

# Larval dispersal underlies demographically important intersystem connectivity in a Great Lakes yellow perch (*Perca flavescens*) population

Reed M. Brodник, Michael E. Fraker, Eric J. Anderson, Lucia Carreon-Martinez, Kristen M. DeVanna, Daniel D. Heath, Julie M. Reichert, Edward F. Roseman, and Stuart A. Ludsin

**Abstract:** Ability to quantify connectivity among spawning subpopulations and their relative contribution of recruits to the broader population is a critical fisheries management need. By combining microsatellite and age information from larval yellow perch (*Perca flavescens*) collected in the Lake St. Clair – Detroit River system (SC-DRS) and western Lake Erie with a hydrodynamic backtracking approach, we quantified subpopulation structure, connectivity, and contributions of recruits to the juvenile stage in western Lake Erie during 2006–2007. After finding weak (yet stable) genetic structure between the SC-DRS and two western Lake Erie subpopulations, microsatellites also revealed measurable recruitment of SC-DRS larvae to the juvenile stage in western Lake Erie (17%–21% during 2006–2007). Consideration of precollection larval dispersal trajectories, using hydrodynamic backtracking, increased estimated contributions to 65% in 2006 and 57% in 2007. Our findings highlight the value of complementing subpopulation discrimination methods with hydrodynamic predictions of larval dispersal by revealing the SC-DRS as a source of recruits to western Lake Erie and also showing that connectivity through larval dispersal can affect the structure and dynamics of large lake fish populations.

**Résumé :** La capacité de quantifier la connectivité entre sous-populations reproductrices et leur contribution relative de recrues à l'ensemble de la population constitue un besoin fondamental en gestion des pêches. En combinant de l'information de microsatellites et sur l'âge pour des perchaudes (*Perca flavescens*) larvaires prélevées dans le réseau du lac St. Clair et de la rivière Detroit (SC-DRS) et l'ouest du lac Érié à une approche de reconstitution hydrodynamique des déplacements, nous avons quantifié la structure des sous-populations, ainsi que leur connectivité et leurs contributions de recrues juvéniles dans l'ouest du lac Érié en 2006–2007. Après avoir fait ressortir une structure génétique faible (mais stable) entre le SC-DRS et deux sous-populations de l'ouest du lac Érié, les microsatellites ont également révélé un recrutement mesurable de larves du SC-DRS chez les juvéniles de l'ouest du lac Érié (de 17 % à 21 % en 2006–2007). L'intégration, en utilisant la reconstitution hydrodynamique, de trajectoires de dispersion des larves avant le prélèvement s'est traduite par une augmentation des contributions estimées, jusqu'à 65 % en 2006 et 57 % en 2007. En faisant ressortir le fait que le SC-DRS est une source de recrues pour l'ouest du lac Érié et en démontrant qu'une connectivité par l'entremise de la dispersion des larves peut influencer la structure et la dynamique de populations de poissons de grands lacs, nos résultats soulignent l'intérêt d'utiliser des prédictions hydrodynamiques de la dispersion des larves pour compléter des méthodes de discrimination de sous-populations. [Traduit par la Rédaction]

## Introduction

Many aquatic species exhibit a metapopulation or subpopulation structure in which semi-independent, spatially distinct populations are linked by varying degrees through dispersal (Hjort 1926; Levin 2006). These subpopulations often represent breeding or spawning groups, from which individuals disperse to form a “mixed” population. In many marine invertebrate and fish populations, larval dispersal through hydrodynamic advection has been identified as a key driver of such subpopulation connectivity (Caley et al. 1996; Cowen and Sponaugle 2009). Similarly, Ludsin et al. (2014) hypothesized that long-distance dispersal of larvae via hydrodynamic advection would be an important driver of population connectivity and recruitment dynamics in many fishes of

the Laurentian Great Lakes (e.g., walleye (*Sander vitreus*), yellow perch (*Perca flavescens*), alewife (*Alosa pseudoharengus*)) because (i) their life-history traits (e.g., long pelagic larval stage with weak swimming capabilities) are similar to those found in most marine fishes (Miller et al. 1998; North et al. 2008; Pritt et al. 2014), and (ii) the Great Lakes share many of the same physical features (e.g., gyres, longshore currents, upwelling zones) as marine ecosystems (reviewed by Ludsin et al. 2014). Even so, our understanding of metapopulation dynamics and population connectivity remains scant in these (and most other) large lake ecosystems (Ludsin et al. 2014).

Quantification of subpopulation connectivity, including the relative contribution of each subpopulation to the broader mixed

Received 23 March 2015. Accepted 31 August 2015.

Paper handled by Associate Editor Eric Taylor.

R.M. Brodnik,\* M.E. Fraker,\* K.M. DeVanna, and S.A. Ludsin. Aquatic Ecology Laboratory, Department of Evolution, Ecology and Organismal Biology, The Ohio State University, Columbus, OH 43212, USA.

E.J. Anderson. NOAA Great Lakes Environmental Research Laboratory, Ann Arbor, MI 48108-9719, USA.

L. Carreon-Martinez. Department of Biology, The University of Texas at Brownsville, Brownsville, TX 78520, USA.

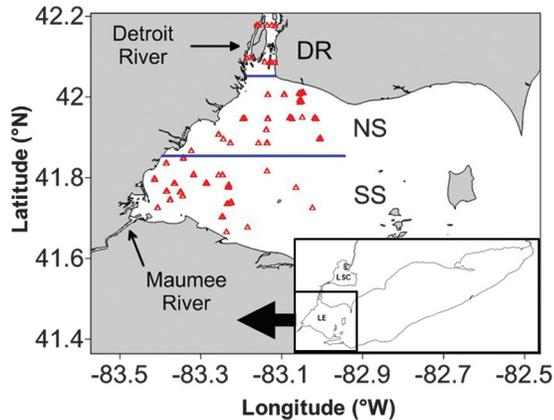
D.D. Heath and J.M. Reichert. Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON N9B 3P4, Canada.

E.F. Roseman. USGS Great Lakes Science Center, Ann Arbor, MI 48105, USA.

Corresponding author: Stuart A. Ludsin (email: ludsin.1@osu.edu).

\*These authors contributed equally to the work.

**Fig. 1.** Map of the collection sites of yellow perch larvae during 2006 and 2007 in the western basin of Lake Erie, with an inset of Lake Erie (LE) and Lake St. Clair (LSC). The horizontal line at 41.83 °N separates the north shore (NS) and south shore (SS), while the horizontal line at 42.05 °N separates the north shore from the Detroit River (DR).



population, can improve our ability to understand the structure and dynamics of the broader population (Turchin 1998; Werner et al. 2007; Kool et al. 2013) and the fisheries that it supports (Begg and Waldman 1999; Hilborn et al. 2003; Cowen and Sponaugle 2009). For example, Schindler et al. (2010), in what they described as a “portfolio effect”, demonstrated how the sockeye salmon (*Oncorhynchus nerka*) population in Bristol Bay, Alaska (USA), is stabilized by the existence of multiple breeding subpopulations undergoing different but complementary dynamics.

Unfortunately, delineating the demographic consequences of population connectivity has remained elusive for most fish populations. For example, limited information exists about dispersal rates and trajectories for most populations, as well as how new immigrants into a population (i.e., dispersers from another population) affect the overall recruitment rate of the broader (recipient) population (Lowe and Allendorf 2010). Likewise, inefficient and ineffective techniques for discriminating among individuals from different subpopulations and for tracking survival of their progeny have historically limited the ability to identify subpopulation structure (Begg and Waldman 1999).

Fortunately, several advancements have improved our ability to understand dispersal dynamics and the relative contributions of recruits to the broader population. Improved hydrodynamic models, for example, offer better tracking of larval dispersal trajectories (North et al. 2009). In particular, hydrodynamic models can now be run backward in time to estimate the most likely dispersal paths and origins of passively dispersed larvae (Christensen et al. 2007; Hinrichsen et al. 2011). Likewise, recent technological advances have provided methods for using genetic data (Kochzius 2009; Seeb et al. 2011) and otolith microchemical and growth rate information (Campana 1999; Swearer et al. 1999) as “natural” tags to identify subpopulation structure and the relative contribution of recruits to the broader population (Begg and Waldman 1999; Gillanders 2009), with the greatest success coming when multiple discrimination approaches are used simultaneously (Swearer et al. 1999; Miller et al. 2005). Further, Fraker et al. (2015a) showed that combining hydrodynamic backtracking approaches with individual-based or subpopulation-specific natural tags can lead to a more complete description of population connectivity.

Herein, we utilize the approach introduced by Fraker et al. (2015a) to determine whether western Lake Erie’s yellow perch population is connected to the Lake St. Clair – Detroit River system (SC-DRS; Fig. 1) through larval exchange, as well as whether this connectivity might be important to understanding recruit-

ment dynamics in Lake Erie. While multiple breeding subpopulations are thought to support western Lake Erie’s yellow perch population (e.g., Reichert et al. 2010; Sepulveda-Villet and Stepien 2011; Kocovsky et al. 2013; Sullivan and Stepien 2014; Carreon-Martinez et al. 2015), which is not unlike other exploited fish populations within and outside of the Great Lakes basin, the relative contributions of recruits to Lake Erie’s fishable population from potential external sources such as the SC-DRS remains unknown. Understanding the degree to which these systems are connected holds great potential to alter how yellow perch are managed in Lake Erie, given that current catch quotas are based on geographically defined management units without regard to population structure or recruits from external sources such as the SC-DRS (YPTG 2013).

While never documented in the field or quantified, much circumstantial evidence exists to suggest that demographically important connectivity through larval exchange exists between the SC-DRS and western Lake Erie. For example, during 2006–2009, larval yellow perch were consistently captured in open waters of western Lake Erie near the Detroit River outflow (along the north shore) at densities 5- to 10-fold greater than those captured near the Maumee River outflow (along the south shore) (Reichert et al. 2010; Ludsin et al. 2011). Whether these north-shore larvae originated in Lake Erie or were exported from the SC-DRS remains unknown; however, the likelihood of flow-assisted transport is strong, since (i) high densities of larval yellow perch were found in Detroit River during 2006–2010 (EFR, unpublished data), (ii) Detroit River flow rates as measured by the USGS consistently exceed the swimming speed of yellow perch larvae (Houde 1969), and (iii) hydrodynamic backtracking modeling that traced dispersal trajectories of yellow perch larvae captured in western Lake Erie during 2006–2007 showed that a substantial portion of these larvae likely originated from the SC-DRS (Fraker et al. 2015a). Moreover, recent otolith microchemical and genetic research has demonstrated that 50% to 90% of the yellow perch that survive to the age-0 juvenile stage — which is a strong indicator of future recruitment to the fishery at age-2 (YPTG 2013; Farmer et al. 2015) — spend their larval stages in northern waters located near the Detroit River outflow (Reichert et al. 2010; Ludsin et al. 2011; Carreon-Martinez et al. 2015).

To determine if and how the SC-DRS and western Lake Erie are connected, with the ultimate intention of improving the ability of agencies to understand and manage western Lake Erie’s yellow perch population, we sought to test two hypotheses: (1) the SC-DRS and western Lake Erie are connected through larval dispersal; and (2) this connectivity has demographic consequences for western Lake Erie’s fishable (adult) population by contributing larvae that recruit to the age-0 juvenile stage. Towards this end, we described population structure by complementing microsatellite information from larvae captured in both the SC-DRS and northern and southern shores of western Lake Erie during 2006 and 2007 with larval age information (from otoliths) and a hydrodynamic backtracking approach that estimates pre-collection larval dispersal (Fraker et al. 2015a). Afterwards, we used this structure to estimate the relative contributions of recruits from the SC-DRS and two western Lake Erie subpopulations to western Lake Erie’s age-0 juvenile population, which is when adult recruitment is set in this population (YPTG 2013; Farmer et al. 2015).

## Materials and methods

### Study system and species

Lake Erie is a part of the Laurentian Great Lakes system and is highly productive across all trophic levels. It contains several ecologically and economically important fishes, including yellow perch, which supports Lake Erie’s largest commercial fishery and also a strong recreational fishery (YPTG 2013). Recruitment to

these fisheries has fluctuated widely through time for reasons that remain largely unknown (YPTG 2013).

Lake Erie consists of three geomorphologically distinct basins (western, central, and eastern) that vary in depth and productivity, with a trend of mean depth increasing from west to east and productivity decreasing along the same west-to-east trajectory (Ludsin et al. 2001). The western basin, which is the focus of this study (Fig. 1), is the shallowest (mean depth = 7.4 m) and most highly productive of the three basins and is a major producer of yellow perch (Reichert et al. 2010; YPTG 2013). The western basin is a hydrodynamically active system, characterized by inflows from the Detroit and Maumee rivers (Baker 2011), large-scale circulation that is primarily driven by Detroit River inflows from the north and basin-wide winds (Beletsky et al. 2013), and the formation of a turbid river plume driven by Maumee River inflows from the south (Reichert et al. 2010).

While yellow perch spawning locations are poorly described, they are likely numerous (Goodyear et al. 1982; Ludsin et al. 2010), with larval production areas documented in the southern and northern shores of the lake (Ludsin 2000; Ludsin et al. 2006; Reichert et al. 2010). In addition, yellow perch larvae have been recently captured in the Detroit River (EFR, unpublished data; see below), although whether they are produced there or drift from Lake St. Clair is unknown. Lake Erie yellow perch larvae hatch at ~5 mm in total length (TL), have weak swimming abilities until ~9.5 mm TL, and spend about 30–35 days in the water column feeding on zooplankton before becoming demersal as juveniles (Houde 1969; Gopalan et al. 1998; Ludsin 2000).

## Field collections

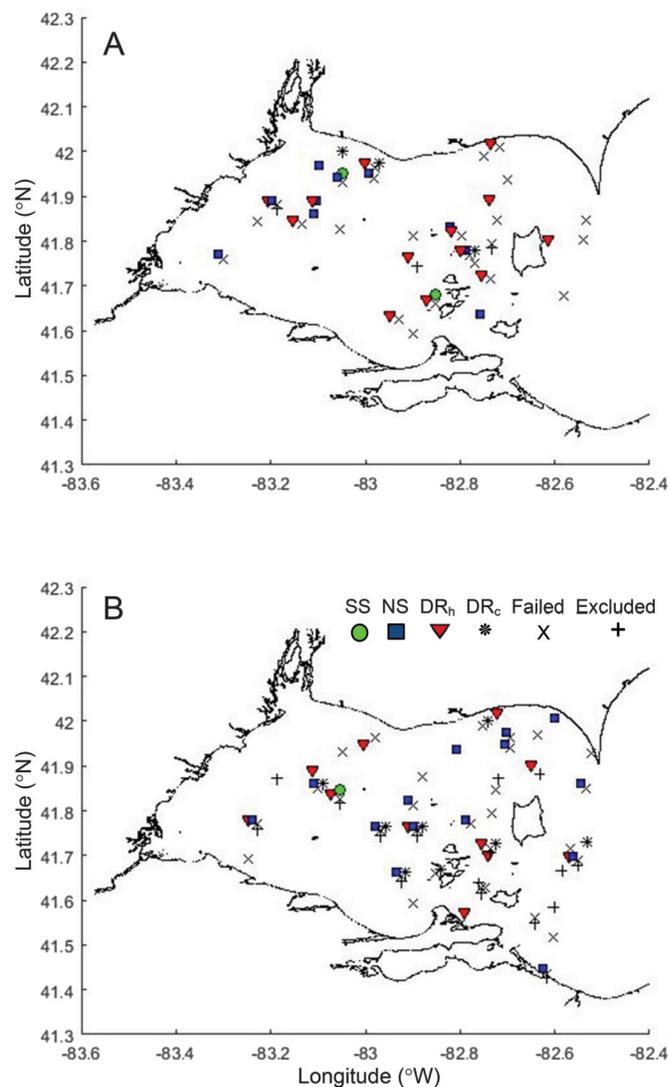
### Larvae

Larval yellow perch were used to define unique, group-level, genetic patterns and estimate hatch dates from three disparate areas that could be contributing recruits to western Lake Erie's fishery. Although exact spawning locations are unknown, larvae used in this study were collected during April–May 2006 and 2007 at three locations: (i) in the Detroit River proper (the "DR<sub>c</sub>" subpopulation; north of 42.05°N); (ii) along the north shore of western Lake Erie in and around the outflow of the Detroit River (the "NS" subpopulation; between 42.05°N and 41.8°N); and (iii) along the south shore of western Lake Erie in and around the outflow of the Maumee River (the "SS" subpopulation; south of 41.8°N; Fig. 1; Table S1<sup>1</sup>). Weekly collections of larval yellow perch were conducted at up to 12 sites in both the north- and south-shore regions (Reichert et al. 2010) and at up to 11 sites within the southern portion of the Detroit River proper (Fig. 1). All larvae were collected with paired (1 m diameter) bongo nets towed ~1 m from the bottom of the lake to the surface (500 µm mesh). These larvae were preserved in 100% ethanol until identification and were transferred to 95% ethanol for storage. In total, larvae of varying size and age (Table S1<sup>1</sup>) were collected during 2006 ( $N = 90$  from SS,  $N = 154$  from NS,  $N = 53$  from DR<sub>c</sub>) and 2007 ( $N = 81$  from SS,  $N = 282$  from NS,  $N = 64$  from DR<sub>c</sub>).

### Juveniles

Age-0 juveniles were collected during late August in both 2006 and 2007 ( $N = \sim 70$  sites per year) via annual fisheries-independent bottom-trawl (10 m head rope; 3 km·h<sup>-1</sup> tow speed) surveys conducted across western Lake Erie by the Ohio Department of Natural Resources – Division of Wildlife and the Ontario Ministry of Natural Resources (Reichert et al. 2010). We conducted molecular analyses on 119 (2006) and 167 (2007) juveniles that were randomly chosen from trawl collection sites based on proportional catches

**Fig. 2.** Subpopulation classification of yellow perch juveniles collected in western Lake Erie during 2006 (A) and 2007 (B). Juvenile genetic classification reflects assignment using backtracking-revised larval groupings. Note that symbols of juveniles collected at the same site and classified to the same subpopulation overlap. Symbols are slightly offset if juveniles from a site were assigned to different subpopulations so that the range of subpopulation classifications at a site is visible.



(Reichert et al. 2010; Fig. 2). All individuals were stored frozen (-20 °C) until processing.

### Larval age estimation

Daily increment counts from sagittal otoliths were used to estimate the hatch date and age at capture (Campana 1999) of larvae collected in each capture area. Methods for otolith extraction and age analysis followed those of Ludsin et al. (2006) and Reichert et al. (2010). Data for NS and SS larvae were taken from archived collections that had been previously analyzed for a different purpose (Reichert et al. 2010). Sagittal otoliths from larvae collected in the DR<sub>c</sub> during 2006 and 2007 ( $N = 30$  random individuals per year) were extracted and newly analyzed. Utilizing NIS-Elements imaging software (Media Cybernetics, Inc., Rockville, Maryland, USA)

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2015-0161>.

and a Nikon E200 compound microscope (100× and 50× magnification, oil immersion, Nikon Inc., Melville, New York, USA), post-hatch daily increments were counted, and the total otolith radius (core to otolith edge), hatch radius (hatch check to otolith edge), and daily growth increments of each otolith were measured. For all subpopulations, larval age was determined from a single count for larvae estimated to be  $\leq 25$  days old, as previous research conducted with Lake Erie yellow perch less than this age has shown that single increment counts are reliable (Ludsin et al. 2001; Table S1<sup>1</sup>). For larvae estimated to be  $> 25$  days of age, at least one additional blind count was conducted, with additional counts being performed as needed (see Reichert et al. 2010 for details). Daily increment count information was used to estimate each larva's hatch date. This information was used in our backtracking procedure to correct hatch locations based on pre-collection dispersal (see below). Because subpopulation- and growth-dependent survival of larvae has been documented in western Lake Erie yellow perch (Reichert et al. 2010; Ludsin et al. 2011; Carreon-Martinez et al. 2015), ageing each larva also allowed us to determine whether individuals collected in each region were of the same relative age, thus helping ensure that no bias was introduced in identifying larval recruitment patterns to the juvenile stage because of age-at-collection differences among subpopulations.

### Hydrodynamic backtracking of larval dispersal

Model simulations were carried out with hydrodynamic conditions (e.g., currents, temperature) 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 (3D) primitive equations in a second-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 successful prediction of water levels, temperatures, and currents in the lake (Schwab and Bedford 1994; Chu et al. 2011). Although recent work has shown that the interpolated meteorology can cause errors in the summer circulation in the central basin of Lake Erie (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 owing 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 perch in western Lake Erie. The particle model used a second-order Lagrangian scheme (Bennett and Clites 1987) to simulate passive, neutrally buoyant particle movement in 3D. 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 ( $0.0005 \text{ m}^2 \cdot \text{s}^{-1}$ ).

The dispersal pathway of each larvae was tracked from the time of hatch until collection by using otolith age information (per above) in combination with a hydrodynamic particle-backtracking procedure (Fraker et al. 2015a). Briefly, we simulated the dispersal of an individual larva by spreading 5000 particles over a 5 m radius at the location (and time) that larva was collected by our nets. We ran hydrodynamic simulations backward in time, starting from the time of capture until the estimated hatch date (from otoliths). We used the backtracked daily locations of the 5000 particles to determine the most likely posthatch dispersal path of that individual from time of collection to its (earlier) time of hatch. To do

so, we calculated a grid-based probability of daily larva location using the percentage of the 5000 particles present within each region (NS, SS, or DR) on each posthatch day. The region that had the highest percentage of the 5000 particles on the day of hatching was predicted to be the most likely hatch site for that individual (see Fraker et al. 2015a for further discussion of method). Throughout this process, water-current uncertainties and variability were accounted for by the calibrated diffusion coefficients and schemes, as described above.

### DNA extraction procedure

Nine microsatellite loci were genotyped per individual using the following procedure. DNA from tissue samples was extracted using a plate-based extraction protocol (Elphinstone et al. 2003). DNA was dissolved in 50  $\mu\text{L}$  of Tris–EDTA buffer (10  $\text{mmol} \cdot \text{L}^{-1}$  Tris, 1.0  $\text{mmol} \cdot \text{L}^{-1}$  EDTA, pH 8.0) for larval samples, whereas 100  $\mu\text{L}$  of the buffer was used for juvenile samples. PCR amplification consisted of 25  $\mu\text{L}$  reactions with 1.5  $\mu\text{L}$  of template DNA (20  $\text{ng} \cdot \mu\text{L}^{-1}$ ), 2.5  $\mu\text{L}$  10× PCR buffer, 2.5  $\mu\text{L}$  of  $\text{MgCl}_2$  (25  $\text{mmol} \cdot \text{L}^{-1}$ ), 0.3  $\mu\text{L}$  of dNTPs (50  $\mu\text{mol} \cdot \text{L}^{-1}$  each), 0.2  $\mu\text{L}$  (0.5  $\mu\text{mol} \cdot \text{L}^{-1}$ ) of dye-labeled primer, 0.2  $\mu\text{L}$  (0.5  $\mu\text{mol} \cdot \text{L}^{-1}$ ) of the reverse primer, and 0.10 U Taq polymerase. PCR conditions included initial denaturation at 94 °C for 2 min, followed by 35 to 40 cycles of denaturing at 94 °C for 15 s, various annealing temperatures for 30 s (following Li et al. 2007), extension at 72 °C for 30 s, and a final extension at 72 °C for 10 min. DNA fragment sizes were determined using the LI-COR 4300 DNA analyzer (LI-COR, Inc., Lincoln, Nebraska, USA) and scored using GenElmage IR 4.05 (LI-COR, Inc.).

### Molecular genetics analyses

#### Subpopulation groupings

We determined yellow perch subpopulation structure in two ways, with each annual cohort (year) analyzed separately. The first way assigned each larva to one of three initial groups (i.e., the SS, NS, or DR<sub>c</sub> subpopulation) based on its original capture location. The second way considered hydrodynamic backtracking results, using the most probable hatch location to assign each larvae to one of four possible initial groups of origination (i.e., SS, NS, or DR<sub>c</sub> and DR<sub>h</sub> subpopulation). The SS and NS are the same western Lake Erie subpopulations as described above. The DR<sub>c</sub> subpopulation consisted of larvae that were predicted to have hatched in the SC-DRS and that also were captured in the Detroit River. Because no larvae collected in the Detroit River were predicted to have originated (hatched) in Lake Erie (see Results below), the group of DR<sub>c</sub> larvae used in this second set of analyses is identical to the group of larvae used in the first set of analyses (based on collection location only). The DR<sub>h</sub> subpopulation consisted of larvae that were predicted to have hatched in the SC-DRS, but that were captured in western Lake Erie proper (i.e., they were predicted to have dispersed from their original SC-DRS hatch location into western Lake Erie prior to capture). All analyses were conducted using only larvae  $\leq 8$  mm TL, which appear highly vulnerable to passive dispersal given their weak swimming abilities in relation to the high flow rates associated with the Detroit River (Houde 1969; [http://waterdata.usgs.gov/mi/nwis/uv/?site\\_no=04165710&PARAMETER\\_cd=00065,00060](http://waterdata.usgs.gov/mi/nwis/uv/?site_no=04165710&PARAMETER_cd=00065,00060)). Sample sizes for these analyses are reported in Table S2<sup>1</sup> (subpopulations based on collection location) and Table S3<sup>1</sup> (subpopulations based on backtracked hatch location).

#### Subpopulation genetic structure

Multiple approaches were used to explore structure among the SS, NS, DR<sub>c</sub>, and DR<sub>h</sub> subpopulations, using microsatellite information. Fisher's exact tests for Hardy–Weinberg Equilibrium (HWE) were conducted using Arlequin (version 3.5.1.2; Excoffier et al. 2005), and tests for linkage disequilibrium were run for all pairs of loci in all larval and juvenile groups using Genepop (version 4.0.7; Rousset 2008). Second, pairwise  $F_{ST}$  estimates were calculated using Genepop (version 4.0.7; Rousset 2008; following Weir and

**Table 1.** Pairwise  $F_{ST}$  values for yellow perch larvae collected in the Lake St. Clair – Detroit River system (SC-DRS) and western Lake Erie during 2006 and 2007.

Subpopulation	Capture				Hatch					
	2006		2007		2006			2007		
	DR <sub>c</sub>	NS	DR <sub>c</sub>	NS	DR <sub>h</sub>	NS	SS	DR <sub>h</sub>	NS	SS
NS	0.013*	—	0.017*	—	0.004	—	—	0.005	—	—
SS	0.017*	0.002*	0.025*	0.002	0.005	0.011*	—	0.006	0.009*	—
DR <sub>c</sub>	—	—	—	—	0.017*	0.014*	0.016*	0.024*	0.017*	0.025*

**Note:** The initial assignment locations of larvae (NS, north shore of western Lake Erie; SS, south shore of western Lake Erie; DR<sub>c</sub>, Detroit River) were based on larval collection locations (Capture), whereas the revised (most probable) hatch locations (Hatch) were based on the backtracking results. For analyses based on backtracking-modified hatch locations, larvae captured in western Lake Erie proper but that were predicted to have hatched in the SC-DRS were designated as DR<sub>h</sub>, whereas those captured in the Detroit River and predicted to have hatched in the SC-DRS were designated as DR<sub>c</sub>. The same individuals were used for the DR<sub>c</sub> in both sets of analyses within a year. Only larvae <8 mm total length were included in these analyses. Asterisks denote significant differences in allele frequency distributions, using Fisher exact tests with a Bonferroni-corrected  $\alpha$  level = 0.0167 (Capture) or 0.0083 (Hatch).

Cockerham 1984). Third, an analysis of molecular variance (AMOVA; following Weir and Cockerham 1984; Excoffier et al. 2005) was conducted. Year, subpopulation nested within year, and within-subpopulation effects were considered in our AMOVA model.  $P$  values < 0.05 were considered statistically significant, unless otherwise noted because of a Bonferroni correction.

Importantly, in describing genetic structure, we were not concerned with identifying population substructure per se. Instead, we sought to determine if enough (i.e., significant) structure existed among larval production areas such that we could develop reliable functions to determine the natal source area of juvenile recruits (e.g., Hogan et al. 2012). Indeed, previous studies have demonstrated that the assignment tests used herein are robust to low differentiation among subpopulations (e.g., low  $F_{ST}$ ) and violations of assumptions of HWE (Hauser et al. 2006; Bradbury et al. 2008).

#### Larval genetic self-assignment

A rank-based self-assignment analysis (GENECLASS 2.0; Paetkau et al. 1995; Piry et al. 2004; Carreon-Martinez et al. 2015), using larvae from all subpopulations, was conducted for two purposes. First, it was used to assess the consistency of subpopulation-specific genetic signatures for the subsequent classification of juveniles of unknown origin (see below). This analysis used a bootstrapping approach wherein each individual larva was removed from the dataset (one at a time) and subsequently treated as an “unknown” larva that is then assigned to one of the subpopulations, based on the genotypes of all other individuals (Paetkau et al. 1995). By determining the percentage of larvae successfully assigned back to their collection site, as well as exploring posterior probabilities of assignment for each individual, reliability in assignments for each subpopulation could be assessed. Second, this analysis was used to characterize genetic similarity among subpopulations. Genetic similarity was assessed by considering to which subpopulation each misclassified individual was assigned. Our expectation was that the DR<sub>c</sub> and DR<sub>h</sub> subpopulations would be misclassified as the NS subpopulation (or vice versa) more often than either DR subpopulation would be misclassified as the SS subpopulation, owing to the close geographical proximity of the Detroit River mouth to the north shore of western Lake Erie (see Fig. 1).

#### Juvenile genetic classification

A two-step process was used to classify juvenile recruits of unknown origin to a larval source population (Beneteau et al. 2009). First, a Bayesian assignment was conducted (Rannala and Mountain 1997) with Monte Carlo resampling, using a simulation algorithm (10 000 simulated individuals at an assignment threshold  $P = 0.05$ ; GENECLASS 2.0; Paetkau et al. 2004). Following Bayesian assignment, juveniles that were unlikely to have originated from any of the larval subpopulations being explored herein (i.e., NS, SS, DR<sub>c</sub>,

and DR<sub>h</sub>) were removed from the analysis. Such a possibility exists, given that enhanced swimming capabilities can allow individuals to actively move between lake basins (e.g., from the central to western basin of Lake Erie) during late larval and juvenile stages (Houde 1969; Beletsky et al. 2007). For this analysis, if a juvenile did not have a probability of assignment to any one of our subpopulations that exceeded 0.3 (i.e., it had a >70% chance of originating from a different subpopulation outside of the basin), it was excluded from analysis (Rannala and Mountain 1997; Carreon-Martinez et al. 2015). In alternate analyses that included these individuals, all were classified as failed assignments (MEF, unpublished data). Second, each remaining juvenile was assigned to a larval source population with an individual-based posterior probability of assignment. Only individuals with a posterior probability of assignment  $\geq 0.7$  were considered reliable (Rannala and Mountain 1997; Carreon-Martinez et al. 2015).

## Results

### Subpopulation genetic structure

Analysis of microsatellites revealed violation of assumptions of HWE for some loci (Tables S2 and S3<sup>1</sup>). For example, when larvae were grouped based on capture location, two, three, and four of the nine microsatellite loci deviated from HWE for larvae collected from the SS, NS, and DR<sub>c</sub>, respectively, with similar numbers of loci violating assumptions in 2007 (five, four, and one loci for SS, NS, and DR<sub>c</sub>, respectively). Similar numbers of violations (i.e., one to five loci) were evident when using backtracked hatch location to group larvae, although no violations were evident for some subpopulations in some years (e.g., DR<sub>c</sub> in 2006; SS in 2007). No single locus deviated from HWE consistently among subpopulations between years for either method of grouping larvae (Tables S2 and S3<sup>1</sup>), indicating that these violations of assumptions did not stem from null alleles or scoring errors. Additionally, no evidence existed for linkage disequilibrium between any loci after Bonferroni correction (MEF, unpublished data).

Based on capture location, pairwise  $F_{ST}$  values indicated some genetic differentiation among subpopulations during both years (Table 1).  $F_{ST}$  values were greatest between the geographically most distant subpopulations (SS and DR<sub>c</sub>), followed by the NS and DR<sub>c</sub> subpopulations, with the two Lake Erie subpopulations (NS and SS) possibly being slightly differentiated. Near identical results were evident during 2007, with the exception that genetic differentiation between the DR<sub>c</sub> and both Lake Erie subpopulations was greater than during 2006 (Table 1). Using predicted hatch locations (from backtracking) increased  $F_{ST}$  values between the NS and SS subpopulations during both years by 4.5- to 5.5-fold (Table 1). The DR<sub>c</sub> subpopulation (larvae hatched in the SC-DRS and captured in the Detroit River) had greater  $F_{ST}$  values than the DR<sub>h</sub> subpopulation (larvae hatched in the SC-DRS but captured in western Lake Erie proper) when compared with the SS and NS

**Table 2.** Genetic self-assignment results (assigned as %) for larval yellow perch collected in the Lake St. Clair – Detroit River system (SC-DRS) or western Lake Erie during 2006 and 2007.

Subpopulation	Capture			Hatch		
	DR <sub>c</sub>	NS	SS	SC-DRS	NS	SS
<b>2006</b>						
DR <sub>h</sub>	—	—	—	83	11	6
DR <sub>c</sub>	68	19	13	60	22	18
NS	12	52	36	17	53	30
SS	8	20	72	7	10	83
<b>2007</b>						
DR <sub>h</sub>	—	—	—	87	8	6
DR <sub>c</sub>	80	11	9	70	18	12
NS	21	49	30	15	52	33
SS	11	21	68	11	14	75

**Note:** The assignment location of larvae was based on their initial collection location (Capture) or their most probable hatch location (Hatch) based on hydrodynamic backtracking. Larvae were collected in the north shore (NS) and south shore (SS) of western Lake Erie, as well as the Detroit River. For analyses based on backtracking-modified hatch locations, larvae captured in western Lake Erie that were predicted to have hatched in the SC-DRS were designated as DR<sub>h</sub>, whereas those captured in the Detroit River and predicted to have hatched in the SC-DRS were designated as DR<sub>c</sub>.

subpopulations (Table 1). The  $F_{ST}$  between the DR<sub>c</sub> and DR<sub>h</sub> subpopulations generally exceeded those between the DR<sub>c</sub> and the NS and SS subpopulations during both years (Table 1).

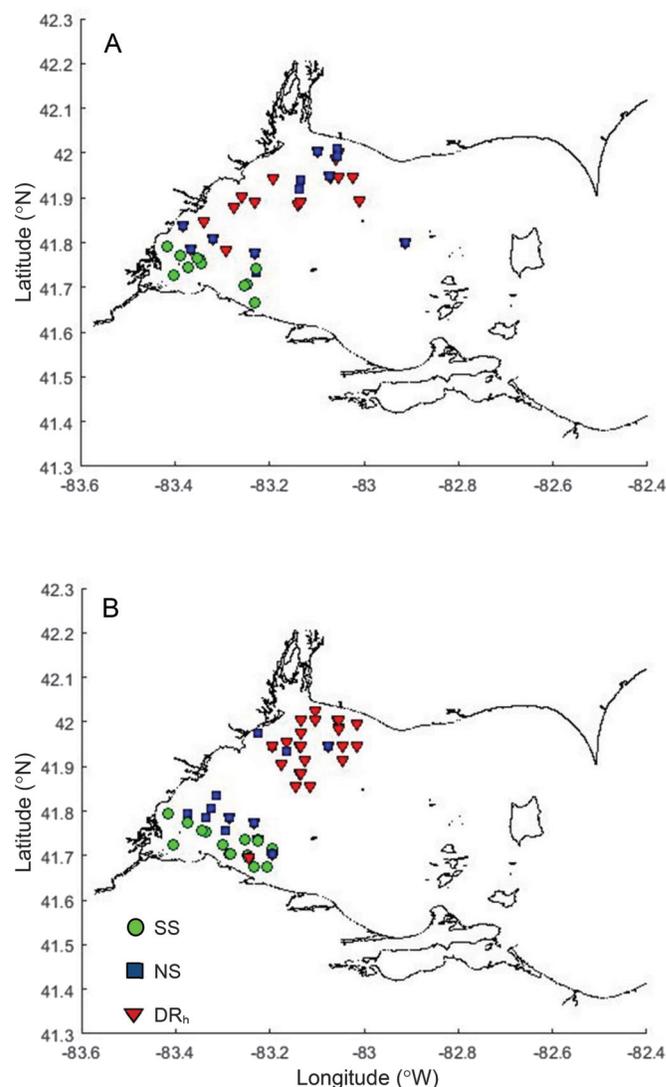
Fisher exact tests revealed generally consistent differences in allele frequency distributions among subpopulations. Using groups assigned based on capture location, allele frequency distributions differed between the DR<sub>c</sub> and NS subpopulations, as well as between the DR<sub>c</sub> and SS subpopulations, during both 2006 and 2007 (all  $P < 0.001$ ,  $df = 18$ ; Table 1). Allele frequencies also differed (marginally) between the NS and SS subpopulations during 2006 ( $P = 0.001$ ,  $df = 18$ ), although no significant difference was detected between these western Lake Erie subpopulations during 2007 ( $P = 0.04$ ,  $df = 18$ ; Table 1). Results based on hatch location were similar, with significant differences found between all subpopulations in both years, with the exception of the comparisons between DR<sub>h</sub> and NS and SS in 2006 and 2007 (Table 1).

Interannual differences in genetic structure among subpopulations was not evident, based on AMOVA results. When capture location is used to define subpopulations, differences in genetic structure between years explained none (0.00%) of the overall variation. Differences among subpopulations within years explained a small fraction (0.44%) of the variation ( $P = 0.5$ ). AMOVA results based on hatch location were similar, with 0.46% of the overall variation being explained by differences among subpopulation within years ( $P = 0.5$ ) and 0.00% due to year differences.

### Larval genetic self-assignment

Rank-based self-assignment tests demonstrated high variation in the potential to accurately assign larvae to a source subpopulation (SS, NS, or SC-DRS) during both years when initial assignment was based upon capture location (Table 2). During 2006, assignment accuracies of 68% and 72% were found for the DR<sub>c</sub> and SS subpopulations, respectively. Larvae collected in the Detroit River were misassigned to the geographically closer NS subpopulation more often than to the SS subpopulation during 2006 (Table 2). Likewise, misassigned larvae from the SS subpopulation were assigned to the geographically closer NS subpopulation than to the DR<sub>c</sub> subpopulation. Assignment accuracy for the NS subpopulation was the lowest at 52%, with larvae being misassigned to the SS and DR<sub>c</sub> subpopulations about evenly (Table 2). During 2007, nearly identical results were produced, with the highest self-assignment accuracies being found in the DR<sub>c</sub> (80%) and SS (68%) subpopulations (Table 2). Similar to 2006, larvae collected in the

**Fig. 3.** Subpopulation assignments of yellow perch larvae collected in western Lake Erie during 2006 (A) and 2007 (B). Larval assignment (SS, NS, or DR<sub>h</sub>) reflects revision after a hydrodynamic backtracking correction was applied (i.e., location shows collection location, while symbol shows subpopulation assignment). Larvae collected in the Detroit River and predicted to have hatched in the Lake St. Clair – Detroit River system (i.e., those collected in the Detroit River north of 42.05°N, DR<sub>c</sub>) are not shown. Note that symbols of larvae collected at the same site and assigned to the same subpopulation overlap. Subpopulation symbols are slightly offset if larvae from a site were assigned to different subpopulations so that the range of subpopulation assignments at a site is visible.



Detroit River were misassigned more often to the NS subpopulation than to the SS subpopulation, and larvae collected in the SS were more often misassigned to the NS subpopulation than to the DR<sub>c</sub> subpopulation. Larvae collected in the NS had a low (49%) self-assignment accuracy, with these larvae being misclassified to the SS subpopulation more often than to DR<sub>c</sub> (Table 2).

Using hatch location (i.e., after backtracking revision; Figs. 3A and 3B) produced a similar pattern as using capture location, but with improved self-assignment accuracies for at least two of the subpopulations. While little improvement in self-assignment accuracy ( $\leq 3\%$ ) was found for the NS subpopulation during both years, self-assignment accuracies for the SS subpopulation increased from 72% to 83% during 2006 and from 68% to 75% during

**Table 3.** Genetic classification results for age-0 juvenile yellow perch recruits captured in western Lake Erie during 2006 and 2007.

Year	SS	NS	DR <sub>c</sub>	DR <sub>h</sub>	Failed	Excluded	Total juveniles
<b>Capture</b>							
2006	6	9	3	—	98	3	119
2007	7	26	9	—	98	27	167
<b>Hatch</b>							
2006	3	10	3	21	79	3	119
2007	1	18	8	17	96	27	167

**Note:** Juveniles that had a <30% likelihood of originating from any of the three larval collection areas (NS, north shore; SS, south shore; DR, Detroit River), following Bayesian correction, were “Excluded” from analyses. Those with probabilities of assignment to a larval production area that ranged 30% to 70% were considered “Failed”. Those juveniles with a >70% probability were assigned to their respective larval population(s) (i.e., SS, NS, DR<sub>c</sub>, or DR<sub>h</sub>). The initial assignment of juveniles was based on larval collection locations (Capture). The revised assignment was based on the most probable hatch location (Hatch) based on the backtracking results. For analyses based on backtracking-modified hatch locations, larvae captured in western Lake Erie proper but that were predicted to have hatched in the SC-DRS were designated as DR<sub>h</sub>, whereas those captured in the Detroit River and predicted to have hatched in the SC-DRS were designated as DR<sub>c</sub>. The numbers of juveniles assigned to an SC-DRS origin are highlighted with bold font.

2007 (Table 2). Correction for precapture dispersal also improved the self-assignment accuracy of larvae predicted to have originated in the SC-DRS (Table 2). For example, the self-assignment accuracies for larvae captured in western Lake Erie proper but that were predicted to have hatched in the SC-DRS (DR<sub>h</sub> subpopulation) were higher (83%–87% for 2006–2007, respectively) when compared with larvae whose capture location was assumed to be their hatch location (i.e., non-backtrack-corrected DR<sub>c</sub> larvae; 68%–80% for 2006–2007, respectively).

### Juvenile genetic classification

Classification juveniles of unknown origin to a source subpopulation indicated that the SC-DRS contributed recruits to western Lake Erie’s population during both years. Based on analyses using larval yellow perch capture location, during 2006 and 2007, three and 27 individuals were excluded from analysis (Table 3), respectively, owing to a Bayesian probability value of <0.3 (i.e., these individuals had less than a 30% chance of originating from one of the three western basin subpopulations; Rannala and Mountain 1997; Carreon-Martinez et al. 2015). Of the remaining juveniles that were classified to a source subpopulation (SS, NS, or DR<sub>c</sub>), 98 were considered failed assignments in each year, owing to a posterior probability of assignment of <0.70 (Table 3). Of the remaining 18 juveniles classified during 2006, six, nine, and three (33%, 50%, and 17%) were typed back to the SS, NS, and DR<sub>c</sub>, respectively (Table 3). During 2007, of the 42 juveniles classified to a source population with high confidence (posterior probability >0.70), seven, 26, and nine (17%, 62%, and 21%) were assigned to the SS, NS, and DR<sub>c</sub>, respectively (Table 3).

When juvenile assignments were based on hatch location instead of capture location (i.e., after backtracking revision), the number of failed assignments decreased slightly ( $N = 79$ ) during 2006, but remained similar during 2007 (Table 3). Backtracking greatly increased the number of juveniles assigned to one of the SC-DRS subpopulations (DR<sub>c</sub> or DR<sub>h</sub>) during both years, with 65% (24 of 37) and 57% (25 of 44) of the juvenile recruits predicted to have originated in the SC-DRS during 2006 and 2007, respectively (Figs. 2A and 2B; Table 3).

### Discussion

Our study revealed that connectivity with the SC-DRS appears to be influencing the yellow perch population in western Lake Erie through the export of larvae that recruit to the age-0 juvenile

stage. Our study also showed how complementing natural tagging approaches (e.g., microsatellites) with physical (e.g., hydrodynamics) models that consider spatiotemporal processes operating during dispersive early life stages can improve our ability to identify population connectivity and the relative contribution of subpopulations to the broader population. More specifically, revision of hatch locations using hydrodynamic backtracking improved our ability to identify genetic structure in our weakly differentiated subpopulations and increased the estimated contribution of juvenile recruits from the SC-DRS system to western Lake Erie’s open-lake population by three- to fourfold. Below, we discuss our findings more fully, including how they can be used to guide research and management within the Lake Erie basin. Finally, we discuss the general implications of our research for addressing questions related to population connectivity and recruitment dynamics in large lake and marine ecosystems.

### Lake Erie yellow perch

#### Population connectivity and demographics

Our study indicated that larval yellow perch are being advected from the SC-DRS into western Lake Erie and that some are recruiting to the juvenile population. In support of this notion, our hydrodynamic modeling showed that a substantial percentage of larvae collected in western Lake Erie proper actually hatched in the SC-DRS (25% in 2006, 64% in 2007), assuming passive transport (Houde 1969). In addition, a conspicuous percentage (17% in 2006, 10% in 2007) of age-0 juveniles — the life stage at which recruitment to the fishery at age-2 is set (YPTG 2013; Farmer et al. 2015) — captured in Lake Erie during 2006 and 2007 assigned back with high confidence to the SC-DRS after using backtracking to revise (and seemingly improve) initial larval hatch locations. These findings support our hypothesis that potentially demographically important population connectivity exists between these systems, with the mechanism of connectivity being larval dispersal from the SC-DRS to western Lake Erie.

While finding evidence for connectivity between the SC-DRS and western Lake Erie, we also documented weak genetic structure between systems. Given the apparent gene flow, the weak structure is not surprising. Fisher’s exact tests showed that larvae collected in the lower Detroit River (DR<sub>c</sub>) proper had significant genetic differentiation from larvae originating in western Lake Erie’s north shore (NS) or south shore (SS) during both 2006 and 2007. Likewise, genetic differentiation was evident between NS and SS larvae during 2006 (and in 2007, but only based on hatch location), although this difference was not as great as found between the DR<sub>c</sub> and either the NS or SS subpopulations. The  $F_{ST}$  values calculated for DR<sub>c</sub> and Lake Erie (NS, SS) yellow perch population pairs in our study (0.013–0.025) are lower than those measured for some freshwater fish populations (e.g., landlocked Atlantic salmon (*Salmo salar*) in Lac-Saint Jean, Canada;  $F_{ST} = 0.109$ ; Fraser et al. 2007), but they are within the range of values for other species that exhibit homing with some degree of straying (e.g., brown trout (*Salmo trutta*);  $F_{ST} = 0.018$  to 0.063; Carlsson et al. 1999; Fraser et al. 2007) and similar to the total  $F_{ST}$  measured for 15 microsatellite loci in 15 spawning groups of yellow perch from lakes St. Clair, Erie, and Ontario ( $F_{ST} = 0.034$ ; Sepulveda-Villet and Stepien 2011). Further, these values are relatively high when compared with the mean global  $F_{ST}$  values found among populations of adult fish within coral reef systems known to exhibit high dispersal rates (e.g., 0.003: Christie et al. 2010; 0.001: Saenz-Agudelo et al. 2011; 0.005: Hogan et al. 2012). Our  $F_{ST}$  values for NS–SS population pairs (~0.002), however, were close to these values.

The relatively large  $F_{ST}$  values between the DR<sub>c</sub> and DR<sub>h</sub> (2006: 0.017; 2007: 0.024) were surprising to us, given that both groups were predicted to have originated from the SC-DRS. However, while both the DR<sub>c</sub> and DR<sub>h</sub> larvae emanate from the SC-DRS, it is important to recognize that this system is large and includes dif-

ferent types of spawning habitats, including both lotic and lentic. As such, larvae from one of these SC-DRS subpopulations could have potentially spawned in Lake St. Clair proper (or even above it) and the other below it (in the Detroit River proper, perhaps even just above the entrance to Lake Erie). In this way, both subpopulations could remain genetically separated even though their larvae share an identical dispersal pathway into Lake Erie. In support of this general idea, Sullivan and Stepien (2014) documented some genetically disparate yellow perch spawning groups across Lake Erie and the SC-DRS, including a genetically distinct subpopulation that spawns at restored habitat at Belle Isle within the Detroit River. Another possibility is that our hydrodynamic backtracking is inaccurately assigning larvae from the western basin to the DR<sub>h</sub> subpopulation, which leads to the large  $F_{ST}$  values between the DR<sub>c</sub> and DR<sub>h</sub> subpopulations. Given the consistent strong outflow of the Detroit River, we have relatively high confidence in the DR<sub>h</sub> larval assignments. However, the possibility exists that these or other assignment errors may account for the unexpected  $F_{ST}$  values. Regardless of the potential explanation, further data are needed to satisfactorily resolve this issue.

We propose three possible mechanisms that can explain how weak genetic structure can be maintained between the SC-DRS and western Lake Erie subpopulations in the face of connected populations via larval dispersal, as well as contributions of SC-DRS individuals to the recruited juvenile population in western Lake Erie. First, homing behavior to natal spawning sites may exist for SC-DRS yellow perch, which can lead to reproductive isolation despite mixing during early life stages. Such homing behavior has been demonstrated in yellow perch in other systems (Kipling and Le Cren 1984; Hodgson et al. 1998; Leung et al. 2011) and other fishes, both freshwater (Neville et al. 2006; Stepien et al. 2009) and marine (Ruzzante et al. 2006; Walther and Thorrold 2008). Second, although remote, the possibility exists that SC-DRS fish transported into Lake Erie remain there in small numbers (perhaps in a different lake basin) and do not subsequently interbreed with grown NS or SS larvae. Such reproductive isolation among sympatric subpopulations may arise via kin recognition, as has been found in Lake Constance, Germany, for European perch (*Perca fluviatilis*), a congener of yellow perch (Gerlach et al. 2001). This mechanism also has been suggested as a possible explanation of similar kin groups found in Lake Erie yellow perch (Kocovsky et al. 2013), but has not yet been studied. Growth-dependent survival may offer a third mechanism. Ludsin et al. (2011) and Carreon-Martinez et al. (2014) provide a wealth of evidence to demonstrate that both predation risk and predation mortality were higher in Lake Erie's north shore than south shore during our study years (2006–2007). This disparity was due to formation of turbid, open-lake plumes by Maumee River (see Fig. 1) inflows in the south shore during the larval yellow perch production period, which provided a refuge from predation for larvae (Ludsin et al. 2011; Carreon-Martinez et al. 2014). In turn, larvae that resided in this south-shore plume recruited disproportionately better to the juvenile stage than those living outside of it during both of our study years (Reichert et al. 2010; Ludsin et al. 2011; Carreon-Martinez et al. 2015). While the Maumee River plume may indeed be crucial to the recruitment success of larval yellow perch in western Lake Erie, we hypothesize that the initial source of the larvae may be the SC-DRS (via larval dispersal) in addition to the Maumee River (south-shore) region.

Because our juvenile classifications require larval subpopulations to be genetically distinct from one another, the connectivity between the SC-DRS and western Lake Erie and within western Lake Erie may reduce our ability to discriminate among larval subpopulations and successfully classify juveniles back to a breeding subpopulation. Reduced discrimination among subpopulations in our study also may emanate from imperfect sampling, owing to river-flow or wind-driven circulation that transports larvae from their natal location into the natal location of another

subpopulation prior to collection for development of a subpopulation-specific genetic signature (Fraker et al. 2015a). In this way, the suite of larvae collected to characterize the north shore, for example, might actually have consisted of a mix of larvae produced locally and individuals that were physically transported there from another location (e.g., the Detroit River or south shore). Indeed, geographically close subpopulations in this study were less genetically distinct than those farther apart. Specifically, the DR<sub>c</sub> and SS subpopulations were more differentiated than were the DR<sub>c</sub> and NS or NS and SS during both of our study years. Our hydrodynamic simulations of larval yellow perch advection suggest that transport of larvae from the SC-DRS into western Lake Erie is fairly common, although revising initial assignments based on the backtracking results tended to have small effects on  $F_{ST}$  values in this study. Similar long-distance transport of larvae via river-flow and wind-driven circulation has been documented both in the Great Lakes (Mion et al. 1998; Hook et al. 2006; Beletsky et al. 2007) and marine ecosystems (Cowen et al. 2003; Hogan et al. 2012).

#### Future Lake Erie research and management

We encourage continued research that is focused on quantifying contributions of the SC-DRS to the western basin yellow perch population, as this source may have been important historically. While the degree to which the SC-DRS contributes juvenile recruits to western Lake Erie is only known for 2006 and 2007, which were years of below average and average recruitment (YPTG 2013), the possibility exists that contributions from this subpopulation might be higher under different ecosystem conditions. Such conditions might arise owing to high Detroit River inflows that transport more larvae into western Lake Erie or possibly higher Maumee River inflows that cause a greater proportion of the western basin to be encompassed by the “protective” turbid Maumee River plume during the springtime larval production period (Ludsin et al. 2010, 2011; Reichert et al. 2010; Carreon-Martinez et al. 2014). Hydrodynamic modeling (both forward and backward in time) in conjunction with genetic analyses or other natural tagging approaches (e.g., otolith microchemistry) that are being used to discriminate yellow perch spawning subpopulations in Lake Erie (Ludsin et al. 2006; Fraker et al. 2015a) also could assist in evaluating annual contributions of larvae from a donor population (e.g., SC-DRS) to its recipient population (Lake Erie). We also see a strong need to better understand yellow perch subpopulation structure within the SC-DRS, including identifying where spawning occurs in this system.

Our findings also have implications for the management of western Lake Erie's yellow perch population. We presented strong evidence for the contribution of age-0 juvenile recruits to the western Lake Erie yellow perch population from at least one external subpopulation (a subpopulation located within the SC-DRS). Thus, modification of Lake Erie's current yellow perch management plan (YPTG 2013) to consider contributions of recruits from the SC-DRS to western Lake Erie seems warranted (but see Sullivan and Stepien 2014 for a landscape genetic analysis that found evidence for historical genetic isolation among these groups, although not always related to distance). The need to better understand how contributions from the SC-DRS to western Lake Erie's population vary temporally seems especially important given that maintaining a diverse “portfolio” of spawning stocks (sensu Schindler et al. 2010) has been shown to stabilize fisheries production in other ecosystems during large-scale ecosystem change (Griffiths et al. 2014). Because human-induced ecosystem change has been prominent in the Laurentian Great Lakes basin during the past century (Bunnell et al. 2014), including Lake Erie (Ludsin et al. 2001; Jones et al. 2006; Scavia et al. 2014), the need to understand subpopulation (stock) structure and maintain stock diversity seems as important as ever in the Great Lakes basin.

### Implications for quantifying connectivity and recruitment

While the importance of larval dispersal to fish recruitment dynamics has long been recognized in marine ecosystems (Caley et al. 1996; Cowen and Sponaugle 2009), larval dispersal has historically been neglected in large freshwater systems. For example, only within recent decades have researchers begun to consider the role of larval dispersal in the fish recruitment process in freshwater ecosystems, including the world's Great Lakes (reviewed by Ludsin et al. 2014). Further, we only know of one other study (Hatcher et al. 1991) that has considered the role of larval dispersal as a mechanism for intersystem population connectivity in the Great Lakes basin. Given that many of the Laurentian Great Lakes' ecologically and economically important fishes (e.g., walleye, yellow perch, alewife) have a prolonged pelagic egg or larval stage that is similar to that of their marine counterparts (Ludsin et al. 2014; Pritt et al. 2014), these species also are highly suited to hydrodynamic transport during early life stages (Ludsin et al. 2014). In turn, demographically important intra- and intersystem connectivity — via dispersal during early life stages — may be as widespread a mechanism of population connectivity in the world's large lakes as it is in marine ecosystems.

Finally, our work points to the need to continue to break down the barriers that exist between freshwater and marine researchers (also see Pritt et al. 2014; Ludsin et al. 2014). Our findings clearly show that population connectivity via larval dispersal, which has historically been considered a marine phenomenon (see review by Cowen and Sponaugle 2009), may play a critical role in structuring fish populations in large lake ecosystems such as Lake Erie. For this reason, we support Ludsin et al.'s (2014) call for the expanded use of coupled biological–physical models in large freshwater ecosystems that are focused on larval fish dispersal and recruitment (e.g., Beletsky et al. 2007; Fraker et al. 2015b). Such models are quite common in marine ecosystems (Christensen et al. 2007; Miller 2007; North et al. 2009; Hinrichsen et al. 2011) and most certainly could help address the current gap in knowledge regarding the demographic consequences of connectivity in fish and other aquatic animal populations in large lake ecosystems (Lowe and Allendorf 2010). The continued joint application of marine approaches (e.g., coupling physical–biological models) and concepts (e.g., population connectivity through larval dispersal) to the world's large lake ecosystems would help maximize our ability to identify general processes that explain why metapopulations fluctuate and how they are structured.

### Acknowledgements

This work was funded by multiple sources and supported by multiple partners, including the Federal Aid in Sport Fish Restoration Program (F-69-P, Fish Management in Ohio), administered jointly by the US Fish and Wildlife Service and the Ohio Department of Natural Resources – Division of Wildlife (ODNR-DOW). Monetary support for genetic analyses and processing of Detroit River fish was provided by The Ohio State University's Chapter of Sigma Xi (to RMB), Department of Evolution, Ecology, and Organismal Biology (to SAL), and College of Arts and Sciences (to RMB), as well as the Natural Sciences and Engineering Research Council of Canada (to DDH). Monetary support for collections of yellow perch larvae and juveniles was provided by the Great Lakes Fishery Commission Fisheries Research Program (to SAL and DDH), with in-kind support provided by the ODNR-DOW, the Ontario Ministry of Natural Resources, NOAA's Great Lakes Environmental Research Laboratory, and the USGS Great Lakes Science Center. We also thank W. Stott and the anonymous reviewers for comments that improved this manuscript. This is GLERL contribution 1776 and contribution No. 1964 of the USGS Great Lakes Science Center. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

### References

- Baker, D.B. 2011. The sources and transport of bioavailable phosphorus to Lake Erie, Final Report: Part 2. US EPA/GLNPO ID: GL 00E75401-1. United States Environmental Protection Agency, Chicago, Ill.
- Begg, G.A., and Waldman, J.R. 1999. An holistic approach to fish stock identification. *Fish. Res.* **43**: 35–44. doi:10.1016/S0165-7836(99)00065-X.
- Beletsky, D., Mason, D.M., Schwab, D.J., Rutherford, E.S., Janssen, J., Clapp, D.F., and Dettmers, J.M. 2007. Biophysical model of larval yellow perch advection and settlement in Lake Michigan. *J. Great Lakes Res.* **33**: 842–866. doi:10.3394/0380-1330(2007)33[842:BMOLYP]2.0.CO;2.
- Beletsky, D., Hawley, N., and Rao, Y.R. 2013. Modeling summer circulation and thermal structure in Lake Erie. *J. Geophys. Res. Oceans*, **118**: 6238–6252. doi:10.1002/2013JC008854.
- Beneteau, C.L., Mandrak, N.E., and Heath, D.D. 2009. The effects of river barriers and range expansion of the population genetic structure and stability in Greenside Darter (*Etheostoma blennioides*) populations. *Conserv. Biol.* **10**: 477–487. doi:10.1007/s10592-008-9627-9.
- Bennett, J.R., and Clites, A.H. 1987. Accuracy of trajectory calculation in a finite-difference circulation model. *J. Comput. Phys.* **68**: 272–282. doi:10.1016/0021-9991(87)90058-1.
- Blumberg, A.F., and Mellor, G.L. 1987. A description of a three-dimensional coastal ocean circulation model. In *Three-dimensional coastal ocean models*. Edited by N. Heaps. American Geophysical Union, Washington, D.C. pp. 1–16.
- Bradbury, I.R., Campana, S.E., and Bentzen, P. 2008. Estimating contemporary early life-history dispersal in an estuarine fish: integrating molecular and otolith elemental approaches. *Mol. Ecol.* **17**: 1438–1450. doi:10.1111/j.1365-294X.2008.03694.x. PMID:18321254.
- Bunnell, D.B., Barbiero, R.P., Ludsin, S.A., Madenjian, C.P., Warren, G.J., Dolan, D.M., Brenden, T.O., Briland, R., Gorman, O.T., He, J.X., Johengen, T.H., Lantry, B.F., Lesht, B.M., Nalepa, T.F., Riley, S.C., Riseng, C.M., Treska, T.J., Tsehaye, I., Walsh, M.G., Warner, D.M., and Weidel, B.C. 2014. Changing ecosystem dynamics in the Laurentian Great Lakes: bottom-up and top-down regulation. *BioScience*, **64**: 26–39. doi:10.1093/biosci/bit001.
- Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P., and Menge, B.A. 1996. Recruitment and the local dynamics of open marine populations. *Annu. Rev. Ecol. Syst.* **27**: 447–500. doi:10.1146/annurev.ecolsys.27.1.477.
- Campana, S.E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. *Mar. Ecol. Prog. Ser.* **188**: 263–297. doi:10.3354/meps188263.
- Carlsson, J., Olsen, K., Nilsson, J., Overli, O., and Stabell, O. 1999. Microsatellites reveal fine-scale genetic structure in stream-living brown trout. *J. Fish Biol.* **55**: 1290–1303. doi:10.1111/j.1095-8649.1999.tb02076.x.
- Carreon-Martinez, L.B., Wellband, K.W., Johnson, T.B., Ludsin, S.A., and Heath, D.D. 2014. Novel molecular approach demonstrates that turbid river plumes reduce predation mortality on larval fish. *Mol. Ecol.* **23**: 5366–5377. doi:10.1111/mec.12927. PMID:25231387.
- Carreon-Martinez, L.B., Walter, R.P., Johnson, T.B., Ludsin, S.A., and Heath, D.D. 2015. Benefits of turbid river plume habitat for Lake Erie yellow perch (*Perca flavescens*) recruitment determined by juvenile to larval genotype assignment. *Plos ONE*, **10**(5): e0125234. doi:10.1371/journal.pone.0125234. PMID:25954968.
- Christensen, A., Daewel, U., Jensen, H., Mosegaard, H., St. John, M., and Schrum, C. 2007. Hydrodynamic backtracking of fish larvae by individual-based modelling. *Mar. Ecol. Prog. Ser.* **347**: 221–232. doi:10.3354/meps06980.
- Christie, M.R., Johnson, D.W., Stallings, C.D., and Hixon, M.A. 2010. Self-recruitment and sweepstakes reproduction amid extensive gene flow in a coral-reef fish. *Mol. Ecol.* **19**: 1042–1057. doi:10.1111/j.1365-294X.2010.04524.x. PMID:20089121.
- Chu, P.Y., Kelley, J.G.W., Mott, G.V., Zhang, A., and Lang, G.A. 2011. Development, implementation, and skill assessment of the NOAA/NOS Great Lakes Operational Forecast System. *Ocean Dynam.* **61**: 1305–1316. doi:10.1007/s10236-011-0424-5.
- Cowen, R.K., and Sponaugle, S. 2009. Larval dispersal and marine population connectivity. *Annu. Rev. Mar. Sci.* **1**: 443–466. doi:10.1146/annurev.marine.010908.163757.
- Cowen, R.K., Paris, C.B., Olson, D.B., and Fortuna, J.L. 2003. The role of long distance dispersal versus local retention in replenishing marine populations. *Gulf Caribb. Res.* **14**: 129–137.
- Elphinstone, M.S., Hinten, G.N., Anderson, M.J., and Nock, C.J. 2003. An inexpensive and high-throughput procedure to extract and purify total genomic DNA for population studies. *Mol. Ecol. Notes*, **3**: 317–320. doi:10.1046/j.1471-8286.2003.00397.x.
- Excoffier, L., Laval, G., and Schneider, S. 2005. Arlequin version 3.0: an integrated software package for population genetics data analysis. *Evol. Bioinform.* **1**: 47–50. PMID:19325852.
- Farmer, T.M., Marschall, E.A., Dabrowski, K., and Ludsin, S.A. 2015. Short winters threaten temperate fish populations. *Nat. Comm.* **6**: 7724. doi:10.1038/ncomms8724.
- Fraker, M.E., Anderson, E.J., Brodnik, R.M., Carreon-Martinez, L., DeVanna, K.M., Fryer, B.J., Heath, D.D., Reichert, J.M., and Ludsin, S.A. 2015a. Particle backtracking improves breeding subpopulation discrimination and natal-source identification in mixed populations. *PLoS ONE*, **10**: e0120752. doi:10.1371/journal.pone.0120752. PMID:25799555.
- Fraker, M.E., Anderson, E.J., Chen, K.-Y., Davis, J.J., DeVanna, K.M., DuFour, M.R.,

- Marschall, E.A., May, C.J., Mayer, C.M., Miner, J.G., Pangle, K.L., Pritt, J.J., Roseman, E.F., Tyson, J.T., Zhao, Y., and Ludsin, S.A. 2015b. Variation in larval advection and early life history of Lake Erie walleye (*Sander vitreus*): insights from an individual-based biophysical model. *J. Gt. Lakes Res.* **41**: 830–845.
- Fraser, D.J., Jones, M.W., McParland, T.L., and Hutchings, J.A. 2007. Loss of historical immigration and the unsuccessful rehabilitation of extirpated salmon populations. *Conserv. Genet.* **8**: 527–546. doi:10.1007/s10592-006-9188-8.
- Gerlach, G., Schardt, U., Eckmann, R., and Meyer, A. 2001. Kin-structured sub-populations of Eurasian perch (*Perca fluviatilis*). *Heredity*, **86**: 213–221. doi:10.1046/j.1365-2540.2001.00825.x. PMID:11380667.
- Gillanders, B.M. 2009. Tools for studying biological marine ecosystem interactions — natural and artificial tags. In *Ecological connectivity among tropical coastal ecosystems*. Edited by I. Nagelkerken. Springer, New York. pp. 457–492.
- Goodyear, C.S., Edsall, T.A., Ormsby, D.M.D., Moss, G.D., and Polanski, P.E. 1982. Atlas of the spawning and nursery areas of Great Lakes fishes. Vol. 9: Lake Erie. US Fish and Wildlife Service, Washington, D.C.
- Gopalan, G., Culver, D.A., Wu, L., and Trauben, B.K. 1998. Effects of recent ecosystem changes on the recruitment of young-of-the-year fish in western Lake Erie. *Can. J. Fish. Aquat. Sci.* **55**(12): 2572–2579. doi:10.1139/f98-130.
- Griffiths, J.R., Schindler, D.E., Armstrong, J.B., Scheuerell, M.D., Whited, D.C., Clark, R.A., Hilborn, R., Holt, C.A., Lindley, S.T., Stanford, J.A., and Volk, E.C. 2014. Performance of salmon fishery portfolios across western North America. *J. Appl. Ecol.* **51**: 1554–1563. doi:10.1111/1365-2664.12341. PMID:25552746.
- Hatcher, C.O., Nester, R.T., and Muth, K.M. 1991. Using larval fish abundance in the St. Clair and Detroit Rivers to predict year-class strength of forage fish in lakes Huron and Erie. *J. Gt. Lakes Res.* **17**: 74–84. doi:10.1016/S0380-1330(91)71343-9.
- Hauser, L., Seamons, T.R., Dauer, M., Naisch, K.A., and Quinn, T.P. 2006. An empirical verification of population assignment methods by marking and parentage data: hatchery and wild steelhead (*Oncorhynchus mykiss*) in Forks Creek, Washington, USA. *Mol. Ecol.* **15**: 3157–3173. doi:10.1111/j.1365-294X.2006.03017.x. PMID:16968262.
- Hilborn, R., Quinn, T.P., Schindler, D.E., and Rogers, D.E. 2003. Biocomplexity and fisheries sustainability. *Proc. Natl. Acad. Sci. U.S.A.* **100**: 6564–6568. doi:10.1073/pnas.1037274100. PMID:12743372.
- Hinrichsen, H.H., Dickey-Collas, M., Hurat, M., Peck, M.A., and Vikebo, M.E. 2011. Evaluating the suitability of coupled biophysical models for fishery management. *ICES J. Mar. Sci.* **68**: 1478–1487. doi:10.1093/icesjms/fsr056.
- Hjort, J. 1926. Fluctuations in the year classes of important food fishes. *J. Cons. Int. Explor. Mer.* **1**: 5–38. doi:10.1093/icesjms/1.1.5.
- Hodgson, J.R., Schindler, D.E., and He, X. 1998. Homing tendency of three piscivorous fish in a north temperate lake. *Trans. Am. Fish. Soc.* **127**: 1078–1081. doi:10.1577/1548-8659(1998)127<1078:HTOTPF>2.0.CO;2.
- Hogan, J.D., Thiessen, R.J., Sale, P.F., and Heath, D.D. 2012. Local retention, dispersal and fluctuating connectivity among populations of a coral reef fish. *Oecologia*, **168**: 61–71. doi:10.1007/s00442-011-2058-1. PMID:21735201.
- Hook, T.O., McCormick, M.J., Rutherford, E.S., Mason, D.M., and Carter, G.S. 2006. Short-term water mass movements in Lake Michigan: implications for larval fish transport. *J. Gt. Lakes Res.* **32**: 728–737. doi:10.3394/0380-1330(2006)32[728:SWMMIL]2.0.CO;2.
- 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**(6): 1647–1659. doi:10.1139/f69-148.
- Jones, M.L., Shuter, B.J., Zhao, Y., and Stockwell, J.D. 2006. Forecasting effects of climate change on Great Lakes fisheries: models that link habitat supply to population dynamics can help. *Can. J. Fish. Aquat. Sci.* **63**(2): 457–468. doi:10.1139/f05-239.
- Kipling, C., and Le Cren, E.D. 1984. Mark-recapture experiments on fish in Windermere, 1943–1982. *J. Fish Biol.* **24**: 395–414. doi:10.1111/j.1095-8649.1984.tb04811.x.
- Kochzius, M. 2009. Trends in fishery genetics. In *The future of fisheries science in North America*. Edited by R.J. Beamish and B.J. Rothschild. Springer, New York. pp. 453–493.
- Kocovsky, P.M., Sullivan, T.J., Knight, C.T., and Stepien, C.A. 2013. Genetic and morphometric differences demonstrate fine-scale population substructure of the yellow perch *Perca flavescens*: need for redefined management units. *J. Fish Biol.* **82**: 2015–2030. doi:10.1111/jfb.12129. PMID:23731149.
- Kool, J.T., Moilanen, A., and Treml, E.A. 2013. Population connectivity: recent advances and new perspectives. *Landsc. Ecol.* **28**: 165–185. doi:10.1007/s10980-012-9819-z.
- Leung, C., Magnan, P., and Angers, B. 2011. Genetic evidence for sympatric populations of yellow perch (*Perca flavescens*) in Lake Saint-Pierre (Canada): the crucial first step in developing a fishery management plan. *J. Aquac. Res. Dev.* **56**: 001. doi:10.4172/2155-9546.56.001.
- Levin, L.A. 2006. Recent progress in understanding larval dispersal: new directions and digressions. *Integr. Comp. Biol.* **46**: 282–297. doi:10.1093/icb/cj024. PMID:21672742.
- Li, L., Wang, H.P., Givens, C., Czesny, S., and Brown, B. 2007. Primer note: Isolation and characterization of microsatellites in yellow perch (*Perca flavescens*). *Mol. Ecol. Notes*, **7**: 600–603. doi:10.1111/j.1471-8286.2006.01645.x.
- Lowe, W.H., and Allendorf, F.W. 2010. What can genetics tell us about population connectivity? *Mol. Ecol.* **19**: 3038–3051. doi:10.1111/j.1365-294X.2010.04688.x. PMID:20618697.
- Ludsin, S.A. 2000. Exploration of spatiotemporal patterns in recruitment and community organization of Lake Erie fishes: a multiscale, mechanistic approach. Ph.D. dissertation, Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, Columbus, Ohio.
- Ludsin, S.A., Kershner, M., Blocksom, K., Knight, R., and Stein, R. 2001. Life after death in Lake Erie: nutrient controls drive fish species richness, rehabilitation. *Ecol. Appl.* **11**: 731–746. doi:10.1890/1051-0761(2001)011[0731:LADILE]2.0.CO;2.
- Ludsin, S.A., Fryer, B.J., and 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. doi:10.1577/T04-165.1.
- Ludsin, S.A., Pangle, K.L., and Tyson, J.T. 2010. Using satellite imagery for fisheries management. Final completion report. Lake Erie Protection Fund, Toledo, Ohio.
- Ludsin, S.A., Pangle, K., Carreon-Martinez, L., Legler, N., Reichert, J.M., and Heath, D.D. 2011. River discharge as a predictor of Lake Erie yellow perch recruitment. Final completion report. Great Lakes Fishery Commission, Fisheries Research Program, Ann Arbor, Mich.
- Ludsin, S.A., DeVanna, K.M., and Smith, R.E.H. 2014. Physical-biological coupling and the challenge of understanding fish recruitment in freshwater lakes. *Can. J. Fish. Aquat. Sci.* **71**(5): 775–794. doi:10.1139/cjfas-2013-0512.
- Michalak, A.M., Anderson, E.J., Beletsky, D., Boland, S., Bosch, N.S., Bridgeman, T.B., Chaffin, J.D., Cho, K., 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., Verhamme, E., Wright, D.M., and Zagorski, M.A. 2013. Record-setting algal bloom in Lake Erie caused by agricultural and meteorological trends consistent with expected future conditions. *Proc. Natl. Acad. Sci. U.S.A.* **110**: 6448–6452. doi:10.1073/pnas.1216006110. PMID:23576718.
- Miller, J.A., Banks, M.A., Gomez-Uchida, D., and 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**(10): 2189–2198. doi:10.1139/f05-133.
- 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. doi:10.3354/meps06973.
- Miller, T.J., Crowder, L.B., Rice, J.A., and Marschall, E.A. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Can. J. Fish. Aquat. Sci.* **45**(9): 1657–1670. doi:10.1139/f88-197.
- Mion, J., Stein, R., and Marschall, E. 1998. River discharge drives survival of larval walleye. *Ecol. Appl.* **8**: 88–103. doi:10.1890/1051-0761(1998)008[0088:RDDSOL]2.0.CO;2.
- Neville, H.M., Isaak, D.J., Dunham, J.B., Thurow, R.F., and Rieman, B.E. 2006. Fine-scale natal homing and localized movement as shaped by sex and spawning habitat in Chinook salmon: insights from spatial autocorrelation analysis of individual genotypes. *Mol. Ecol.* **15**: 4589–4602. doi:10.1111/j.1365-294X.2006.03082.x. PMID:17107485.
- North, E.W., Schlag, Z., Hood, R.R., Li, M., Zhong, L., Gross, T., and Kennedy, V.S. 2008. Vertical swimming behavior influences the dispersal of simulated oyster larvae in a coupled particle-tracking and hydrodynamic model of Chesapeake Bay. *Mar. Ecol. Prog. Ser.* **359**: 99–115. doi:10.3354/meps07317.
- North, E.W., Gallego, A., and Petigas, P. 2009. Manual of recommended practices for modeling physical-biological interactions during early fish life. ICES Report 295, ICES, Copenhagen.
- Paetkau, D., Calvert, W., Stirling, I., and Strobeck, C. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Mol. Ecol.* **4**: 347–354. doi:10.1111/j.1365-294X.1995.tb00227.x. PMID:7663752.
- Paetkau, D., Slade, R., Burden, M., and Estoup, A. 2004. Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. *Mol. Ecol.* **13**: 55–65. doi:10.1046/j.1365-294X.2004.02008.x. PMID:14653788.
- Piry, S., Alapetite, A., Cornuet, J.M., Paetkau, D., Baudouin, L., and Estoup, A. 2004. GENECLASS2: a software for genetic assignment and first-generation migrant detection. *J. Hered.* **95**: 536–539. doi:10.1093/jhered/esh074. PMID:15475402.
- Pritt, J.J., Roseman, E.F., and 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. doi:10.1093/icesjms/fsu080.
- Rannala, B., and Mountain, J.L. 1997. Detecting immigration by using multilocus genotypes. *Proc. Natl. Acad. Sci. U.S.A.* **94**: 9197–9201. doi:10.1073/pnas.94.17.9197. PMID:9256459.
- Reichert, J.M., Fryer, B.J., Pangle, K.L., Johnson, T.B., Tyson, J.T., Drelich, A.B., and Ludsin, S.A. 2010. River-plume use during the pelagic larval stage benefits recruitment of a lentic fish. *Can. J. Fish. Aquat. Sci.* **67**(6): 987–1004. doi:10.1139/F10-036.
- Rousset, F. 2008. Genepop'007: a complete reimplementation of the Genepop software for Windows and Linux. *Mol. Ecol. Res.* **8**: 103–106. doi:10.1111/j.1471-8286.2007.01931.x.
- Ruzzante, D.E., Mariani, S., Bekkevold, D., André, C., Clausen, H., Dahlgren, L.A., Hutchinson, T.G., Hatfield, W.F., Torstensen, E.M.C., Brigham, E., Simmonds, J., Laikre, E.J., Larsson, L., Stet, L.C., Ryman, R.J.M., Carvalho, N.,

- G.R. 2006. Biocomplexity in a highly migratory pelagic marine fish, Atlantic herring. *Proc. R. Soc. B Biol. Sci.* **273**: 1459–1464. doi:10.1098/rspb.2005.3463.
- Saenz-Agudelo, P., Jones, G.P., Thorrold, S.R., and Planes, S. 2011. Connectivity dominates larval replenishment in a coastal reef fish metapopulation. *Proc. R. Soc. B Biol. Sci.* **278**: 2954–2961. doi:10.1098/rspb.2010.2780.
- Scavia, D., Allan, J.D., Arend, K.K., Bartell, S., Beletsky, D., Bosch, N.S., Brandt, S.B., Briland, R.D., Daloğlu, 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., and Zhou, Y. 2014. Assessing and addressing the re-eutrophication of Lake Erie: Central Basin Hypoxia. *J. Gt. Lakes Res.* **40**: 226–246. doi:10.1016/j.jglr.2014.02.004.
- Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Rogers, L.A., Quinn, T.P., Rogers, L.A., and Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited species. *Nature*, **465**: 609–612. doi:10.1038/nature09060.
- Schwab, D.J., and Bedford, K.W. 1994. Initial implementation of the Great Lakes Forecasting System: a real-time system for predicting lake circulation and thermal structure. *Water Pollut. Res. J. Can.* **29**: 203–220.
- Seeb, J.E., Carvalho, G., Hauser, L., Naish, K., Roberts, S., and Seeb, L.W. 2011. Single-nucleotide polymorphism (SNP) discovery and applications of SNP genotyping in nonmodel organisms. *Mol. Ecol. Resour.* **11**: 1–8. doi:10.1111/j.1755-0998.2010.02979.x. PMID:21429158.
- Sepulveda-Villet, O.J., and Stepien, C.A. 2011. Fine-scale population genetic structure of the yellow perch *Perca flavescens* in Lake Erie. *Can. J. Fish. Aquat. Sci.* **68**(8): 1435–1453. doi:10.1139/f2011-077.
- Stepien, C.A., Murphy, D.J., Lohner, R.N., Sepulveda-Villet, O.J., and Haponski, A.E. 2009. Signatures of vicariance, postglacial dispersal, and spawning philopatry: population genetics of the walleye, *Sander vitreus*. *Mol. Ecol.* **18**: 3411–3428. doi:10.1111/j.1365-294X.2009.04291.x. PMID:19659479.
- Sullivan, T.J., and Stepien, C.A. 2014. Genetic diversity and divergence of yellow perch spawning populations across the Huron–Erie corridor, from Lake Huron through western Lake Erie. *J. Gt. Lakes Res.* **40**(Suppl. 2): 101–109. doi:10.1016/j.jglr.2012.12.004.
- Swearer, S.E., Caselle, J.E., Lea, D.W., and Warner, R.R. 1999. Larval retention and recruitment in an island population of coral-reef fish. *Nature*, **402**: 799–802. doi:10.1038/45533.
- Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in plants and animals. Sinauer Associates, Sunderland, Mass.
- Walther, B.D., and Thorrold, S.R. 2008. Geochemical signatures in otoliths record natal origins of American shad. *Trans. Am. Fish. Soc.* **137**: 57–69. doi:10.1577/T07-029.1.
- Weir, B.S., and Cockerham, C.C. 1984. Estimating F-statistics for the analysis of population structure. *Evolution*, **38**: 1358–1370. doi:10.2307/2408641.
- Werner, F.E., Cowen, R.K., and Paris, C.B. 2007. Coupled biological and physical models: present capabilities and necessary developments for future studies of population connectivity. *Oceanography*, **20**: 54–69. doi:10.5670/oceanog.2007.29.
- YPTG. 2013. Report of the Lake Erie Yellow Perch Task Group. Report to the Standing Technical Committee, Lake Erie Committee of the Great Lakes Fishery Commission, Yellow Perch Task Group, Ann Arbor, Mich.