 2007; Haponski and Stepien, 2014), we do not have a full understanding of the degree of mixing among stocks during any life stage.

Study years

Similar to all other year-classes produced during 2004–2013, weak walleye year-classes were produced during our focal years of study, 2011 and 2012 (Walleye Task Group, 2013). Despite these similar levels of recruitment between years, several key physical drivers differed between our study years that might have caused different habitat conditions for larval walleye. For example, precipitation was higher during spring 2011 (March–June total precipitation at Toledo Express Airport: 0.42 m) than 2012 (March–June total precipitation at Toledo Express

Airport: 0.28 m), which led to higher mean monthly discharges from the Maumee River during March through June larval walleye production period (Table 1). By contrast, air temperatures were higher during March through May in 2012 than 2011, although air temperatures became similar by June (Table 1).

General description of the model and data inputs

Many information gaps exist in our understanding of Lake Erie walleye, which caused us to both make (and also avoid) many simplifying assumptions in the ICPBM that we developed to explore stock-specific larval dispersal and growth. For example, similar to nearly all other freshwater fishes and most marine fishes (Leis, 2007; Willis, 2011), little is known about larval walleye movement behavior, including what factors drive movement decision-making and how movement decisions are made. Correspondingly, we strictly modeled walleye as passive particles in this study, which also seems justified given that previous larval walleye research has not demonstrated behavioral competency for the sizes of larvae explored herein (Houde, 1969; Humphrey et al., 2012). Similarly, our understanding of how biological components of habitat quality such as zooplankton prey availability, potential competitors for prey, and predation risk vary spatially and temporally across western Lake Erie during the larval production period is scant. In the absence of this information, we ignored the potential for inter- and intra-

Table 1

Monthly means for several meteorological and physical variables during 2011 and 2012 measured at Toledo Express Airport, OH (meteorology) and Waterville, OH (discharge). Meteorological data were provided by from National Climatic Data Center (ncdc.noaa.gov), whereas Maumee River discharge data came from the United States Geological Survey (waterdata.usgs.gov).

	Air temperature (°C)	Wind direction (° past N)	Wind speed (m/s)	Cloud cover (%)	Maumee River discharge (m ³ /s)
2011					
March	2.3	0	3.9	37	599
April	8.9	250	5.0	49	467
May	16.2	40	3.3	63	685
June	21.6	260	3.3	74	144
2012					
March	10.5	230	4.1	51	270
April	9.7	320	3.9	50	42
May	18.3	0	3.0	66	53
June	21.7	260	3.2	73	15

specific interactions, and assumed zooplankton prey availability to be both constant and homogeneous during the larval stage. As a result of this suite of assumptions about larval behavior and biological processes, our resulting ICPBM essentially describes larval walleye dispersal and growth primarily as a function water currents and temperature, two physical factors that have been shown to drive larval dispersal and growth for other marine and Great Lakes fishes (North et al., 2009) and that we feel confident in our ability to depict with our physical model (see below).

Hydrodynamic modeling and field data input

Model simulations were carried out with hydrodynamic conditions (currents, temperature, etc.) provided by the NOAA Great Lakes Coastal Forecasting System (GLCFS; Schwab and Bedford, 1994). The GLCFS is based on the Princeton Ocean Model (Blumberg and Mellor, 1987), which solves the hydrostatic, three-dimensional (3-d) primitive equations in a 2nd order finite difference framework. The GLCFS is operated in a real-time nowcast/forecast framework, with hourly output made available on a 2-km structured grid for Lake Erie (21 vertical sigma layers). Horizontal diffusion in the GLCFS is prescribed by the Smagorinsky parameterization and vertical diffusion is governed by the Mellor–Yamada level 2.5 turbulence closure scheme. Forcing conditions for the hydrodynamic model are prescribed using a natural-neighbor interpolation from land- and buoy-based observations, which have yielded a successful prediction of water levels, temperatures, and currents in the lake (Schwab and Bedford, 1994; Beletsky and Schwab, 2001; Chu et al., 2011). While discrepancies between observed temperatures and model output tend to be most pronounced during the spring warmup period (e.g., Beletsky et al., 2013), our model reasonably approximated observed mean west basin (west of -82.5°N) surface temperatures during the spring period (compared to GLSEA data in Electronic Supplementary Material (ESM) Figs. S1a and b and Fig. S2; but see also comparison to NDBC Buoy 45005 data in ESM Fig. S3). Also, although recent work has shown that the interpolated meteorology can cause errors in the summer circulation in the central basin (Beletsky et al., 2013), our study focuses on spring transport (April–May) in the western basin, in which wind-field-induced errors are presumed to be reduced due to the influence of hydraulically-driven flow and the density of meteorological stations surrounding the western basin.

Hydrodynamic output from the GLCFS was used to drive a Lagrangian particle transport model to simulate the trajectories of larval walleye in western Lake Erie. The particle model used a 2nd-order Lagrangian scheme (Bennett and Clites, 1987) to simulate passive, neutrally buoyant particle movement in three dimensions. The Smagorinsky parameterization was used for horizontal diffusion (coefficient of 0.005), based on previous calibrations (Michalak et al., 2013), and a random-walk approach was used for vertical diffusion ($0.0005\text{ m}^2/\text{s}$).

We tracked the advection and growth of weekly cohorts of walleye larvae during the entire spawning season of 2011 and 2012. Because we were primarily interested in exploring intra- and inter-annual variabilities in stock mixing and its impact on stock-specific growth (not stock-specific survival through the larval stage), we did not model observed densities of larvae. Instead, we tracked the advection and growth performance of weekly cohorts of larvae, with each cohort consisting of 5000 individuals (represented by a group of 5000 particles in the model). Each set of larvae was seeded at 1 of 4 known larval walleye production locations (Maumee River mouth: 41.68° , -83.49° ; Detroit River mouth: 42.02° , -83.16° ; midpoint of the Ohio reef complex: 41.63° , -83.02° ; Sandusky Bay mouth: 41.48° , -82.72° ; Fig. 1). Although walleye larvae from the Sandusky River were collected in the river proper, particles in our model were released at the point at which the Sandusky Bay opens into Lake Erie because Sandusky Bay is not included in the GLCFS model domain. All particles in the model were released at 4 m of depth, spread over a 5 m radius.

The release date of each weekly cohort was determined from field observations of walleye larvae (Detroit, Maumee, and Sandusky rivers) or eggs (Ohio reef complex), using a temperature-dependent development function to determine larval emergence, based on McElman and Balon (1979). During 2011, walleye eggs were observed on the Ohio reef complex during 30 April–14 May (3 weekly cohorts modeled), and larvae were observed in the Sandusky River during 26 April–17 May (4 weekly cohorts modeled), in the Maumee River during 26 April–31 May (6 weekly cohorts modeled), and in the Detroit River during 26 April–24 May (5 weekly cohorts modeled). During 2012, the spawning season began earlier with eggs being observed on the Ohio reef complex during 13 April–11 May (5 weekly cohorts modeled), and larvae collected in the Sandusky River during 4–26 April (4 weekly cohorts modeled), in the Maumee River during 21 March–2 May (7 weekly cohorts modeled), and in the Detroit River during 11 April–16 May (6 weekly cohorts modeled). Because the number of weekly cohorts observed at a spawning location varied among sites and between years, the total number of larvae modeled for a site in any given year also varied (i.e., 5000 larvae per weekly cohort was modeled).

Simulations were performed forward in time for 30 d, starting at the time of release from the four spawning sites. The location of each particle (larva) and the temperature in each cell were recorded at 3 h intervals. The current uncertainties and variability were accounted for by the calibrated diffusion coefficients/schemes, as described above, and the resultant particle patch.

Individual-based model (IBM) of walleye larvae

The IBM was constructed from previously published models (Madon and Culver, 1993; Hanson, 1997; Johnston, 1999) with a large majority of model parameters being experimentally derived using walleye. The IBM can be broken into foraging, growth, and survival subcomponents. The mass-specific larval walleye foraging rate (F ; $\mu\text{g zooplankton/g larval mass/d}$), which was derived by Madon and Culver (1993) from controlled hatchery pond experiments, was a function of available zooplankton biomass, water temperature, and individual larval walleye mass. Larvae were assumed to be free foraging from hatch (i.e., we assumed that no energy was available from a yolk sac). A bioenergetics model developed specifically for larval walleye (Madon and Culver, 1993; Johnston, 1999) was used to convert energy intake (zooplankton consumption) into daily growth (G , $\mu\text{g/g/d}$), while also accounting for daily energetic losses due to respiration (R , $\mu\text{g/g/day}$), specific dynamic action (SDA, unitless; i.e., costs of digestion), egestion (E , unitless), and excretion (U , unitless), using the following equation:

$$G = (F - F \cdot E) - R - (F - F \cdot E) \cdot (SDA - U). \quad (1)$$

Specific dynamics action was modeled as a constant proportion of assimilated energy, E and U were modeled as functions of water temperature, and R was modeled as a function of water temperature and larval walleye mass (Hanson, 1997). The mean temperature experienced by each individual during each day (8 measurements) and its foraging success were used to determine the individual's growth for that day based on Eq. (1) above and modeled environmental conditions. Because of the trends in the physical model to overestimate (2011) and underestimate (2012) surface water temperature compared to observed temperatures at NDBC Buoy 45005 (ESM Figs. S3 a and b), we also ran the IBM using the Buoy 45005 temperatures (http://www.ndbc.noaa.gov/station_page.php?station=45005) for both years, assuming a homogeneous temperature across the lake. This allowed us to compare variation in larval growth between years in order to determine how much any differences in modeled growth may be due to the physical model versus variation in physical conditions. As spatiotemporal heterogeneity in warming may occur in the lake, this is a somewhat limited comparison; however, the Buoy 45005 data are the

most complete available observations for the time and area of interest. Additionally, because the other potential observed data (GLSEA satellite data) are more similar to the simulated temperatures of our physical model (ESM Fig. S2), comparison to the Buoy 45005 data gives a better sense of the potential interannual variation in simulated larval growth based on the source of temperature data. All larvae/particles were assumed to have an initial wet mass of 3.8 mg and an initial total length of 7.8 mm (McDermott and Rose, 2000). Zooplankton biomass (equal proportions of copepods and cladocerans) was assumed to be homogeneous and constant at a level of 0.5 mg/L. The model also was run with a zooplankton biomass of 0.2 mg/L to begin to test sensitivity. Zooplankton biomass levels were chosen to fall within ranges observed in the western basin of Lake Erie during May 2000–2013 (R. D. Briland, The Ohio State University, 2014, personal communication; Frost and Culver, 2001). In the western basin, particularly in recent years, zooplankton biomass may be lower when the earliest walleye cohorts enter the lake (i.e., during April; CJM, personal data) and also is likely to be spatially heterogeneous due to various biological and physical processes. The IBM was built and run in Matlab 2012b (The Mathworks, Inc., 2012).

Analyses

Because our modeled particles (i.e., larvae) tended to be found near the water surface in the hydrodynamic/Lagrangian trajectory model (>95% within the upper 3 sigma levels; EJA and MEF, unpublished data), we focused on the two horizontal dimensions. In addition to visualizing the advection pathways of individuals and weekly cohorts, we used a variety of summary statistics to describe advection and growth patterns. First, we calculated the weighted mean center of each stock's advection pathway, which gives a sense of the concentration and spread of larvae over time due to passive drift. To do so, we combined cohorts from each stock within a year, irrespective of release day, and plotted the advection pathways of all individuals from each weekly cohort together. We then calculated the location of the center of the population by weighting the density of larvae after 15 d and 30 d of advection. Second, to identify the degree and location of stock mixing, we calculated mixing proportions among stocks over time based on grid-cell co-occupancy. Mixing was calculated only while larvae were in the system (i.e., weekly cohorts were not combined as was done above to calculate the weighted mean center). Third, from the larval growth data, we used a simple linear regression to test for relationships between release day and total predicted growth. Analyses were performed in Minitab 16 (Minitab, Inc. 2013) and Matlab 2012b (The Mathworks, Inc. 2012).

Results

Larval advection patterns

While advection patterns and stock mixing varied within and between years, some patterns also emerged. First, the combined advection pathways of each larvae from each stock show that the full-season, basin-scale advection patterns were strikingly similar during both 2011 and 2012 (Fig. 2; also see ESM Video S1 and S2 for movies of the advection patterns of the peak weekly cohorts from each stock). Most larvae produced on the Ohio reef complex remained near the reefs, with some being advected to the west, to the north, or southeast into the central basin (especially in 2012; Figs. 2 and 3A; see ESM Figs. S4 and S5 for advection patterns of all weekly cohorts). The weighted mean center of this stock moved only slightly eastward between day 15 and day 30 during 2011 (<5 km) with a much stronger eastward movement during 2012 (~25 km; Figs. 2 and 3). Most Maumee River larvae cohorts were advected north in both 2011 and 2012, with some weekly cohorts being advected to the east, along the southern shoreline in 2012 (Fig. 2; also see middle panels in ESM Figs. S4 and S5). The weighted mean center of this stock moved only slightly northeast

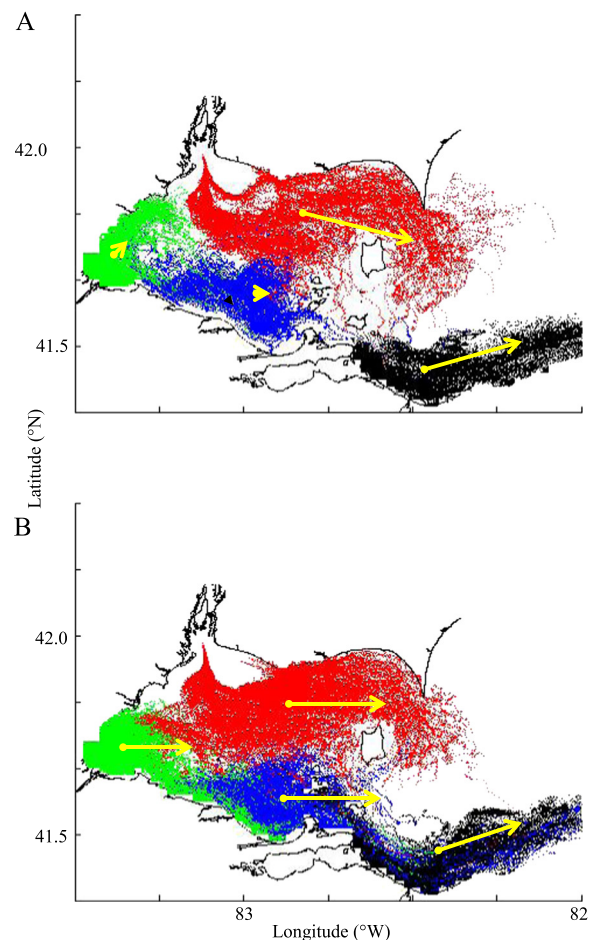


Fig. 2. The combined advection patterns of simulated walleye larvae (all weekly cohorts for each stock) in western Lake Erie during 2011 (A) and 2012 (B). Each point marks the daily location of each larva released from each stock (Detroit River, red; Maumee River, green; Ohio reef complex, blue; and Sandusky River, black). The beginning and end of each yellow arrow show the weighted population centers for each stock after 15 d and 30 d, respectively (all weekly cohorts combined). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

between day 15 and day 30 during 2011 (<5 km) and strongly east during 2012 (~15 km; Fig. 2). Detroit River larvae were advected south before spreading to the east and north, many toward and through the Pelee Passage into the central basin (Figs. 2 and 3; ESM Video S1 and S2 and ESM Figs. S4 and S5). The weighted mean center of this stock moved southeast in 2011 (~30 km) and due east in 2012 (~25 km; Fig. 2). Sandusky River larvae were largely advected east toward the central basin, although some also drifted north toward the Ohio reef complex, especially in 2012 (Figs. 2 and 3D). The weighted mean center of this stock moved northeast between day 15 and day 30 during both 2011 (~25 km) and 2012 (~20 km; Fig. 2).

The Detroit River and Ohio reef complex stocks generally had the greatest spatial coverage at any particular time (Figs. 4A and B) and over the full season (Fig. 2). In 2011, the total number of 2×2 km cells occupied by larvae at some point were 871 (Detroit River), 607 (Ohio reef complex), 275 (Sandusky River), and 237 (Maumee River). The number of cells occupied at some point increased for all spawning stocks in 2012 as compared to 2011 (Figs. 4A and B; Detroit River = 1103 cells; Ohio reef complex = 969 cells; Maumee River = 562 cells; and Sandusky River = 475 cells).

Mixing among stocks showed both similarities and differences between years. When stock mixing was defined as at least one larva from at least two different stocks being present in the same 2×2 km cell at the same time, substantially higher mixing for a longer duration

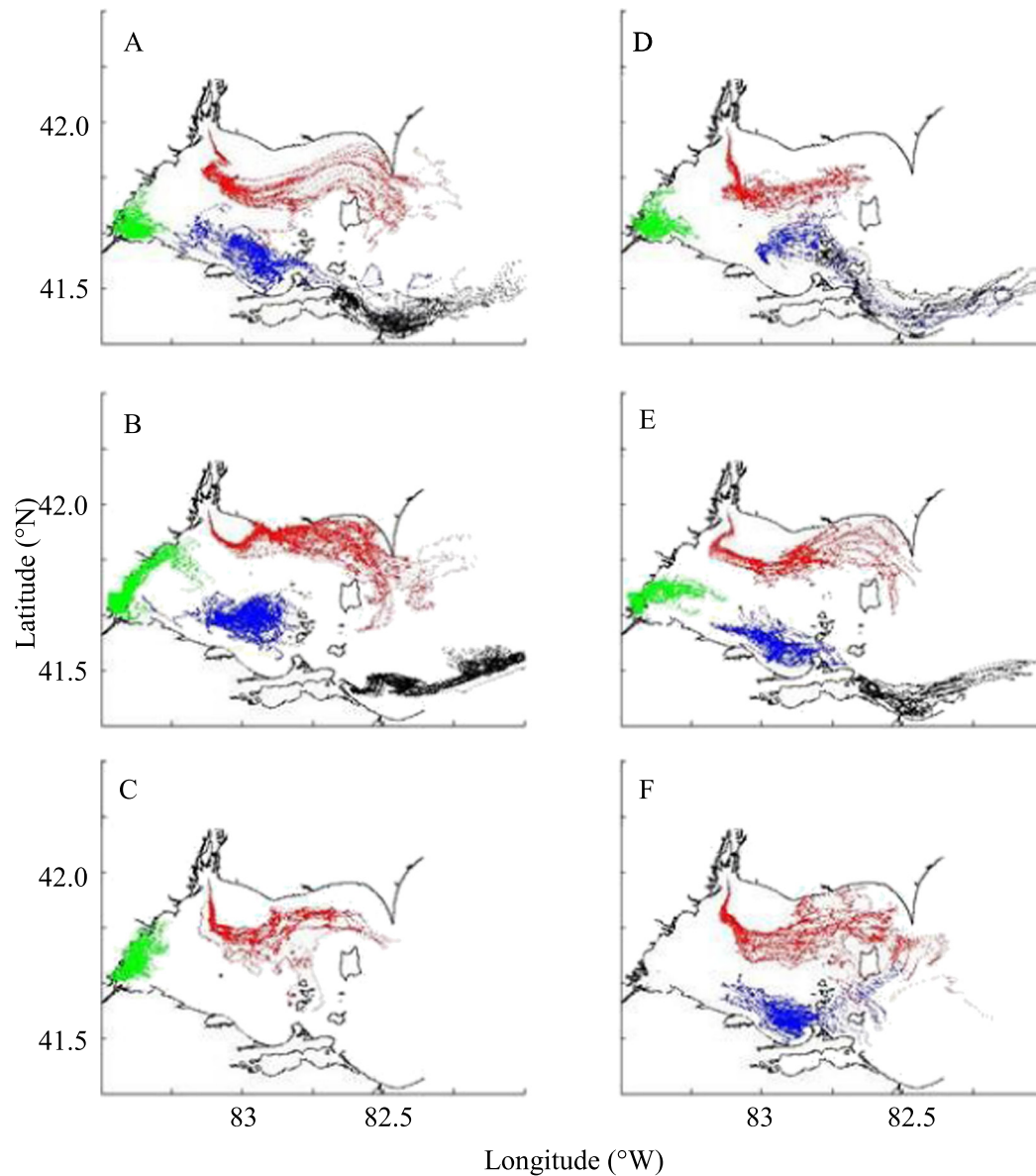


Fig. 3. Advection patterns of weekly cohorts of walleye larvae from four western Lake Erie spawning locations (Detroit River, red; Maumee River, green; Ohio reef complex, blue; and Sandusky River, black) during 26 April (A), 9 May (B), 24 May (C) 2011 and 11 April (D), 25 April (E), and 10 May (F) 2012. These weeks represent early, middle, and late cohorts, respectively, for each year. Note that not all stocks had larvae released during each week. In each panel, 5000 larvae were released from each spawning location. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

occurred in 2012 than during 2011 (Fig. 4C). Additionally, mixing was more spatially widespread in 2012 than in 2011 (Fig. 5). Substantial mixing of Ohio reef complex and Maumee River larvae occurred during both years in cells located in the westernmost part of the west basin (in Ohio waters near the Maumee River; green circles in Fig. 5), whereas mixing of Ohio reef complex and Detroit River larvae was most prevalent in offshore waters west of the islands (red circles in Fig. 5). Likewise, substantial mixing of Ohio reef complex and Sandusky River larvae was predicted to occur along the southern shore of the central basin located east of Sandusky Bay (black circles in Fig. 5). Despite these commonalities, inter-annual variation in stock mixing occurred. For example, Ohio reef complex and Detroit River larvae mixing occurred farther north (nearer to the northern shoreline) in 2012 than in 2011, whereas mixing of Maumee River and Detroit River larvae occurred over most of the southern shoreline (including the entire western basin and western part of the central basin) in 2012 but not in

2011 (blue crosses in Fig. 5). Additionally, during 2012, a small degree of mixing among Maumee, Detroit, and Sandusky River larvae was observed (primarily near and to the east of the mouth of Sandusky Bay); but during 2011, virtually none was detected (Fig. 5).

We also found that stock mixing varied within and between years and among cohorts within a year when mixing was measured as the *proportion of cells* that contained at least one individual from two or more stocks (Figs. 6A and C) and the *proportion of individuals* of a stock that were found in a cell with at least one individual from another stock (Figs. 6B and D). Mixing between stocks was generally less pronounced during 2011 (Fig. 6A) than during 2012 (Fig. 6C), although a peak of ~60% of the cells in which Maumee River larvae occurred also contained at least one Ohio reef complex larva during the 2011 simulation (day 145; see M-R in Fig. 6A) and 2012 simulation (day 125; see M-R in Fig. 6C). Variable cohort-specific advection led to this pattern, including asymmetries in stock mixing. Most notably, during 2011,

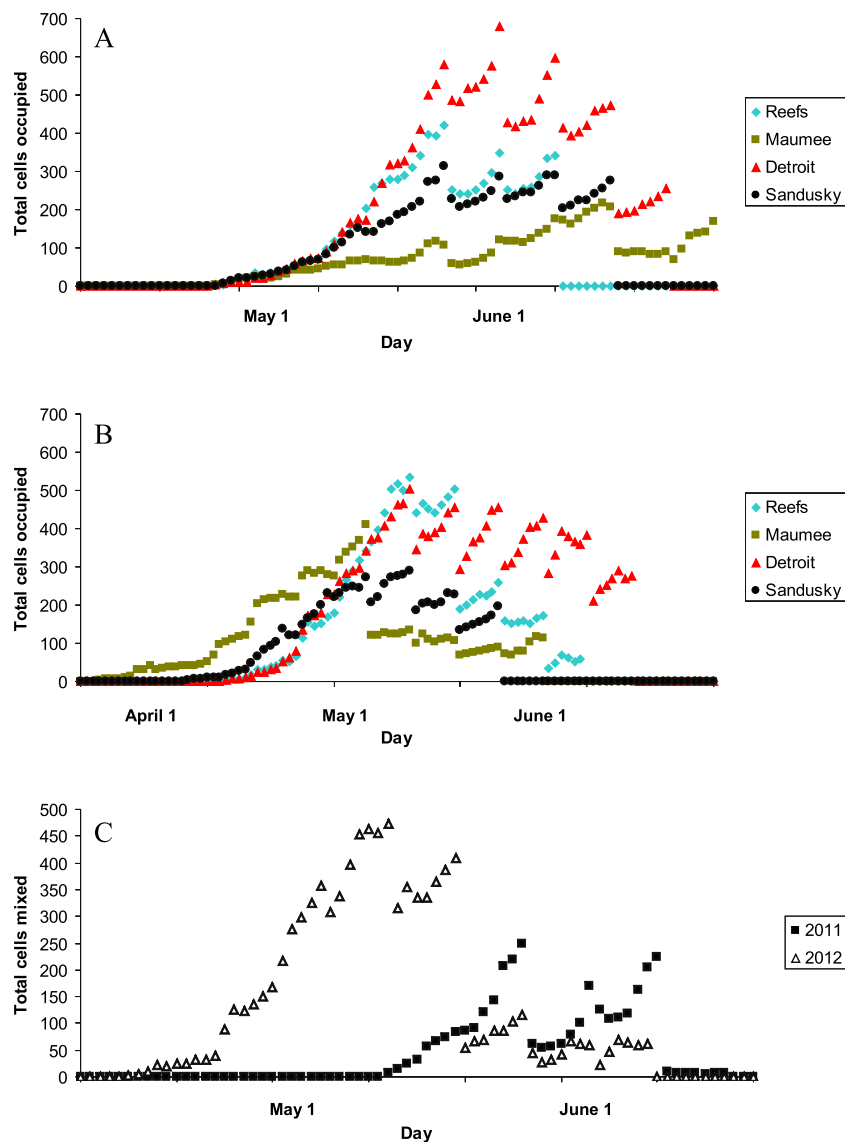


Fig. 4. The total number of 2×2 km cells in western Lake Erie that were occupied during 2011 (A) and 2012 (B) by walleye larvae from the Detroit River, Maumee River, Ohio reef complex, and Sandusky River spawning stocks. Also reported is the total number of cells co-occupied by larvae from at least two stocks during 2011 and 2012 (C).

~70% of the Sandusky larvae were predicted to co-occur with at least one Ohio reef complex larva during days 135–145 of the simulation (see S-R in Fig. 6B) whereas only 0–5% of Ohio reef complex larvae were predicted to co-occur with Sandusky River larvae during the same time period (see R-S in Fig. 6B). This result occurred due to a relatively small number of the Ohio reef larvae being advected south and east along the southern shore of the central basin at a time when Sandusky River larvae were in the system (e.g., Fig. 3A, ESM Video S1), whereas few Sandusky larvae were advected northward where the majority of the Ohio reef complex larvae remained (Figs. 2 and 3; ESM Video S1). The Maumee River and Ohio reef complex larvae provide a second example. Ohio reef complex larvae were predicted to consistently co-occur in cells with larvae from the Maumee River early in the larval production season during 2012 (days 105–125; see R-M in Fig. 6C), whereas cells with at least one Maumee River larva that also had an Ohio reef complex larvae were increasing during this same time period (see M-R in Fig. 6C). After day 125, mixing of these two stocks strongly decreased (Fig. 6C), owing to changing advection patterns (Figs. 2 and 3; ESM Video S2 and ESM Fig. S5). This pattern also is reflected in the proportion of individual larva that co-occurred with the other stock,

although the proportion of Maumee River larvae that co-occurred with Ohio reef complex was relatively low (see M-R in Fig. 6D) when compared to the proportion of shared cells (see M-R in Fig. 6C).

Inter-cohort and stock-specific differences in growth patterns

We also explored how different release dates and advection paths could influence growth patterns among cohorts and stocks, as well as how the scale of heterogeneity in habitat quality related to stock-specific patterns in growth. In terms of habitat quality, we focused on temperature at the surface (0 m depth) because larvae were concentrated there in the model, the water column was isothermal during the larval production season (MEF and EJA, unpublished data), and surface temperature can have a strong influence on larval fish bioenergetics and zooplankton (prey) productivity (Frost and Culver, 2001; Roderick and Kapoor, 2008; but see Myers, 1997).

During 2011 and 2012, our model showed that surface water in western Lake Erie warmed earlier along the southern and western shoreline relative to the rest of the shoreline, with open waters warming later (Fig. 7; ESM Video S3 and S4). Intermittent patches of

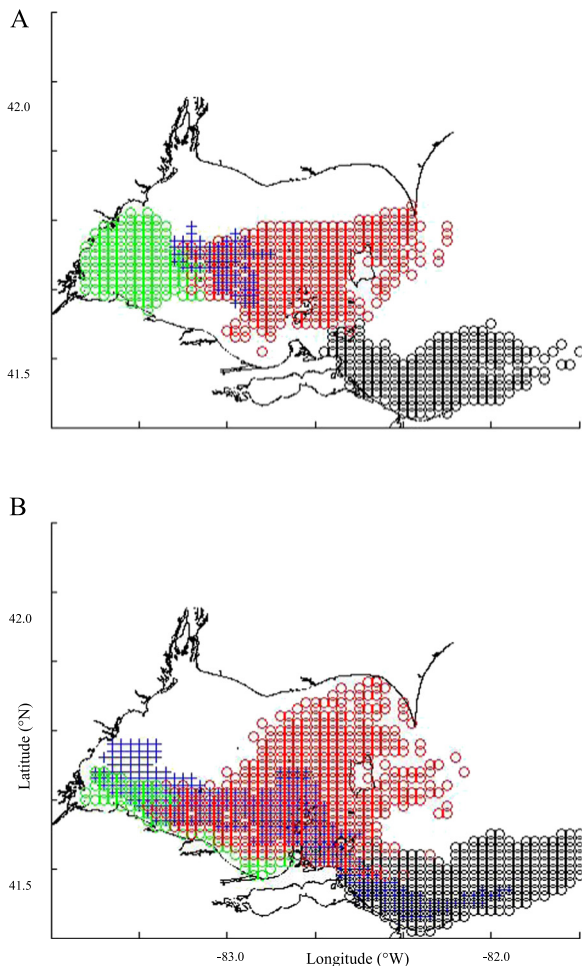


Fig. 5. Spatial distribution of mixing of walleye larvae in western Lake Erie during 2011 (A) and 2012 (B). Cells (2×2 km) in which larvae from two stocks co-occurred in space and time are denoted as follows: green circles denote mixing of Ohio reef complex and Maumee River larvae; red circles denote mixing of Ohio reef complex and Detroit River larvae; black circles denote mixing of Ohio reef complex and Sandusky River larvae; and blue crosses denote mixing of Maumee River and Detroit River larvae. Low levels of mixing between some stocks not shown to reduce clutter. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

cooler water also occurred throughout the season, which were associated with Detroit River inflow (based on their location and movement). Warming occurred earlier during 2012 than during 2011; however, by day 140 (19–20 May), temperatures were similar between years (Figs. 7 and 8). These findings are supported by basin-wide observations of surface temperature recorded by Great Lakes Surface Environmental Analysis (GLSEA) satellite imagery (ESM Fig. S1a, but see also NDBC Buoy 45005 temperature data in ESM Fig. S1b).

Inter-stock differences in the thermal regime experienced by larvae were evident. During 2011, larvae from all stocks experienced mean 30 d temperatures that were intermediate relative to the modeled minimum and maximum temperatures in the lake (Fig. 8A). The mean temperatures experienced by weekly cohorts also generally increased in a simple linear fashion with a release date. During 2012, the mean temperature experienced by larvae from different stocks and cohorts was more variable. For example, several Detroit River weekly cohorts experienced near-maximum temperatures, whereas others experienced near-minimum temperatures, with no obvious linear warming trends being evident for any stock (Fig. 8B). Likewise, the temperatures experienced by cohorts from different stocks released during the same week also varied more widely in 2012 than 2011 (compare vertical

spread in points between Figs. 8B and A, respectively). Additionally, unlike 2011, later-produced weekly cohorts of larvae did not always experience warmer temperatures than their earlier-produced counterparts during 2012 (e.g., see Detroit and Maumee River cohorts in Fig. 8B).

Within-stock differences in temperature experienced by larvae were related to advection patterns. For example, early cohorts released from the Maumee River during 2012 were advected into the early warming water near the Maumee River mouth and experienced near maximum temperatures. By contrast, and counter to our predictions (sensu Roseman et al., 2005), Maumee River cohorts produced in the middle of the larval production period experienced intermediate temperatures with increased advection toward the southern shore (Fig. 8B; ESM Fig. S5). Also, early season cohorts from the Detroit River during 2012 were advected along the northern shore of the west basin, which was warmer than the more southerly waters of the open lake that later-spawned Detroit River cohorts experienced (Fig. 8B, ESM Video S2). The earlier Sandusky River cohorts of 2012 were primarily advected eastward along the southern shoreline of the central basin, where they tended to experience warmer temperatures than the last weekly cohort (Fig. 8B), which was primarily advected away from the shore (ESM S5).

Because the prey resource environment was held constant in our model and all larvae began at the same size in our model, growth in our simulations could only vary as a function of experienced temperature. The temperature differences experienced by individuals from the various cohorts and stocks (Fig. 8) led to small differences in observed daily growth rates, which in turn, led to large differences in the biomass accumulated over the 30 d simulations. During 2011, the mean wet mass of cohorts of 30 d old larvae increased linearly with release date (linear regression, $r = 0.97$; ANOVA regression $F_{1,19} = 269.0$, $P < 0.001$; Fig. 9A), whereas during 2012, growth rates were unrelated to release date (linear regression, $r = 0.24$; ANOVA regression $F_{1,24} = 1.4$, $P = 0.252$, Fig. 9B). Biomass accrual was greater for larvae released before day 120 (29–30 April) during 2012 than during 2011, but greater for larvae released after day 120 during 2011 than during 2012 (Fig. 9). The range in the final mass at 30 d among weekly cohorts from different stocks also was substantially higher in 2011 than in 2012 (Fig. 9).

The 30 d growth trends suggest more variable growth rates among stocks and weekly cohorts observed during 2012 relative to 2011 (Fig. 10). Although early produced cohorts typically had slow growth rates during both years, nearly all of these cohorts were larger than later-produced cohorts when comparing individual mass at a particular day during 2011 (i.e., on any given day, older larvae often tended to be larger than younger larvae; Fig. 10A). This finding was less apparent in 2012 (Fig. 10B), owing to less uniformity in temperatures experienced by weekly cohorts (Fig. 8B). These findings also appear robust to zooplankton density, as lowering zooplankton density to 0.2 mg/L resulted in a proportional reduction in growth that was similar across all cohorts (i.e., the pattern was similar, but final larval sizes were reduced; ESM Figs. S6a and b).

The wider range of advection among stocks during 2012, as compared to 2011, also generated more variability in growth rates within and among weekly cohorts (Fig. 11). The ratio of the range of 30 d wet mass (maximum–minimum) to mean 30 d wet mass within weekly cohorts gives a sense of the range of habitat quality (i.e., temperature) experienced by larvae within each cohort. During 2012, the ratio tended to be more variable across the full season than during 2011 although the ratio also was high during the early part of 2011 (Fig. 11). With exception of the Detroit and Maumee River stocks in 2011, which demonstrated consistently low ratios, high variability in ratios among weekly cohorts within a stock was evident during both years (especially for the Ohio reef complex and Sandusky River larvae; Fig. 11).

When larval growth was modeled using the NDBC Buoy 45005 surface water temperatures, similar and temporally linear trends in growth occurred during 2011 and 2012, although growth was initially greater

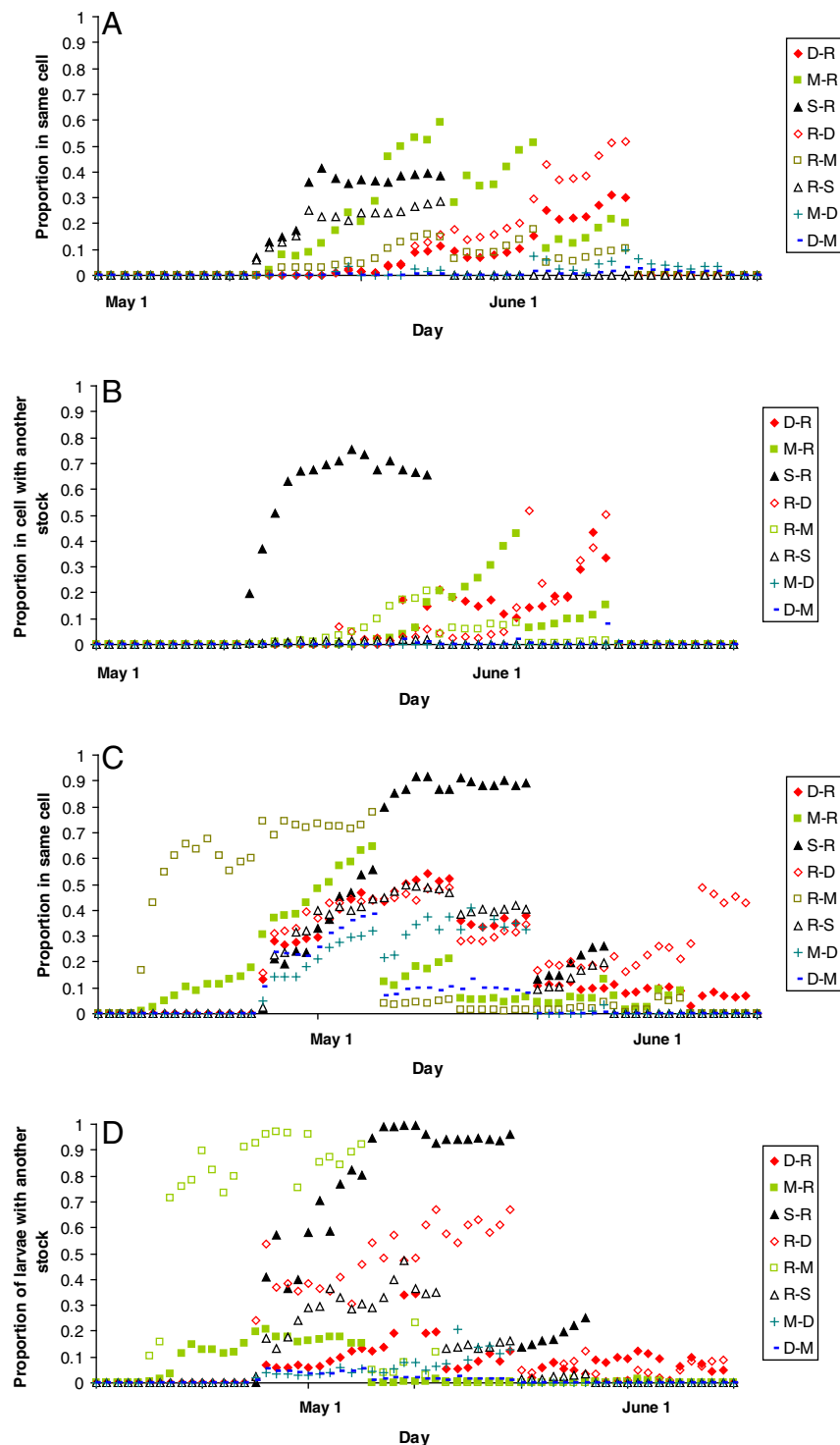


Fig. 6. The proportion of 2×2 km cells in western Lake Erie in which a walleye larva from a focal stock co-occurred with at least one larva from a different stock during 2011 (A) and 2012 (C) and the proportion of walleye larvae from a focal stock that co-occurred with at least one larva from a different stock during 2011 (B) and 2012 (D). In each legend, the focal stock is listed first (Detroit River, D; Ohio reef complex, R; Maumee River, M; Sandusky River, S).

during 2012 among the earliest larval cohorts compared to growth using the physical model's simulated temperatures (ESM Fig. S7). Larval growth tended to be lower during 2011 when using water temperatures simulated by the physical model than growth using the Buoy 45005 data. During 2012, larval growth initially tended to be greater using water temperatures simulated by the physical model than growth using the Buoy 45005 data before becoming lesser for the later cohorts.

Discussion

Our model simulations demonstrate some of the ways in which ICPBMs can be used to help begin to understand fish recruitment patterns and variability in large freshwater ecosystems, including western Lake Erie. Below, we discuss how our ICPBM has improved our understanding of stock-specific advection and growth patterns of larval walleye in western Lake Erie, as well as illustrate some of the ways

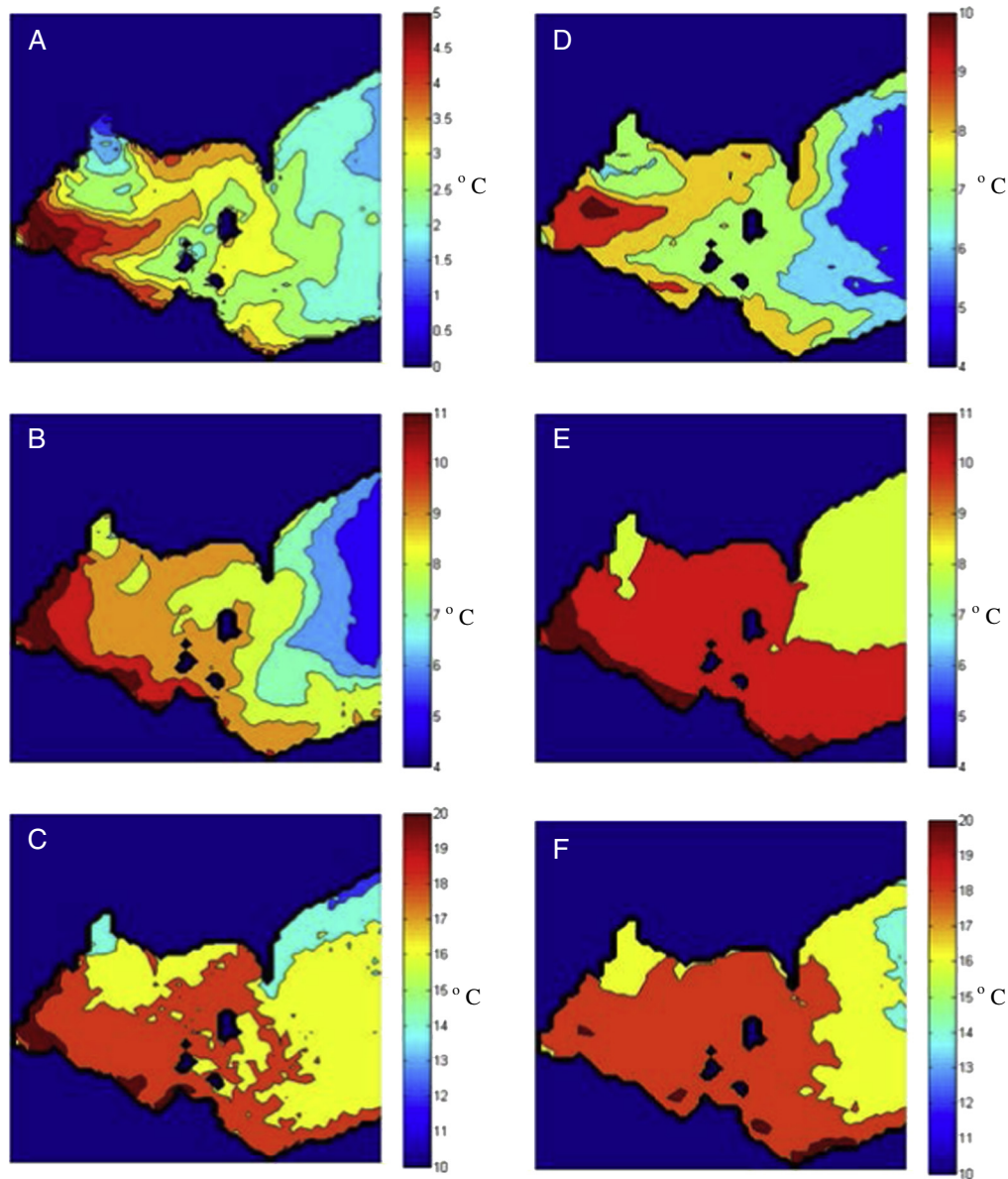


Fig. 7. Surface water temperatures in the western basin simulated during April 1 (A), May 1 (B), and June 1 (C) 2011, and during April 1 (D), May 1 (E), and June 1 (F) 2012. Please note that the range of temperatures included in each panel may differ.

in which this understanding could benefit the management of Lake Erie walleye. Afterwards, we identify some limitations to our ICPBM and point out key information gaps that could improve the use of ICPBMs for fish recruitment investigations in general. Finally, we close with a synopsis of the key benefits that ICPBMs can offer Great Lakes fisheries investigations.

Larval advection, habitat quality, and growth

Specific to Lake Erie walleye, our findings indicate that 1) advection can differ among stocks for several reasons, including the timing and location of spawning and variability in wind-driven circulation, and 2) variation in advection patterns can interact with spatiotemporal variation in water temperature to produce stock-specific and inter- and intra-cohort differences in larval growth. In turn, variable advection and warming patterns, both within and between years, hold great potential to influence recruitment to older life stages through their direct effect on larval growth (reviewed by Peck and Hufnagl, 2012). Further,

our findings suggest that different mechanisms may operate during the larval stage to cause poor walleye growth. For example, during 2011, temporal variation in water temperature interacting with timing of spawning was the primary driver of growth variation, whereas in 2012, spatial variation in water temperature interacting with larval advection patterns was more important to explaining growth patterns. In this way, the weak year-classes produced during both 2011 and 2012 (Walleye Task Group, 2013) could have resulted from very different processes operating during the larval stage. Comparison of our results with future modeling of strong year-classes (e.g., 1996, 2003; Walleye Task Group, 2013) could help identify patterns that enable strong larval growth and recruitment. The qualitative pattern of higher growth rates among later cohorts in 2011 compared to 2012 was observed in the field as well although simulated mean individual growth rates were somewhat higher than observed in southern western basin field sampling during spring (mid-April through May) of 2011 and 2012 (CJM, unpublished data; 2011: $TL = 7.74 + 0.13^*(\text{age in days})$, $P < 0.0001$, $R^2 = 0.42$, $F_{1,136} = 97.33$; 2012: $TL = 7.57 + 0.11^*(\text{age in days})$, $P < 0.0001$, $R^2 =$

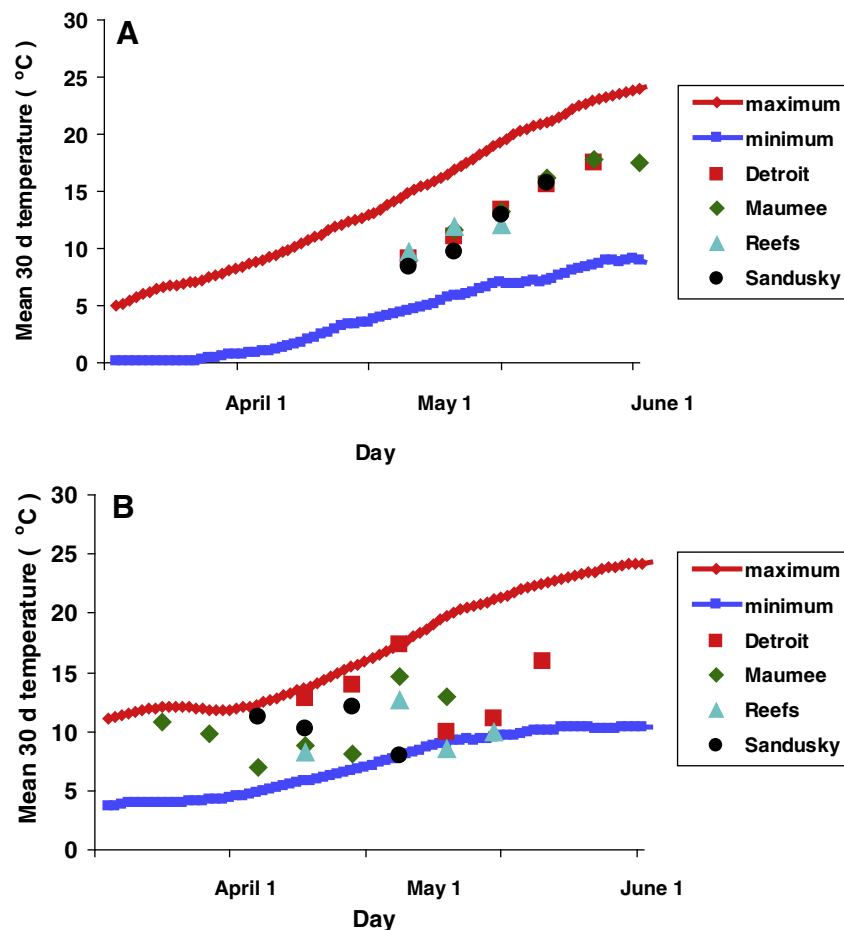


Fig. 8. Temperatures experienced by walleye larvae in western Lake Erie during our 30 d simulation during 2011 (A) and 2012 (B). Mean 30 d temperatures experienced by weekly cohorts of larvae ($n = 5000$ individuals per cohort) from the Detroit River, Maumee River, Ohio reef complex, and Sandusky River spawning stocks are plotted by release day. Minimum and maximum water temperatures for the entire west basin also are plotted for each day of the simulations.

0.42, $F_{1,64} = 45.69$). This likely reflects the assumption of a homogeneous zooplankton field, in addition to other simplifications and assumptions in the physical and bioenergetics models.

In general, growth and recruitment (or year-class strength) should depend on the relationship between the spatiotemporal advection pattern and the spatiotemporal extent of high-quality habitat (area and duration). The match–mismatch hypothesis (Cushing, 1990) suggests that timing of the larval production period in relation to prey (zooplankton) availability is critical. However, given the dependence of larval dispersal on hydrodynamic advection, spatial overlap may be equally as important (Durant et al., 2007).

In addition to the considering the overlap of larvae with habitat in both space and time, we need to consider the scale/magnitude of heterogeneity in habitat quality when trying to understand stock-specific patterns in growth. From our results, we can hypothesize that, if optimal conditions are found only in small areas or for short durations, individual-level larval advection may be largely irrelevant, and growth and future recruitment would be low since a large proportion of larvae are likely to end up in an area of low or intermediate habitat quality. For example, regardless of whether the advection kernel of a stock is large or small, the probability that many or most of the larvae are advected into the high-quality region is low because of its limited spatial extent. However, at the population level, these conditions, especially if the location of high-quality habitat varies, may favor broad advection (e.g., through larval release from multiple spawning sites), so that at least some recruitment occurs. If optimal or near-optimal conditions are broadly distributed (homogeneous) in space and time, individual-

level larval advection also may not be particularly important because a large proportion of individual larvae and the population are likely to experience high-quality conditions regardless of their advection trajectories. Under these conditions, growth and recruitment rates would be expected to be higher relative to the preceding poor habitat-quality condition. By contrast, when heterogeneity in high-quality habitat is great, individual-level larval advection would be expected to play an important role in determining growth and recruitment rates as the potential for larvae to find suitable habitat could range from high to low (depending on the timing of spawning, water circulation, and spatiotemporal variability in habitat conditions). Under these conditions, growth variation at the population level may also be common, since spawning site location and circulation patterns may be more likely to lead to advection into either more or less favorable habitat (i.e., larvae from particular stocks may perform consistently better than larvae from other stocks).

Consistent with other freshwater and marine studies that have shown temperature to be a major driver of larval growth (Roderick and Kapoor, 2008), our modeling showed how different advection patterns could lead to different growth patterns by influencing only the amount of available thermal habitat to larval walleye (Fig. 9). This dependence of growth on temperature, in turn, led to some unexpected stock-specific growth patterns. For example, because previous research has suggested the southern nearshore area to have the highest-quality habitat for walleye larvae in western Lake Erie (Roseman et al., 2005), we expected those stocks with high average larval advection rates over this area (e.g., Maumee River and the Ohio reef complex stocks;

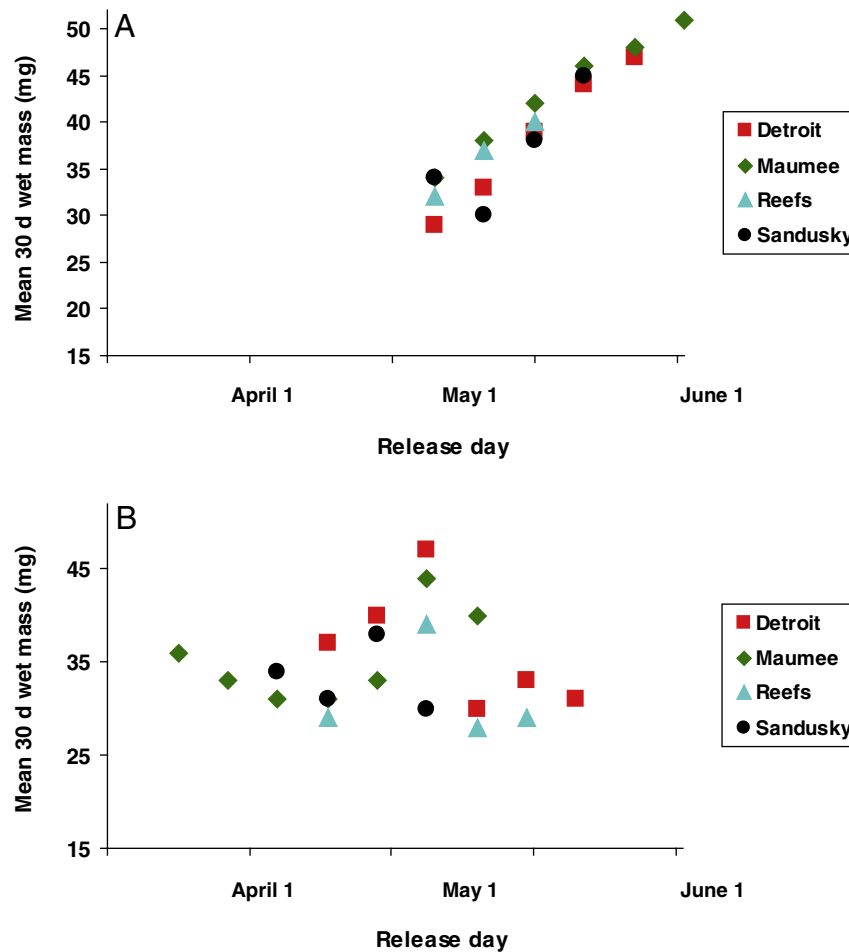


Fig. 9. Mean (± 1 SE) wet mass of walleye larvae from each weekly cohort from four western Lake Erie spawning stocks (Detroit River, Maumee River, Ohio reef complex, and Sandusky River) after 30 d during 2011 (A) and 2012 (B). Weekly cohorts are plotted by release day.

Fig. 2) to have a growth advantage over other stocks. While this southern portion of the western basin did tend to have earlier warming surface water, as well as more high quality thermal habitat relative to offshore waters, it was not uniformly high in quality. As a result, high variation in growth rates was observed for Maumee River and Ohio reef complex larvae despite their frequent advection into southern nearshore areas. Further, areas of high-quality habitat developed elsewhere in the basin, particularly later in the larval production season, which leads to other stocks demonstrating rapid growth (e.g., Detroit River stock). This disparity in our results relative to previous field studies (e.g., Roseman et al., 2005) points to: 1) a gap in our understanding of zooplankton prey availability in offshore waters of the west basin, 2) the need for future modeling efforts to consider more realistic (e.g., heterogeneous) zooplankton prey fields, and 3) model simulations that are conducted during years of strong recruitment (e.g., 1996, 2003; Walleye Task Group, 2013) in which advection patterns and habitat quality likely differ. With respect to this last point, we would expect to often find an intermediate to large proportion of walleye larvae from all stocks being dispersed into areas of sub-optimal habitat quality. Advection and mixing of some or all stocks might be more concentrated in high-quality habitat and (or) high-quality habitat may be more spatially and temporally widespread during years of strong recruitment relative to our study years.

Lake Erie fisheries management implications

Because larval growth can influence future growth and survival, variation in the timing of spawning, larval advection, and habitat (thermal

quality that eventually cause differences in stock-specific larval growth should be expected to drive inter-annual variability in the contribution that each stock makes to the new year-class. As a result, Lake Erie's walleye population is likely supported by different stocks during different time periods, analogous to Pacific salmonines (Schindler et al., 2010) and other marine species (Thibault et al., 2012; Yates et al., 2012). Given the high variability in habitat conditions experienced by our focal western Lake Erie walleye stocks, we strongly encourage agencies to protect spawning stock diversity, as a diverse "portfolio" of stocks can help buffer the population (and the fisheries it supports) against wide swings in recruitment, not to mention protect the population in the face of continued human-drive change (Schindler et al., 2010). Most certainly, continued modeling in which multi-year comparisons are conducted that also consider the numbers of eggs or larvae produced at each site will help to identify how the relative contributions of each stock to the new year-class vary and how this variance relates to biophysical processes.

In addition to helping to understand recruitment, accounting for the advection of eggs and larvae and the degree to which discrete spawning stocks overlap or mix during early life stages can help to improve efforts to discriminate among stocks. With improved stock discrimination capabilities, management agencies would be better positioned to understand the contribution of recruits that each stock makes to the broader population (and fisheries that it supports). For example, we now know from our modeling that wind-driven advection can cause geographically discrete spawning stocks to mix considerably in both space and time during the larval stage (e.g., larvae produced on the Ohio reef complex frequently mixed with larvae from other stocks and

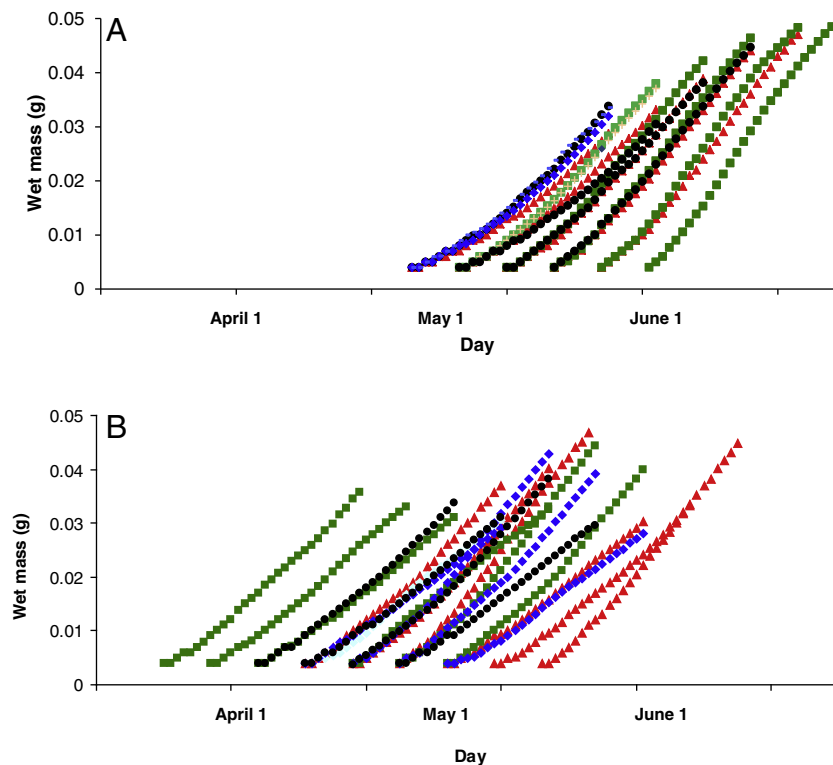


Fig. 10. Mean daily wet mass of Lake Erie walleye over a simulated 30 d larval period during 2011 (A) and 2012 (B). Each point represents the mean of 5000 larvae from weekly cohorts released from 1 of 4 locations (Detroit River, red; Maumee River, green; Ohio reef complex, blue; Sandusky River, black). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Maumee and Detroit larvae also mixed at times; see Figs. 5 and 6). Not accounting for this mixing prior to the collection of individuals (i.e., larvae) in seemingly isolated spawning locations for stock discrimination purposes, which has been a common practice in the fisheries stock discrimination literature, might limit our ability to use natural tags (e.g., otolith microchemistry, genetics; Campana, 1999; Miller et al., 2005; Ludsins et al., 2006; Perrier et al., 2011) as stock markers for identifying the natal origins of recruits to the fishery. For this reason, using biophysical models to account for advection pathways by backtracking or hindcasting individual larvae to their hatching location (Christensen et al., 2007) may improve stock discrimination in mixed populations by allowing initial group assignments to be revised, especially in species in which adult spawning locations are uncertain (Fraker et al., in review).

ICPBMs: key limitations and research needs

While our ICPBM has provided insight into the degree to which discrete spawning stocks likely mix during early life stages and how spawning time and location, advection patterns, and heterogeneity in thermal habitat can potentially influence larval walleye growth, addressing some of the limitations and simplifications of our model will undoubtedly improve its value in understanding the walleye recruitment process. For example, smaller scale processes (e.g. vertical mixing and bottom topography/velocities; North et al., 2009; Thygesen, 2011) that can be important to larval transport and foraging may not be represented in our hydrodynamic and particle tracking model. Likewise, the grid resolution of most ICPBMs, including our own, tends to range from tens of meters to a few kilometers (e.g., ours has a 2×2 km resolution), which is a resolution that is larger than that at which most individual-level interactions occur (e.g., foraging and predator-prey interactions occur at the scale of a few millimeters to a few meters; Peck and Hufnagl, 2012). This mismatch in scale can

pose difficulty in realistically accounting for the role that small-scale physical processes play in influencing larval foraging, growth, and survival (e.g., Langmuir cells that may concentrate zooplankton; turbulence that can influence larval foraging; chemotaxis that may influence predator-prey interactions; Ledbetter, 1979; Tollrian and Harvell, 1999; Pepin, 2004; Hay, 2012; North et al., 2009; Peck and Hufnagl, 2012). In turn, ability to use ICPBMs to truly describe larval foraging, growth, and survival might remain somewhat circumspect until these types of small-scale interactions can be practically captured in lake- or basin-scale level models.

In addition to these limitations of the physical model, our ICPBM also could be improved from a biological standpoint. For example, late in the larval period, individuals often do become large enough to exhibit horizontal swimming behavior (Leis, 2007; Willis, 2011) and could exhibit similar types of responses to predation risk-foraging gain tradeoffs observed in older individuals (Lima, 2002; Fiksen and Jørgensen, 2011). While the sizes of larvae modeled herein were small enough that horizontal swimming behavior should be a non-factor (Houde, 1969; Humphrey et al., 2012), no research has been conducted to know exactly when larval walleye become competent enough to adjust their vertical position in the water column, as well as what environmental cues might motivate active vertical movement of walleye larvae. Thus, a better understanding of vertical movement behavior is needed, and accounting for it in our model could prove highly beneficial, as active vertical movement has been shown to greatly affect larval fish dispersal trajectories in marine ecosystems (Willis, 2011). Additionally, accounting for possible variation in initial larval size at hatch and individual-level physiological variation (Rice et al., 1993; Peck and Hufnagl, 2012) also may have led to improved estimates of the impact of thermal habitat on walleye growth. Although overcoming some of these limitations will be challenging, these collaborations should prove fruitful, given the value that ICPBMs to fisheries science in other ecosystems (Miller, 2007; Peck and Hufnagl, 2012).

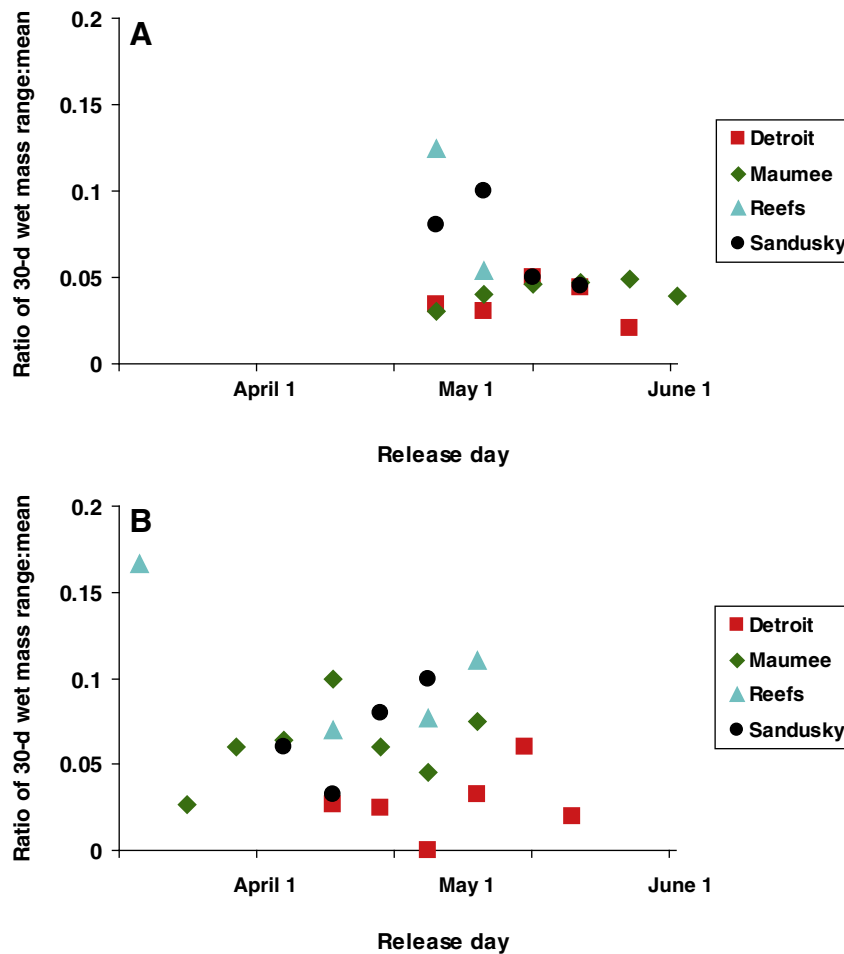


Fig. 11. Ratio of the range of 30 d wet mass to the mean 30 d wet mass for each weekly cohort of walleye larvae from each Lake Erie spawning stock during 2011 (A) and 2012 (B). Each point represents the mean of 5000 larvae from weekly cohorts released from 1 of 4 locations (Detroit River, red; Maumee River, green; Ohio reef complex, blue; Sandusky River, black). Weekly cohorts are plotted by release day. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Benefits of ICPBMs to Great Lakes fisheries investigations

Biophysical processes have long been considered important drivers of marine fish early life history, and are increasingly recognized as potentially important to many Great Lakes species (Ludsin et al., 2014). The variable patterns in larval advection, stock mixing, and growth that we found for walleye have been observed in some marine systems (e.g., Searcy and Sponaugle, 2000; Sponaugle and Pinkard, 2004; Siegel et al., 2008) and seem likely to occur in other Great Lakes species with pelagic larvae (e.g., yellow perch, lake whitefish *Coregonus clupeaformis*), although specific patterns may depend on the species or lake. ICPBMs should continue to be useful to identifying which large scale biophysical processes matter and why. A potentially fruitful method in future studies is to contrast years of strong and weak year-classes. If sufficient meteorological and biological data are available, the biophysical patterns in these years can be simulated and identified. The ICPBM could then be used to test the sensitivity of recruitment to various inputs (e.g., warming rates, wind direction, timing of precipitation, timing and location of spawning) under hypothetical conditions. Processes identified as important could then be tested, using observed data or data from other years, with hypotheses being refined as needed. This approach requires access to monitoring data and collaboration between multiple groups (e.g., physical modelers, fisheries ecologists, state, provincial, and Federal agencies); fortunately, these kinds of data are often available, especially for large lakes such as the Laurentian Great Lakes (e.g., Zhao et al., 2009; Ludsin et al., 2014).

The use of ICPBMs can complement and even change our existing understanding of the biology of many species and may produce important ideas for their management and conservation. For example, ICPBMs offer an approach to better understand population connectivity that might be important to fisheries management (Peck and Hufnagl, 2012). In the case of Lake Erie, those walleye larvae advected out of the western basin may end up providing the recruits that support the large walleye populations found in both the central and eastern basins of the lake (Walleye Task Group, 2013). While this hypothesis needs testing, if true, then managing those spawning stocks that contribute recruits to the central and eastern basin of the lake might be even more important than previously thought. Similarly, ICPBMs offer a means to better understand population demographics, structure, and dynamics. For example, an understanding of the degree to which stocks mix and experience similar environmental conditions can help us potentially understand why annual recruitment events are large (e.g., all stocks experience favorable conditions for growth and survival during the larval stage), intermediate (e.g., some, but not all, stocks experience favorable conditions), or small (e.g., all stocks experience unfavorable conditions) in size. Likewise, ICPBMs can improve our understanding of stock-specific contributions of recruits to the fishery by improving stock discrimination capabilities (Fraker et al., in review), as well as by allowing us to account for prior, stock-specific environmental histories. Finally, ICPBMs may offer a complementary, or potentially improved, approach to fishery management by offering ways to bring an ecological, mechanistic viewpoint into management and providing a means

for ecosystem-based management to be practiced. These abilities, in turn, offer a great opportunity to improve our understanding of the recruitment process, which can only help agencies keep their important fisheries sustainable in the face of continued human-induced ecosystem change (Scavia et al., 2014). For this reason, we encourage continued efforts by fisheries scientists to collaborate with physical scientists and ecologists to continue to develop ICPBMs in freshwater ecosystems such as the Laurentian Great Lakes.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jglr.2015.04.008>.

Acknowledgments

We thank Maura C. O'Brien for producing the bathymetric map of Lake Erie. We also thank two anonymous reviewers for providing comments that improved this work. This work was primarily funded by the Federal Aid in Sport Fish Restoration Program (F-69-P, Fish Management in Ohio), administered jointly by the U.S. Fish and Wildlife Service and the Ohio Division of Wildlife (FADR69 to SAL and MEF). Additional support was provided by the Great Lakes Restoration Initiative Project 70, "Developing Fish Habitat Restoration Strategies for the Huron-Erie Corridor", the USGS Great Lakes Science Center, the Ontario Ministry of Natural Resources, and the Canada-Ontario Agreement (7-16) Respecting to the Great Lakes Basin Ecosystem to YZ. The funding sources had no role in study design, data collection, analysis, and interpretation, or reporting of results. This is contribution number 1928 of the USGS Great Lakes Science Center and contribution number 1762 of the NOAA Great Lakes Environmental Research Laboratory. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

- Allain, G., Petitgas, P., Lazure, P., Grellier, P., 2007. Biophysical modelling of larval drift, growth and survival for the prediction of anchovy (*Engraulis encrasicolus*) recruitment in the Bay of Biscay (NE Atlantic). *Fish. Oceanogr.* 16, 489–505.
- Bailey, K.M., Houde, E.D., 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Adv. Mar. Biol.* 25, 1–83.
- Bartnik, S.E.H., 2005. Population Dynamics of Age-0 Walleye in Western Lake Erie. (Master's thesis). University of Windsor, Windsor, ON, Canada.
- Beletsky, D., Schwab, D.J., 2001. Modeling circulation and thermal structure in Lake Michigan: annual cycle and interannual variability. *J. Geophys. Res.* 106, 19745–19771.
- Beletsky, D., Mason, D.M., Schwab, D.J., Rutherford, E.S., Janssen, J., Clapp, D.F., Dettmers, J.M., 2007. Biophysical model of larval yellow perch advection and settlement in Lake Michigan. *J. Great Lakes Res.* 33, 842–866.
- Beletsky, D., Hawley, N., Rao, Y.R., 2013. Modeling summer circulation and thermal structure in Lake Erie. *J. Geophys. Res. Oceans* 118, 6238–6252. <http://dx.doi.org/10.1002/2013JC008854>.
- Bennett, J.R., Clites, A.H., 1987. Accuracy of trajectory calculation in a finite-difference circulation model. *J. Comput. Phys.* 68, 272–282.
- Bigg, J.L., 2006. Determining Stream Origin of Four Purported Walleye Stocks in Lake Erie Using Otolith Elemental Analysis. (Master's thesis). The Ohio State University, Columbus, Ohio, USA.
- Blumberg, A.F., Mellor, G.L., 1987. A description of a three-dimensional coastal ocean circulation model. In: Heaps, N. (Ed.), *Three-dimensional Coastal Ocean Models*. American Geophysical Union, Washington DC, pp. 1–6.
- Bruce, L.C., Hamilton, D., Imberger, J., Gal, G., Gophen, M., Zohary, T., Hambricht, K.D., 2006. A numerical simulation of the role of zooplankton in C, N, and P cycling in Lake Kinneret. *Israel. Ecol. Model.* 193, 412–436.
- Busch, W.D.N., Scholl, R.L., Hartman, W.L., 1975. Environmental factors affecting the strength of walleye (*Stizostedion vitreum vitreum*) year-classes in western Lake Erie, 1960–1970. *J. Fish. Res. Board Can.* 32, 1733–1742.
- Campana, S.E., 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. *Mar. Ecol. Prog. Ser.* 188, 263–297.
- Christensen, A., Daewel, U., Jensen, H., Mosegaard, H., St. John, M., Schrum, C., 2007. Hydrodynamic backtracking of fish larvae by individual-based modeling. *Mar. Ecol. Prog. Ser.* 347, 221–232.
- Chu, P.Y., Kelley, J.G.W., Mott, G.V., Zhang, A., Lang, G.A., 2011. Development, implementation, and skill assessment of the NOAA/NOS Great Lakes Operational Forecast System. *Ocean Dyn.* 61, 1305–1316.
- Cowen, R.C., Sponaugle, S., 2009. Larval dispersal and marine population connectivity. *Ann. Rev. Mar. Sci.* 1, 443–466.
- Cushing, D.H., 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv. Mar. Biol.* 26, 249–293.
- DeAngelis, D.L., Gross, L.J., 1992. *Individual-based Models and Approaches in Ecology: Populations, Communities, and Ecosystems*. Chapman and Hall, New York.
- Doyle, M.J., Mier, K.L., 2012. A new conceptual framework for evaluating early life history aspects of recruitment processes among marine fish species. *Can. J. Fish. Aquat. Sci.* 69, 2112–2129.
- Durant, J.M., Hjermann, D.O., Ottersen, G., Stenseth, N.C., 2007. Climate and the match or mismatch between predator requirements and resource availability. *Clim. Res.* 33, 271–283.
- Fiksen, O., Jørgensen, C., 2011. Model of optimal behaviour in fish larvae predicts that food availability determines survival, but not growth. *Mar. Ecol. Prog. Ser.* 432, 207–219.
- Frost, P.C., Culver, D.A., 2001. Spatial and temporal variability of phytoplankton and zooplankton in western Lake Erie. *J. Freshw. Ecol.* 16, 435–443.
- Fuller, K., Shear, H., Wittig, J., 1995. *The Great Lakes: An Environmental Atlas and Resource Book*. Environment Canada and U.S. Environmental Protection Agency, Chicago, Illinois, USA.
- Gatt, M.H., McParland, T., Halyk, L.C., Ferguson, M.M., 2003. Mitochondrial DNA variation and mixed-stock analysis of recreational and commercial walleye fisheries in eastern Lake Erie. *N. Am. J. Fish. Manag.* 23, 431–440.
- Goodyear, C.S., Edsall, T.A., Ormsby Dempsey, D.M., Moss, G.D., Polanski, P.E., 1982. *Atlas of the Spawning and Nursery Areas of Great Lakes Fishes*. FWS/OBS-82/52. U.S. Fish and Wildlife Service, Washington, DC.
- Gopalan, G., Culver, D.A., Wu, L., Trauben, B.K., 1998. The effect of recent ecosystem changes on the recruitment of young-of-year fish in western Lake Erie. *Can. J. Fish. Aquat. Sci.* 55, 2572–2579.
- Grimes, C.B., Kingsford, M.J., 1996. How do riverine plumes of different sizes influence fish larvae: do they enhance recruitment? *Mar. Freshw. Res.* 47, 191–208.
- Grimm, V., Railsback, S.F., 2005. *Individual-based Modeling and Ecology*. Princeton University Press, Princeton, NJ, USA.
- Hanson, P.C., 1997. Fish bioenergetics. University of Wisconsin Sea Grant Institute, Madison, WI, USA.
- Haponski, A.E., Stepien, C.A., 2014. Genetic connectivity and diversity of walleye (*Sander vitreus*) spawning groups in the Huron–Erie corridor. *J. Great Lakes Res.* 40 (Suppl. 2), 89–100.
- Hatch, R.W., Nepzy, S.J., Muth, K.M., Baker, C.T., 1987. Dynamics of the recovery of the western Lake Erie walleye (*Stizostedion vitreum vitreum*) stock. *Can. J. Fish. Aquat. Sci.* 44 (Suppl. 2), 15–22.
- Hay, M.E., 2012. Marine chemical ecology: chemical signals and cues structure marine populations, communities, and ecosystems. *Annu. Rev. Mar. Sci.* 1, 193–212.
- Hedges, K.J., 2002. Use of Calcified Structures for Stock Discrimination in Great Lakes Walleye (*Stizostedion vitreum*). Master's thesis. University of Windsor, Windsor, ON, Canada.
- Hilborn, R., Quinn, T.P., Schindler, D.E., Rogers, D.E., 2003. *Biocomplexity and Fisheries Sustainability*. PNAS USA 100pp. 6564–6568.
- Hinrichsen, H.H., Dickey-Collas, M., Hurat, M., Peck, M.A., Vikebo, F.B., 2011. Evaluating the suitability of coupled biophysical models for fishery management. *ICES J. Mar. Sci.* 68, 1478–1487.
- Hook, T.O., McCormick, M.J., Rutherford, E.S., Mason, D.M., Carter, G.S., 2006. Short-term water mass movements in Lake Michigan: implications for larval fish transport. *J. Great Lakes Res.* 32, 728–737.
- Houde, E.D., 1969. Sustained swimming ability of larvae of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*). *J. Fish. Res. Board Can.* 26, 1647–1659.
- Houde, E.D., 1987. Fish early life dynamics and recruitment variability. *Am. Fish. Soc. Symp.* 2, 17–29.
- Houde, E.D., 1989. Subtleties and episodes in the early life of fishes. *J. Fish Biol.* 35 (Suppl. A), 29–38.
- Houde, E.D., 2008. Emerging from Hjort's shadow. *J. Northwest Atl. Fish. Sci.* 41, 53–70.
- Houde, E.D., 2009. Recruitment variability. In: Jakobsen, T., Fogarty, M.J., Megrey, B.A., Moksness, E. (Eds.), *Fish Reproductive Biology: Implications for Assessment and Management*. Wiley-Blackwell, West Sussex, pp. 91–171.
- Humphrey, S., Zhao, Y., Higgs, D., 2012. The effects of water currents on walleye (*Sander vitreus*) eggs and larvae and implications for the early survival of walleye in Lake Erie. *Can. J. Fish. Aquat. Sci.* 69, 1959–1967.
- James, M.K., Armsworth, P.R., Mason, L.B., Bode, L., 2002. The structure of reef fish metapopulations: modelling larval dispersal and retention patterns. *Proc. R. Soc. Lond. B* 269, 2079–2086.
- Johnston, T.A., 1999. Factors affecting food consumption and growth of walleye, *Stizostedion vitreum*, larvae in culture ponds. *Hydrobiologia* 400, 129–140.
- Jones, M.L., Netto, J.K., Stockwell, J.D., Mion, J.B., 2003. Does the value of newly accessible spawning habitat for walleye (*Stizostedion vitreum*) depend on its location relative to nursery habitats? *Can. J. Fish. Aquat. Sci.* 60, 1527–1538.
- Ledbetter, M., 1979. Langmuir circulations and plankton patchiness. *Ecol. Model.* 7, 289–310.
- Leis, J.M., 2007. Behaviour as input for modelling dispersal of fish larvae: behaviour, biogeography, hydrodynamics, ontogeny, physiology, and phylogeny meet hydrography. *Mar. Ecol. Prog. Ser.* 347, 185–193.
- Leon, L.F., Imberger, J., Smith, R.E.H., Hecky, R.E., Lam, D.C.L., Schertzer, W.M., 2005. Modelling as a tool for nutrient management in Lake Erie: a hydrodynamics study. *J. Great Lakes Res.* 31 (Suppl. 2), 309–318.
- Leon, L.F., Smith, R.E.H., Hipsey, M.R., Bocainov, S.A., Higgins, S.N., Hecky, R.E., Antenucci, J.P., Guildford, S.J., 2011. Application of a 3D hydrodynamic-biological model for seasonal and spatial dynamics of water quality and phytoplankton in Lake Erie. *J. Great Lakes Res.* 37, 41–53.
- Lima, S.L., 2002. Putting predators back into behavioral predator–prey interactions. *TREE* 17 pp. 70–75.

- Ludsin, S.A., 2000. Exploration of Spatiotemporal Patterns in Recruitment and Community Organization of Lake Erie Fishes: A Multiscale, Mechanistic Approach. (Ph.D. thesis). The Ohio State University, Columbus, OH, USA.
- Ludsin, S.A., DeVries, D.R., 1997. First-year recruitment of largemouth bass: the interdependency of early life stages. *Ecol. Appl.* 7, 1024–1038.
- Ludsin, S.A., Fryer, B.J., Gagnon, J.E., 2006. Comparison of solution-based versus laser-ablation ICPMS for analysis of larval fish otoliths. *Trans. Am. Fish. Soc.* 135, 218–231.
- Ludsin, S.A., Pangle, K.L., Tyson, J.T., 2010. Using Satellite Imagery for Fisheries Management. Final Completion Report. Lake Erie Protection Fund, Toledo, OH.
- Ludsin, S.A., DeVanna, K.M., Smith, R.E., 2014. Physical–biological coupling and the challenge of understanding fish recruitment in freshwater lakes. *Can. J. Fish. Aquat. Sci.* 71, 775–794.
- Madon, S.P., Culver, D.A., 1993. Bioenergetics model for larval and juvenile walleye: an in-situ approach using experimental ponds. *Trans. Am. Fish. Soc.* 122, 797–813.
- McDermott, D., Rose, K.A., 2000. An individual-based model of lake fish communities: application to piscivore stocking in Lake Mendota. *Ecol. Model.* 125, 67–102.
- McElman, J.F., Balon, E.K., 1979. Early ontogeny of walleye *Stizostedion vitreum*, with steps of saltatory development. *Environ. Biol. Fish.* 4, 309–348.
- Merker, R.J., Woodruff, R.C., 1996. Molecular evidence for divergent breeding groups of walleye (*Stizostedion vitreum*) in tributaries of western Lake Erie. *J. Great Lakes Res.* 22, 280–288.
- Michalak, A.M., Anderson, E.J., Beletsky, D., Boland, S., Bosch, N.S., Bridgeman, T.B., Chaffin, J.D., Cho, K.H., Confesor, R., Daloglu, I., DePinto, J.V., Evans, M.A., Fahnenstiel, G.L., He, L., Ho, J.C., Jenkins, L., Johengen, T.H., Kuo, K.C., Laporte, E., Liu, X., McWilliams, M., Moore, M.R., Posselt, D.J., Richards, R.P., Scavia, D., Steiner, A.L., Vaerhamme, E., Wright, D.M., Zagorski, M.A., 2013. Record-setting algal bloom in Lake Erie caused by agricultural and meteorological trends consistent with expected future conditions. *PNAS USA*. 110 pp. 6448–6452.
- Miller, T.J., 2007. Contribution of individual-based coupled physical–biological models to understanding recruitment in marine fish populations. *Mar. Ecol. Prog. Ser.* 347, 127–138.
- Miller, T.J., Crowder, L.B., Rice, J.A., Marschall, E.A., 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Can. J. Fish. Aquat. Sci.* 45, 1657–1670.
- Miller, J.A., Banks, M.A., Gomez-Uchida, D., Shanks, A.L., 2005. A comparison of population structure in black rockfish (*Sebastes melanops*) as determined with otolith microchemistry and microsatellite DNA. *Can. J. Fish. Aquat. Sci.* 62, 2189–2198.
- Minitab Inc., 2013. Minitab 16 Statistical Software. State College PA, USA.
- Mion, J.B., Stein, R.A., Marschall, E.A., 1998. River discharge drives survival of larval walleye. *Ecol. Appl.* 8, 88–103.
- Myers, R.A., 1997. Recruitment variation in fish populations assessed using meta-analysis. In: Chambers, R.C., Trippel, E.A. (Eds.), *Early Life History and Recruitment in Fish Populations*. Chapman and Hall, London, pp. 451–467.
- North, E.W., Gallego, A., Petigas, P., 2009. Manual of Recommended Practices for Modeling Physical–Biological Interactions During Early Fish Life. ICES Report 295. The International Council for Exploration of the Sea, Copenhagen.
- Peck, M.A., Hufnagel, M., 2012. Can IBMs tell us why most larvae die in the sea? Model sensitivities and scenarios reveal research needs. *J. Mar. Syst.* 93, 77–93.
- Pepin, P., 2004. Early life history studies of prey predator interactions: quantifying the stochastic individual responses to environmental variability. *Can. J. Fish. Aquat. Sci.* 61, 659–671.
- Perrier, C., Grandjean, F., Le Gentil, J., Cherbonnel, C., Evanno, G., 2011. A species-specific microsatellite marker to discriminate European Atlantic salmon, brown trout, and their hybrids. *Conserv. Genet. Resour.* 3, 131–133.
- Pineda, J., Hare, J.A., Sponaugle, S., 2007. Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography* 20, 22–39.
- Pritt, J.J., Roseman, E.F., O'Brien, T.P., 2014. Mechanisms driving recruitment variability in fish: comparisons between the Laurentian Great Lakes and marine systems. *ICES J. Mar. Sci.* 71, 2252–2267.
- Reichert, J.M., Fryer, B.J., Pangle, K.L., Johnson, T.B., Tyson, J.T., Drelich, A.B., Ludsin, S.A., 2010. River-plume use during the pelagic larval stage benefits recruitment of a lentic fish. *Can. J. Fish. Aquat. Sci.* 67, 987–1004.
- Rice, J.A., Miller, T.J., Rose, K.A., Crowder, L.B., Marschall, E.A., Trebitz, A.S., DeAngelis, D.L., 1993. Growth rate variation and larval survival: inferences from an individual-based size-dependent predation model. *Can. J. Fish. Aquat. Sci.* 50 (133), 142.
- Roderick, N.F., Kapoor, B.G., 2008. *Fish Larval Physiology*. CRC Press, Boca Raton, FL.
- Roseman, E.F., 1997. Factors Influencing the Year-class Strength of Reed-spawned Walleye in Western Lake Erie (MS thesis). Michigan State University East Lansing MI, USA.
- Roseman, E.F., Taylor, W.W., Hayes, D.B., Tyson, J.T., Hass, R.C., 2005. Spatial patterns emphasize the importance of coastal zones as nursery areas for larval walleye in western Lake Erie. *J. Great Lakes Res.* 31 (Suppl. 1), 28–44.
- Scavia, D., Allan, J.D., Arend, K.K., Bartell, S., Beletsky, D., Bosch, N.S., Brandt, S.B., Briland, R.D., Daloglu, I., DePinto, J.V., Dolan, D.M., Evans, M.A., Farmer, T.M., Goto, D., Han, H., Höök, T.O., Knight, R., Ludsin, S.A., Mason, D., Michalak, A.M., Richards, R.P., Roberts, J.J., Rucinski, D.K., Rutherford, E., Schwab, D.J., Sesterhenn, T., Zhang, H., Zhou, Y., 2014. Assessing and addressing the re-eutrophication of Lake Erie: Central Basin hypoxia. *J. Great Lakes Res.* 40, 226–246.
- Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Rogers, L.A., Quinn, T.P., Webster, M.S., 2010. Population diversity and the portfolio effect in an exploited species. *Nature* 465, 609–612.
- Schwab, D.J., Bedford, K.W., 1994. Initial implementation of the Great Lakes Forecasting System: a real-time system for predicting lake circulation and thermal structure. *Water Poll. Res. J. Can.* 29, 203–220.
- Searcy, S., Sponaugle, S., 2000. Variable larval growth in a coral reef fish. *Mar. Ecol. Prog. Ser.* 206, 213–226.
- Sesterhenn, T.M., Roswell, C.R., Stein, S.R., Klaver, P., Verhamme, E., Pothoven, S.A., Hook, T.O., 2014. Modeling the implications of multiple hatching sites for larval dynamics in the resurgent Saginaw Bay walleye population. *J. Great Lakes Res.* 40 (Suppl. 1), 113–122.
- Siegel, D.A., Mitarai, S., Costello, C.J., Gaines, S.D., Kendall, B.E., Warner, R.R., Winters, K.B., 2008. The stochastic nature of larval connectivity among nearshore marine populations. *PNAS USA*. 105 pp. 8974–8979.
- Smith, R.E.H., Zhao, Y., 2011. Bio-physical Forcing of Walleye Recruitment in Western Lake Erie. Completion Report. Great Lakes Fishery Commission, Ann Arbor, MI, USA.
- Sponaugle, S., Pinkard, D.R., 2004. Impact of variable pelagic environments on natural larval growth and recruitment of the reef fish *Thalassoma bifasciatum*. *J. Fish Biol.* 64, 34–54.
- Steinhart, G.B., Leonard, N.J., Stein, R.A., Marschall, E.A., 2005. Effects of storms, angling, and nest predation during angling on smallmouth bass (*Micropterus dolomieu*) nest success. *Can. J. Fish. Aquat. Sci.* 62, 2649–2660.
- Strange, R.M., Stepien, C.A., 2007. Genetic divergence and connectivity among river and reef spawning populations of walleye (*Sander vitreus*) in Lake Erie. *Can. J. Fish. Aquat. Sci.* 64, 437–448.
- The Mathworks Inc., 2012. Matlab Release 2012b. Natick, MA, USA.
- Thibault, L.M., Connolly, S.R., Sweatman, S.P.A., 2012. Diversity and stability of herbivorous fishes on coral reefs. *Ecology* 93, 891–901.
- Thygesen, U.H., 2011. How to reverse time in stochastic particle tracking models. *J. Mar. Syst.* 88, 159–168.
- Tollrian, R., Harvell, C.D., 1999. *The Ecology and Evolution of Inducible Defenses*. Princeton University Press, Princeton, NJ, USA.
- Walleye Task Group, 2013. Report of the Lake Erie Walleye Task Group to the Standing Technical Committee, Lake Erie Committee. Great Lakes Fishery Commission, Ann Arbor, MI, USA.
- Werner, F.E., Cowen, R.K., Paris, C.B., 2007. Coupled biological and physical models: present capabilities and necessary developments for future studies of population connectivity. *Oceanography* 20, 54–69.
- Willis, J., 2011. Modelling swimming aquatic animals in hydrodynamic models. *Ecol. Model.* 222, 3869–3887.
- Yates, P.M., Heupel, M.R., Tobin, A.J., Simpfendorfer, C.A., 2012. Diversity on young shark habitats provides the potential for portfolio effects. *Mar. Ecol. Prog. Ser.* 458, 269–281.
- Zhao, Y., Jones, M.L., Shuter, B.J., Roseman, E.F., 2009. A biophysical model of Lake Erie walleye (*Sander vitreus*) explains interannual variation in recruitment. *Can. J. Fish. Aquat. Sci.* 66, 114–125.