Evidence across multiple scales for offshore transport of yellow perch (Perca flavescens) larvae in Lake Michigan

John M. Dettmers¹, John Janssen², Bernard Pientka¹,³, Richard S. Fulford⁴,⁵, and David J. Jude⁶

¹Lake Michigan Biological Station, Center for Aquatic Ecology, Illinois Natural History Survey, 400 17th Street, Zion, Illinois 60099
²Great Lakes WATER Institute, 600 E. Greenfield Avenue, Milwaukee, Wisconsin 53204
³Present address: Vermont Department of Fish and Wildlife, 111 West Street, Essex Junction, Vermont 05452
⁴Department of Zoology, North Carolina State University, Campus Box 7617, Raleigh, North Carolina 27595
⁵Present address: Smithsonian Environmental Research Center, 647 Contees Wharf Road, Edgewater, Maryland 21037
⁶School of Natural Resources and the Environment, 430 East University, University of Michigan, Ann Arbor, Michigan 48109
Abstract

Most freshwater fishes have short pelagic early life stages. Lake Michigan presents an interesting scenario for yellow perch (*Perca flavescens*), a species with a long pelagic larval stage that may not be well adapted to lakes with an expansive pelagic environment and extensive offshore transport. We investigated the possibility that early life stages of yellow perch were transported well offshore from their nearshore spawning grounds and explored whether food resources were more or less favorable offshore. To determine the extent to which pelagic age-0 yellow perch moved offshore, we sampled at multiple scales ranging from local (< 2 km) to across the lake (>120 km). Evidence of offshore movement by larvae occurred at each scale. Yellow perch larvae were quickly transported offshore from nearshore spawning sites and remained in the offshore pelagia to sizes of at least 30 mm. Zooplankton density was greater offshore than nearshore, suggesting that pelagic age-0 yellow perch find improved food resources offshore than at their nearshore spawning sites. Currents operating at oceanographic scales likely influenced the offshore movement of pelagic age-0 yellow perch in Lake Michigan. These currents, coupled with prey availability for pelagic age-0 individuals, may influence the recruitment success of this species.

Keywords: yellow perch, offshore transport, zooplankton, Lake Michigan, advection
Introduction

Pelagic early life stages in freshwater fishes typically are very short (Houde 1994). Yellow perch (*Perca flavescens*) is an unusual freshwater fish in that, while the eggs are demersal and deposited in shallow water, it has a relatively long pelagic period spent offshore in ponds and medium to large lakes (Urho 1996). Typically, this period lasts 30-40 days before juveniles return to nearshore nursery areas (Whiteside et al. 1985). The practical effects of a long pelagic larval stage may have little impact on yellow perch when the nearshore-offshore distance is generally < 1 km and depths are < 20 m. For instance, larval yellow perch occurred well offshore in Oneida Lake (Houde 1969), a relatively large inland lake with a surface area of 207 km$^2$ (Clady and Hutchinson 1975). Houde suspected that these fish were transported offshore by currents, but year-class strength of yellow perch was driven primarily by walleye predation (Nielsen 1980). Similarly, most other studies have concluded that biotic factors, especially predation, limit recruitment of yellow perch (Johnson et al. 1992; Rudstam et al. 1996).

In the Great Lakes, predation remains the dominant factor cited in regulation of yellow perch year-class strength (Brandt et al. 1987; Hartman and Margraf 1993; Shroyer and McComish 2000), although these studies were in shallow portions of lakes or in embayments. However, recruitment of yellow perch in lakes Erie and St. Clair was influenced by water temperature (Henderson and Nepszy 1985). In the much larger Lake Michigan (surface area = 57 753 km$^3$), both biotic [e.g., maternal effects (Heyer et al. 2001), prey availability (Dettmers et al. 2003), and predation (Shroyer and McComish 2000)] and abiotic [e.g, water temperature and currents (Clapp and Dettmers 2004)] mechanisms affect recruitment of yellow perch. Typically, yellow perch larvae have been sampled only very close to shore in Lake Michigan (Marsden and
Dettmers et al. 2004), so the question of whether pelagic age-0 yellow perch consistently move well offshore remains uncertain. However, age-0 yellow perch have been incidentally observed offshore, primarily in July and August (Nash and Geffen 1988). Similarly, we have observed age-0 yellow perch offshore as much as 56 km from the Wisconsin shore during July - September at sizes ranging 20 – 70 mm (J. Dettmers, J. Janssen, R. Fulford, unpublished data).

Lake Michigan is large enough to have significant currents (Beletsky et al. 1999). The lake also is large enough to have effects such as Ekman transport due to the rotation of the earth, but the biological impact of these currents is mostly unstudied. Water currents in offshore areas of Lake Michigan during late summer have been measured at up to 55 cm·s$^{-1}$, with a median value of 17 cm·s$^{-1}$ (Pickett et al. 1983). Early studies on Lake Michigan water currents identified many areas of upwelling or downwelling currents along both western and eastern shorelines (Ayers et al. 1958). Taken together, these observations suggest that the hydrodynamics of Lake Michigan interact with the developmental ontogeny of yellow perch to produce an extended pelagic period that might distribute age-0 yellow perch far from where they were hatched. Such a phenomenon might affect basin-wide fluctuations in yellow perch recruitment success (Clapp and Dettmers 2004).

Due to developing evidence that pelagic yellow perch are found well offshore and the limited understanding of how physical forces affect early life stages of yellow perch in Lake Michigan, we developed the following questions that required sampling across multiple scales: Is there evidence that yellow perch larvae are advected by water mass movements in Lake Michigan (small-scale sampling, ~ 1.6 km)? If yellow perch larvae are advected, how far offshore do they travel (mesoscale sampling, ~ 13 km and cross-lake sampling, ~120 km)? Are larger (older) larvae found farther offshore (mesoscale sampling)? Is there a difference between...
nearshore and offshore food resources (mesoscale sampling)? Our work focuses on the first few weeks of life when the fish will be most susceptible to hydrodynamic transport.

**Methods**

To address our hypotheses, we sampled larval and pelagic age-0 yellow perch in a variety of locations and years (Table 1; Figure 1), using similar gear described below. Yellow perch were collected at night with 1- x 2-m neuston nets towed horizontally just beneath the water surface between June and August in each year. Tows were conducted at speeds of 2-3 knots for lengths of time varying between 5 min and 30 min, depending on the scale addressed (see below). Mesh sizes of the neuston nets were varied depending on expected size of larvae, from 500 µm the first 2-3 weeks after hatching, to 1000 µm by the end of June, and 1800 µm thereafter, usually until the first week of August. A flowmeter mounted in the center of the mouth of the net allowed estimation of the volume of water filtered, which was used to calculate density of larvae. Samples were preserved in ethanol for later sorting and identification in the laboratory.

**Small-scale sampling**

To determine how upwelling and downwelling affected advection, two near-shore stations (within 1.6 km of shore) were selected based on water depth (Table 1). For purposes of comparison, the deeper station was considered offshore relative to the shallow station. At each station, three replicate surface neuston tows, each 5 min long, were taken once to twice each week, depending on weather. Stations were located on the western side of Lake Michigan off Evanston, Illinois in 1998, 1999, and 2000 and Milwaukee, Wisconsin in 2001 and 2002 (Figure 1). There was no river plume near Evanston, but near Milwaukee, a substantial, usually warmer, water plume discharges from the Milwaukee River via Milwaukee Harbor. To avoid this plume,
which would alter larval yellow perch densities, we checked temperature, longshore current direction, and visually checked color in the harbor and north and south of the harbor. We then sampled either north or south of Milwaukee Harbor to avoid the discharge. Data for determining the effect of upwelling events were analyzed as an analysis of covariance (ANCOVA) with corrected relative offshore/nearshore abundance \(100 \times \frac{(\text{density offshore})}{(\text{density offshore} + \text{density inshore})}\), henceforth "relative offshore percentage", as the dependent variable. Relative offshore percentage varies between 0 and 1.0 and was arcsine square root transformed for statistical analysis. The covariate was the difference between the shallow station surface temperature and the National Oceanic Atmospheric Administration mid-lake buoy surface temperature. A more extreme upwelling resulted in a more negative \(\Delta T\) whereas a more extreme downwelling generated a more positive \(\Delta T\). Location (Wisconsin vs. Illinois) was a group variable; location and year are confounded. For each depth and date, we employed the mean density from the three samples.

**Mesoscale sampling**

We interpret mesoscale to mean a bounded but sufficiently large area where the hydrodynamics of the area are governed by oceanographic phenomena such as strong wind-driven currents and earth-spin (Beletsky et al. 2004). To investigate offshore transport at a mesoscale level, we sampled an east-west transect of about 12 km, roughly 1.5 km north of Waukegan Harbor, Illinois between late May and early August during 2000 – 2002 (Table 1; Figure 1). Five stations along the transect were selected for larval fish sampling, at the following distances from shore: 1.8, 4.6, 7.4, 10.1 and 12.9 km. Larval fish sampling occurred approximately weekly, weather depending. In the laboratory, larval fishes were identified, counted and total lengths of up to 50 individuals from each tow were measured to the nearest 0.1
mm using an image analysis program. Length data for each year were analyzed using ANCOVA with week as the group variable and distance from shore as the covariate. We also examined the week x distance offshore interaction.

Additional mesoscale samples were taken on nine nights between 22 June and 31 July in 2001 using both a Tucker trawl and a neuston net, and three nights between June 17 and June 30 in 2002 off of Milwaukee using a neuston net for comparison with the Waukegan samples taken by neuston net during the same time frame each year (Table 1; Figure 1).

On the same nights as larval fish sampling, we collected epilimnetic (top 10 m of water) zooplankton samples at distances from shore of 1.8 km and 12.9 km to compare the availability of food in nearshore vs. offshore locations. At each station, two replicate vertical lifts were taken using a 0.5-m diameter, 73-μm mesh conical zooplankton net. The net was unmetered and we assumed 100% net efficiency when calculating zooplankton density. Although this assumption was not always valid, the data are still valid from a comparative perspective, given that changing conditions throughout the season affected our sampling in the same way and that our primary interest was comparing zooplankton abundance between nearshore and offshore locations. Samples were immediately preserved in 5% sugar formalin. In the laboratory, zooplankton were enumerated and identified into the following categories: cladocerans to genus, cyclopoid copepodes, calanoid copepodes, copepod nauplii, Macrothrididae spp., Sididae spp., and rotifers. Uncommon taxa were noted. For each sample, up to three 5-mL subsamples were taken from adjusted volumes that provided a count of at least 20 individuals of most taxa. Upon completion of each subsample, counting ceased for each taxon in which 100 individuals were additively counted. During the counting procedure, length measurements also were taken so that up to 20 individuals for each species and replicate were measured. Weekly zooplankton
densities and lengths for each year were analyzed using a split-plot repeated measures analysis of variance (Maceina et al. 1994) with density or length as the dependent variable and year, week, and sampling station (i.e., distance offshore) as class variables.

**Cross-lake sampling**

In 2002, we sampled across Lake Michigan on 26-28 June using neuston nets as described above to assess the distribution of yellow perch from the Illinois/Wisconsin side to the Michigan side. There were three segments to this sampling. A cross-lake sample was composed of two of these segments with one segment being from Muskegon to about mid-lake and the second being from Milwaukee to about mid-lake (Table 1; Figure 1). For the cross-lake transect samples the tows were 30 min. The cross-lake sampling was complemented with a third segment that included the mesoscale samples in Illinois to confirm very nearshore densities along the western side of the lake.

**Results**

**Small-scale sampling**

Only yolk-sac larvae were collected. Densities of newly hatched yellow perch larvae ranged from 0 to 600·100 m$^{-3}$. Highest densities occurred at the nearshore station on the most extreme downwelling night ($\Delta T = 3.8 ^\circ C$) at Evanston, Illinois (57-600 larvae·100 m$^{-3}$ for the three individual samples) and at the offshore station on the most extreme upwelling night ($\Delta T = -5 ^\circ C$) at Milwaukee, Wisconsin (177 –228 larvae·100 m$^{-3}$ for the three individual samples).

**ANCOVA** revealed a strong negative relationship with $\Delta T$ ($F_{1,10} = 15.4$, $P < 0.003$) and no location effect ($F_{1,10} = 0.1$, $P > 0.5$). Hence, larval yellow perch were relatively more abundant at nearshore stations along the west shoreline for downwellings and at offshore stations.
for upwellings (Figure 2). Several strong upwelling samples for Illinois are not included because there were no larval yellow perch in either the nearshore or offshore sites. Presumably the larvae were farther offshore than our offshore station on those sampling occasions.

**Mesoscale sampling**

Primarily post-yolk sac larvae and age-0 yellow perch were collected. Larval yellow perch patterns of appearance were qualitatively similar for all years sampled (Figure 3). Yellow perch larvae initially were collected closest to shore but within two weeks, they were found at all sampling stations. Hatching continued for about four weeks, during which time yellow perch larvae were small regardless of distance from shore. Yellow perch larvae continued to be detected at all sampling stations for several weeks, but after mid-July were found only at our site farthest from shore. In 2000 and 2002, larval yellow perch densities were qualitatively similar but densities were much lower in 2001 (Figure 3). In all years, the highest densities occurred at 4.6 km offshore, even under the different density conditions (years).

Generally, the size of yellow perch larvae increased through time within years and increased with distance from shore, but these patterns were complex in nature, with consistently significant interaction terms (Figure 4). Newly hatched larvae were collected at our nearshore location 1.8 km from shore during a five-week period each year (Figure 4), indicating that this was the primary hatching location. These newly hatched larvae also were collected at sites well offshore, but only before week 26. After week 25, the size of larvae increased in all years.

Analysis of the patterns during weeks 26-31 revealed that yellow perch grew with time (\(F_{3,766} = 149.02, P < 0.0001\); Figure 4a). Specifically, pelagic yellow perch were longer during week 29 than in week 28; larvae from both of these weeks were longer than larvae collected during weeks 26-27, which did not differ from each other (Tukey’s multiple comparison, \(P < 0.05\)). Yellow
perch length also increased with distance from shore in 2000 ($F = 97.01, P < 0.0001$). During 2001, no significant growth patterns were detected for either week ($P = 0.87$) or distance from shore ($P = 0.17$), largely because yellow perch were not collected consistently across enough sites to allow for statistical differentiation (Figure 4b). Mean yellow perch length did not differ by week in 2002 ($F_{2,361} = 1.61, P = 0.20$) but did increase with increasing distance from shore ($F_{1,361} = 283.6, P < 0.0001$; Figure 4c).

Comparison of Waukegan and Milwaukee samples from 2001 and 2002 revealed that larval yellow perch moved offshore along the entire western side of Lake Michigan, regardless of location in the southern basin of the lake. In 2001, larger yellow perch were collected farther from shore than smaller yellow perch (mean length at 1.8 km offshore $= 4.87$ mm, $\pm 0.47$ standard deviation; mean length at 12.9 km offshore $= 7.18$ mm, $\pm 5.21$ mm; $F_{1,518} = 4.21, P = 0.04$), with no effect of location (Waukegan vs Milwaukee: $F_{1,518} = 3.21, P = 0.08$). In 2002, the same pattern followed, with larger yellow perch collected farther from shore (mean length at 1.8 km offshore $= 6.06$ mm, $\pm 0.41$ standard deviation; mean length at 12.9 km offshore $= 9.18$ mm, $\pm 1.75$ mm; $F_{1,1146} = 376.93, P < 0.0001$), again with no effect of location ($F_{1,1146} = 0.33, P = 0.57$).

**Cross-lake sampling**

Yellow perch larvae were consistently found from the west shoreline to about 50 km offshore but were not found farther offshore, or closer to the eastern shore of the lake (Figure 5), suggesting that the source of most larvae occurred along the western shore in 2002 and that, at the time we sampled, about two weeks after the peak of hatching, yellow perch had not yet been transported completely across the lake.
Mesoscale zooplankton sampling

Crustacean zooplankton densities were initially higher offshore than nearshore across all years, but the difference decreased as the season progressed (Figure 6). Statistically, zooplankton density was greater offshore \( (F_{1,12} = 5.89, P = 0.03) \) with no effect of year \( (F_{2,2} = 3.25, P = 0.24) \), no seasonal trend within years \( (F_{8,12} = 0.73, P = 0.66) \), and no location x week interaction \( (F_{8,12} = 1.45, P = 0.27) \). Although mean crustacean zooplankton length also was greater offshore in all three years \( (F_{1,76} = 10.03; P = 0.002; \text{Figure 7}) \), patterns associated with zooplankton length were much more complex than for density. Crustacean zooplankton length differed among years \( (F_{2,2} = 20.39, P = 0.05) \), with mean zooplankton length in 2002 greater than in either 2000 or 2001 (Tukey’s multiple comparison, \( P < 0.05 \)). Furthermore, zooplankton length varied with week, but not consistently \( (F_{17,76} = 2.88, P = 0.0008) \), leading to a location x week interaction \( (F_{9,76} = 3.52, P = 0.001) \).

Discussion

Our results demonstrate that larval yellow perch are transported into the open water areas of Lake Michigan and that larger, pelagic age-0 yellow perch are found farther from shore. Based on analyses of larval yellow perch swimming ability, their distribution was unlikely to be influenced by swimming until after reaching at least 9.5 mm (Houde 1969). In our case, yellow perch were between 6 and 7 mm long when they first appeared 13 km offshore. Age of larval yellow perch was positively related to distance from shore using otoliths from samples taken off of Milwaukee (Fulford 2003). Our small-scale results indicate that larval yellow perch do not actively swim offshore, or if oriented to swim offshore, their swimming is not strong enough to counter an upwelling or downwelling (onshore) movement of water (Houde 1969). Consistent with this is the collection of large amounts of the epilithic green alga *Cladophora* at a station.
about 15 km east of Milwaukee on 24 June 2002, which had the highest density (17.5 ·100 m$^{-3}$) and largest yellow perch collected from the Wisconsin stations that night (part of the mesoscale sampling). *Cladophora* is shed from the Wisconsin shallow rocky areas in June and the dying filaments drift, providing a marker for passive transport.

The transport likely is a phenomenon of two interacting factors: the early life history of yellow perch and the hydrodynamics of a large, deep lake. In smaller and shallower lakes, *Perca* spp. larvae actively move offshore from the littoral zone where the eggs were deposited (Post and McQueen 1988; Urho 1996). Their initial swimming speed is slow, about 1 cm·s$^{-1}$ (Houde 1969), relative to typical Lake Michigan coastal current speeds, which are commonly 10-20 cm·s$^{-2}$ (Mortimer 1975; Sato 1975; Beletsky et al. 2004). Thus, for a pelagic larva, hydrodynamic transport is expected.

Our study confirms the basic principles outlined by Beletsky et al. (2004) for larval yellow perch drift. Their model estimated the drift of passive neutrally-buoyant particles originating along the Illinois coast just north of Chicago using the meteorological conditions for 1998, 1999, and 2000. The model began on 1 June each year, approximately the time of yellow perch swim-up and was based on that of Beletsky and Schwab (2001), incorporating the Princeton Ocean Model (Blumberg and Mellor 1987). Environmental factors driving the model included wind stress, heat flux, free-slip lateral boundary conditions and bottom friction. In general, particles moved offshore and circulated in an anticyclonic direction. Many particles were trapped in a southern Lake Michigan basin gyre, but some escaped to the northern basin via a northward coastal current along the Michigan shore. The predicted dispersion by the end of June varied among years. In 2000, most particles were scattered between the middle of the lake and the eastern shore (to about Muskegon). Particles were most concentrated between the
western shore (to just north of Milwaukee) and the middle of the lake in 1999, but widely dispersed throughout the entire southern basin in 1998. By the end of July of all three years, about the time that age-0 yellow perch appear in shallow water, particles were widely dispersed with a density bias toward the eastern shore and extending up that coast about one third of its length.

Offshore transport may be a contributing mechanism for the genetic homogeneity of yellow perch in southern Lake Michigan reported by Miller (2003). The homogeneity means there must be mixing of yellow perch from the southern basin. The mixing apparently does not occur at the post-demersal stage; Horns (2001) found region-specific growth patterns that Janssen and Luebke (2004) related to differences in habitat and forage base. A long-term mark-recapture study found little evidence of substantial adult movement and some evidence to suggest a large percentage of fish were recaptured close to their initial capture location (D. Glover, Illinois Natural History Survey, 400 17th Street, Zion, Illinois 60099, personal communication). With this lack of movement and recapture near original tagging locations, it seems unlikely that the mixing occurs in adults. Therefore mixing must have occurred at the larval and juvenile stages.

Our cross-lake results, along with the hydrodynamic modeling of Beletsky et al. (2004), suggest that many, or even most, demersal yellow perch along the eastern coast may originate from spawning activity along the western coast. Yellow perch habitat preferences are consistent with this source-sink hypothesis. Adult yellow perch prefer rocky habitat, apparently both for foraging (Wells 1980; Janssen et al. in press) and spawning (Dorr 1982; Robillard and Marsden 2001); rocky habitat is the dominant feature along the western coast whereas the eastern coast is primarily sandy (Powers and Robertson 1968; Janssen et al. in press). Although an overall
annual counter-clockwise water movement exists in Lake Michigan’s southern basin, this average is driven by strong fall and winter winds (Beletsky et al. 1999). During summer, frequent upwelling events are generated by the prevailing southwestern winds augmented by Ekman transport (Mortimer 2004).

Passive transport of larval yellow perch in Lake Michigan means that young yellow perch have an early life history similar to that of marine coastal fishes imposed on them by the hydrodynamics of a macroscopic lake system. An extended pelagic period is the typical habit for marine coastal fishes (Houde 1994, Bonhomme and Planes 2000). When these larvae are pelagic, their survival is frequently determined by an interaction between physical and biological forcing factors. For instance, recruitment of northern anchovy (Engraulis mordax) is lower during windy and stormy conditions because appropriate food resources for first-feeding larvae are not available (Lasker 1975). On a more global scale, recruitment in herring (Clupea harengus) is related, in part, to the North Atlantic Oscillation (Axenrot and Hansson 2003).

Consequently, recruitment of yellow perch in Lake Michigan may show patterns different from those of smaller lakes where recruitment is commonly influenced by nearshore predation on juveniles (Rudstam et al. 1996; Paxton and Winfield 2000). To better understand how larval transport may influence recruitment we address three areas: offshore environment; duration offshore, and the return nearshore.

**Offshore environment**

The nearshore and offshore environments differ in their thermal regime, zooplankton abundance, and potential predators. Overall, the offshore environment offers a more stable thermal environment as the lake stratifies because the stratification is at first intermittent (Mortimer 2004) and easily disrupted by upwellings and downwellings, especially nearshore.
Food resources also appear greater in the offshore environment. We saw greater zooplankton density offshore, a finding consistent with those of Evans (). Upwelling can increase zooplankton abundance in patches offshore where eddies are generated (Megard et al. 1997) so larval yellow perch transported via upwelling may end up in areas of abundant food and reduced predation risk, much like capelin (*Mallotus villosus*) experience in marine systems (Leggett et al. 1984).

**Offshore duration**

Studies in smaller lakes suggest that yellow perch larvae generally spend two to seven weeks in offshore areas (Whiteside et al. 1985; Wang and Eckmann 1994; Post et al. 1995). In southern Lake Michigan, the time spent offshore appears longer. Annual nearshore bottom trawl assessments by the Illinois Natural History Survey at a site near Waukegan during 1988-2002 showed that juveniles appear nearshore during August – September (J. Dettmers, unpublished data), some 10-16 weeks after hatching.

The long offshore duration in southern Lake Michigan may be related to pelagic food resources. Most work has suggested that movement nearshore occurs when larvae reach 25 - 30 mm (Whiteside et al. 1985; Post and McQueen 1988; Wu and Culver 1992). Once age-0 yellow perch become demersal they experience an ontogenetic diet shift from zooplankton to benthic organisms (Whiteside et al. 1985; Post and McQueen 1988; Wu and Culver 1992). This shift may be related to the summer collapse in *Daphnia* populations (Mills and Forney 1981; Wu and Culver 1992; Wang and Eckmann 1994). For Lake Michigan, an explanation based on a *Daphnia* decline is unlikely because the peak in most crustacean zooplankton, including *Daphnia*, occurs in August and September (Torke 1975), at least 60 days after yellow perch have hatched and much longer than the 30-40 days typically ascribed to their early pelagic phase.
(Whiteside et al. 1985). Cladocera in Lake Michigan are negligible in abundance until late July (Lehman and Caceres 1993) and are increasing at the time when yellow perch are expected to become demersal. Hence there may be little energetic advantage for pelagic age-0 yellow perch to seek out benthic food resources, which typically reduce growth of age-0 yellow perch as compared to zooplankton (Prout et al. 1990). Instead, delaying the switch to benthic nursery areas may make sense when offshore zooplankton are plentiful.

**Return to shore**

During the shift to demersal prey, juvenile yellow perch must move from the pelagic open water environment to areas where they can feed on benthic organisms. In most cases this movement would occur in two directions: horizontally (inshore) and/or vertically (towards the bottom). Compared to studies in smaller systems where offshore sites are often only 1 km from shore (Wang and Eckmann 1994; Urho 1996; Anderson et al. 1998), Lake Michigan distances are much greater. Because we have, as yet, only studied the early phase of offshore movement in any detail, we do not know how far yellow perch must swim or be transported to nearshore nursery grounds, or the mechanism by which they return nearshore. Hydrodynamic predictions suggest wide dispersal such that some fish might have to move 60 km or more (Beletsky et al. 2004). Studies on other large scale freshwater systems had sites up to 10 km from shore (Wu and Culver 1992; Post et al. 1995) but in both studies, water depth was much shallower (Post et al. 1995 = 25 m: Wu and Culver 1992 = 10 m). One study found larval *Perca fluviatilis* over water 50 m deep but this was less than 1 km from shore (Wang and Eckmann 1994).

In smaller lakes the distances are not great and an oriented swim by a juvenile in any direction will easily encounter the littoral zone. But based on hydrodynamic modeling of Lake Michigan (Beletsky et al. 2004), substantial numbers of juveniles will be tens of km offshore at a...
size when, in smaller lakes, they are expected to become demersal. Modeling also demonstrates that some age-0 yellow perch should encounter shallow water if they do not orient toward shore on their own (Beletsky et al. 2004).

Settlement of yellow perch may occur rather deep. Geffen & Nash (1991) found juvenile yellow perch at a Diporeia-rich site at 50-75 m, along with juveniles of deepwater sculpin and bloater.

Nonetheless, some fish may never make it to shore or end up in very poor habitat. Yellow perch about 3-5 cm were reported from 25 m deep in late August 1990 at Julian’s Reef (Edsall et al. 1993), which is 13 km from the west shore and surrounded by water about 50 m deep. Adult yellow perch have never been reported from this area and it is likely that these yellow perch would grow very slowly, be eaten, or die if they did not leave. Yellow perch have been indentified in stomachs of lake trout (Salvelinus namaycush) collected at Sheboygan Reef (C. Madenjian, USGS Great Lakes Science Center, 1451 Green Road, Ann Arbor, Michigan, personal communication), which is well offshore and has a minimum depth of about 40 m.

The relatively long pelagic period of Lake Michigan yellow perch may be a consequence of the long distances transported. The scale of the transport, with larvae as far as 25 km offshore about two weeks after hatching, far exceeds the size of “typical” yellow perch lakes. Although growing evidence that marine coastal fishes, which typically have long pelagic periods (Bonhomme and Planes 2000), have behavioral methods of returning to shore (Armsworth et al. 2001), the brief evolutionary history of yellow perch in Lake Michigan (< 10 000 years) makes it unlikely that a fish evolved in smaller lakes will have such behaviors.

The negative relationship between alewife (Shroyer and McComish 2000) and yellow perch, exacerbated by zebra mussels (Janssen and Luebke 2004) suggests that yellow perch
recruitment is not affected by juveniles failing to return from offshore. The relationship between yellow perch recruitment and zooplankton abundance reported by Dettmers et al. (2003) may be consistent with the patterns due to the invasive alewife and zebra mussel because of the impact of these two invaders on zooplankton. In such a case, rapid offshore transport to areas of higher zooplankton abundance should be favorable to yellow perch recruitment. Alternatively, the loss of *Diporeia* from a large area of eastern Lake Michigan (Nalepa et al. 1998) that might be the hydrodynamically favored endpoint of drift from the west side could lower the basin-wide production of yellow perch. In this case, we expect that production from the eastern shore should be substantially diminished compared to historical values and less than that from the western shore. Offshore transport of yellow perch larvae, in conjunction with changes to the food web mediated by invasive species, can help to explain the extended period of poor yellow perch recruitment in Lake Michigan.

**Acknowledgements**

We thank W. Brofka, B. Brylawski, S. Hensler, P. Hirethota, A. Jaeger, M. Luebke, S. Miehls, A. Spencer, J. Thompson, and K. Wolfe for their dedication and help in both the field and lab. Special thanks to K. Stainbrook for help with figures. We also thank the vessel crews of the R/V Blue Heron, R/V Neeskay, and R/V Cyclops, and Wisconsin DNR for providing vessel time. Comments from two anonymous reviewers substantially improved the paper. Funding was provided in part by the Great Lakes Fishery Trust, Illinois-Indiana Sea Grant, Michigan Sea Grant, Wisconsin Sea Grant award number NA86RG0047, the Federal Aid in Sport Fish Restoration Program, Project F-123-R administered by the Illinois Department of Natural Resources, and by the Illinois Natural History Survey.
References


Dettmers et al. 24


Table 1. Summary of the sampling scale, location of sampling, gear used, mesh sizes used, years and dates sampled duration of each tow, and the crews that conducted each type of sampling for pelagic age-0 yellow perch in southern Lake Michigan, 2000-2002.

<table>
<thead>
<tr>
<th>Sample type</th>
<th>Location</th>
<th>Gear</th>
<th>Mesh size (µm)</th>
<th>Years</th>
<th>Dates</th>
<th>Duration</th>
<th>Sample crew</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small-scale</td>
<td>Evanston</td>
<td>Neuston net</td>
<td>500</td>
<td>1998-2000</td>
<td>May, June</td>
<td>5 min</td>
<td>Janssen</td>
</tr>
<tr>
<td>Small-scale</td>
<td>Milwaukee</td>
<td>Neuston net</td>
<td>500</td>
<td>2001-2002</td>
<td>May, June</td>
<td>5 min</td>
<td>Janssen</td>
</tr>
<tr>
<td>Mesoscale</td>
<td>Waukegan</td>
<td>Neuston net</td>
<td>500, 1000, 1800</td>
<td>2000-2002</td>
<td>May-August</td>
<td>30 min</td>
<td>Dettmers</td>
</tr>
<tr>
<td>Cross-lake</td>
<td>Waukegan</td>
<td>Neuston net</td>
<td>1000</td>
<td>2002</td>
<td>26-28 June</td>
<td>30 min</td>
<td>Dettmers, Janssen, Jude</td>
</tr>
</tbody>
</table>
List of Figures

Figure 1. Map of southern Lake Michigan showing locations of sampling for early life stages of yellow perch (*Perca flavescens*). ▲■◊

Figure 2. Corrected percent offshore catch of yellow perch (*Perca flavescens*) in relation to offshore water temperature at two nearshore stations in southwestern Lake Michigan. Sampling occurred in Illinois during 1998 -2000 (●) and in Wisconsin during 2001 - 2002 (○).

Figure 3. Larval yellow perch (*Perca flavescens*) density collected along a 12-km long nearshore-offshore transect near Waukegan Harbor, Illinois with a 1 x 2-meter neuston net towed at the surface at night. Open circles represent weeks when sampling occurred but no yellow perch larvae were collected. Vertical lines on the graph represent changes in mesh size of the neuston net.

Figure 4. Mean (± 1 standard error) total length of larval yellow perch (*Perca flavescens*) from sites ranging 1.8 – 12.9 km offshore along a transect just north of Waukegan Harbor, Illinois during May –August 2000 -2002.

Figure 5. Density of yellow perch (*Perca flavescens*) larvae two weeks after peak hatching across the southern Lake Michigan basin from Waukegan, Illinois to Muskegon Michigan. Sampling was conducted during 26-28 June 2002 by Illinois Natural History Survey (1.8 – 13 km offshore), University of Wisconsin-Milwaukee (7.5 - 55 km offshore) and University of
Michigan (80 – 128 km offshore). All sample densities are referenced as distances offshore from the west shore of Lake Michigan. INHS = Illinois Natural History Survey, UW-M = University of Wisconsin-Milwaukee, U of M = University of Michigan.

Figure 6. Mean weekly crustacean zooplankton density at nearshore and offshore locations near Waukegan Harbor, Illinois during May – August 2000 – 2002. Asterisks (*) indicate weeks where mean densities were significantly different (analysis of variance with P < 0.05).

Figure 7. Mean (± 1 standard error) length of crustacean zooplankton at nearshore and offshore locations near Waukegan Harbor, Illinois during May – August 2000 – 2002. Asterisks (*) indicate weeks where mean lengths were significantly different (analysis of variance with P < 0.05).
Figure 1.

Dettmers et al.
Figure 2.
Figure 3.

Dettmers et al.
Figure 4.
Figure 5.
Figure 6.

Dettmers et al.