Biophysical Model of Larval Yellow Perch Advection and Settlement in Lake Michigan

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ABSTRACT. *Potential for large-scale physical transport processes to affect recruitment of Lake Michigan yellow perch* (Perca flavescens) *was studied by examining the variation in larval distribution, growth rate, and settlement during June–August 1998–2003 using a 3D particle transport model linked with an individual-based bioenergetics growth model. In all years, virtual larvae were released nearshore in southwestern Lake Michigan, a known and important spawning region for yellow perch. For any given year, the same circulation pattern and water temperature either promoted or reduced yellow perch settlement depending on the consumption rates and settlement size chosen in the growth model. Increased consumption increased the number of settled larvae and expanded the total area where larvae settled, whereas increased settlement size reduced the number of settled larvae and reduced the overall settlement area. Interannual variability in circulation patterns and water temperature also resulted in contrasting larval settlement rates, settlement locations, and size of settlement areas between years. Model predictions were most consistent with field observations of age-0 yellow perch from Illinois and Michigan waters when settlement was assumed to occur at 50 mm. Moreover, our model suggests that larvae originating from southwestern Lake Michigan can recruit anywhere within the southern basin and even in the northern basin. Future model improvement will require information on the relative contribution of various sectors to the larval pool, their distribution with reference to the hydrodynamic landscape, the feeding and growth of yellow perch during their pelagic phase, and the size at transition to demersal stage.*

INDEX WORDS: *Larval transport, bioenergetics model, Great Lakes.*

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INTRODUCTION

Yellow perch (*Perca flavescens*) is an ecologically and economically important species in Lake Michigan that has suffered recruitment failures over the last decade (Francis *et al.* 1996, Clapp and Dettmers 2004). Causes for poor recruitment are not fully understood, but are believed to include high mortality during early life stages caused by advection away from suitable habitats, variable temperature regimes, predation by pelagic planktivores, changes in zooplankton prey assemblages, change in spawning stock characteristics, and overfishing (Clapp and Dettmers 2004). In inland lakes, the pelagic stage of yellow perch and the ecologically similar Eurasian perch (*Perca fluviatilus*) begins shortly after larvae hatch and lasts for a few weeks in lakes that are a few hectares to approximately 40 days in lakes on the scale of a few thousand hectares (Whiteside *et al.* 1985, Urho 1996). In Lake Michigan, the length of the pelagic period may be even longer, and at least some individuals have been captured in the pelagia after about 75 days at sizes ranging from 20 to 70 mm (Dettmers *et al.* 2005). This extended pelagic period means the influence of lake physics on recruitment of yellow perch could be significant due to spatially and temporally variable temperature fields and circulation patterns. Because newly hatched yellow perch swim at only about 1 cm sec^{-1} (Houde 1969), much slower than current velocities (>10 cm sec^{-1}) typical of Great Lakes nearshore areas, the extended pelagic period of at least some individuals reported by Dettmers *et al.* (2005) could be a consequence of hydrodynamics rather than an innate biological imperative.

The importance of circulation variability to fish population structure and recruitment variability has long been recognized for marine fish populations (e.g., Hjort 1914). However, only in more recent years have physical transport models been used to understand the impacts of ocean-scale hydrodynamics on recruitment. For example, Heath and Gallego (1998) coupled a particle-tracking model with an individual-based model of larval growth and survival to investigate the spatial and temporal patterns in recruitment processes of North Sea haddock *Melanogrammus aeglefinus*. Hydrodynamic models were also used to explain transport mechanisms for fish larvae recruiting from offshore to coastal estuaries in the South Atlantic Bight (Crowder and Werner 1999). Cowen *et al.* (2005) used a high-resolution biophysical model to study larval dispersal, connectivity, and recruitment in the Caribbean region.

Physical processes in the Great Lakes occur over temporal and spatial scales comparable to the coastal ocean (Beletsky *et al.* 2004, Dettmers *et al.* 2005, Höök *et al.* 2006), yet coupled physical-biological models for recruitment studies are rare. Given the complexity and magnitude of the physical processes in the Great Lakes, it is very likely that these physical processes play an important role in structuring the recruitment dynamics of Great Lakes fishes. The goal of this paper is to explore the effects of physical factors (temperature and circulation) on recruitment variability of yellow perch in Lake Michigan, to gain insight into the decline of the yellow perch population and the potential factors causing poor recruitment.

To gain a better understanding of yellow perch recruitment dynamics in Lake Michigan, we developed a biophysical model that takes into consideration 3-D circulation and thermal processes, physiology and ecology of fish larvae, and trophodynamics. The model belongs to a Lagrangian-type, which tracks trajectories of fish larvae over time (Hofmann and Lascara, 1998). In this approach, the models of physical transport and temperature are linked with individual-based particle models of fish larvae to study variation in larval total length distributions, growth, and settlement. In particular, we focused on the transport of larval yellow perch hatched in the Illinois sector of southern Lake Michigan during 1998–2003 using recently calibrated modeling results of summer hydrodynamics (Beletsky *et al.* 2006). This area of Lake Michigan is known for high concentrations of yellow perch spawners due to the abundance of their preferred rocky habitat (Goodyear *et al.* 1982, Robillard and Marsden 2001) and has the longest record of observations of age-0 yellow perch in Lake Michigan. Targeting this particular area of Lake Michigan allowed us to demonstrate the potential impact that one relatively small but very productive area can have on other regions of the lake. Model sensitivity to critical parameters was studied by varying feeding rates and settlement lengths. Finally, we evaluated model performance by comparing model results with independent observations of age-0 yellow perch abundance from 1998 to 2003.

METHODS

Biophysical Model

We used a 3-dimensional biophysical individual-based model that predicts the transport, growth, and settlement of larval yellow perch. The model con-

sists of a physical particle component and a bioenergetics component. The physical component moves particles with currents on a 3 hour basis and also supplies temperature along the particle route from a 3-dimensional hydrodynamic model. Then the bioenergetics component is applied to particles representing larval fish on a daily basis using daily averages of modeled temperature.

Particle Transport Model

The 3-dimensional particle trajectory code is a combination of the Princeton Ocean Model subroutine TRACE written by Jarle Berntsen (Institute of Marine Research, Bergen-Nordnes, Norway, personal communication) and the second order accurate horizontal trajectory code described by Bennett and Clites (1987). It uses currents from a 3-dimensional circulation model of Lake Michigan (Beletsky *et al.* 2006) that has a uniform horizontal grid size of 2 km (Figure 1). The Lagrangian equations of motion for a particle are:

$$\frac{dx}{dt} = u(x,y,z)$$
$$\frac{dy}{dt} = v(x,y,z) \qquad (1)$$
$$\frac{dz}{dt} = w(x,y,z)$$

where (x,y,z) is the 3-dimensional position of the particle, (u,v,w) is the 3-dimensional velocity, and t is time. In order to solve the equations of motion numerically, the horizontal currents (u,v) are first interpolated from velocity points to grid square corners on the Arakawa-C grid. The particle trajectory code uses a Taylor series expansion of the horizontal velocities (u,v) about the particle position (x,y) in the trajectory equations and first order differences in time to yield

$$\frac{x^{n+1} - x^n}{\Delta t} = u(x^n,y^n) + \frac{1}{2}\frac{\partial u}{\partial x}(x^{n+1} - x^n) + \frac{1}{2}\frac{\partial u}{\partial y}(y^{n+1} - y^n)$$
$$\frac{y^{n+1} - y^n}{\Delta t} = v(x^n,y^n) + \frac{1}{2}\frac{\partial v}{\partial x}(x^{n+1} - x^n) + \frac{1}{2}\frac{\partial v}{\partial y}(y^{n+1} - y^n)$$
$$(2)$$

where superscript n indicates the current time step in the numerical integration, and Δt is the time increment. Values of u and v at point (x^n, y^n) are computed by assuming bilinear variation of the horizontal currents from the corners of the grid

square. The derivatives of u and v are computed by linear interpolation from the sides of the grid squares. Equations (2) represent a pair of simultaneous equations which can be solved for the new particle position (x^{n+1}, y^{n+1}). The time increment Δt is chosen to limit the maximum excursion of a particle during one time step to 1/8 the distance between horizontal grid points.

To calculate vertical motion, the sigma coordinate ($\sigma = z/d$ where d is the water depth) is calculated using a value for the depth that is bilinearly interpolated to the particle position, i.e.,

$$\sigma(x^n,y^n) = z^n/d(x^n,y^n) \qquad (3)$$

The vertical velocity, w, is interpolated vertically from hydrodynamic model vertical velocities at the σ-levels bracketing $\sigma(x^n, y^n)$. Vertical motion is then predicted by

$$z^{n+1} = z^n + w\Delta t \qquad (4)$$

Particles are prevented from crossing the lake bottom or free surface, as well as horizontal boundaries. This method generally predicts more realistic trajectories than traditional first-order horizontal methods and does not allow particles to accumulate in "stagnation" zones at grid square corners along the shoreline. The model was successfully tested with satellite-tracked drifter observations conducted in southern Lake Michigan in 2003 (Beletsky *et al.* 2006).

In the particle transport model, 246 particles (larval yellow perch) were released at a known spawning location north of Chicago, Illinois (Goodyear *et al.* 1982, Robillard and Marsden 2001) (Fig. 1) at bathymetric depths of less than 10 m. This reflects the preference for yellow perch to spawn on the rocky habitat available at this location and that the larvae and pelagic juveniles are in the epilimnion (Fulford *et al.* 2006b). Particles were distributed uniformly with depth: near the surface, at 1/3 and at 2/3 of a grid cell's depth. Particle model runs began on 1 June of each year and ended in late August. Observed hatch dates of yellow perch larvae in this area were between 1 June and 3 June for 4 of 6 years surveyed, and only a few days later during the other 2 years (which should not make a substantial difference in their final dispersion pattern 3 months later). Therefore, particles were released during a 2-day period starting on 1 June in the south and ending on 3 June in the north.
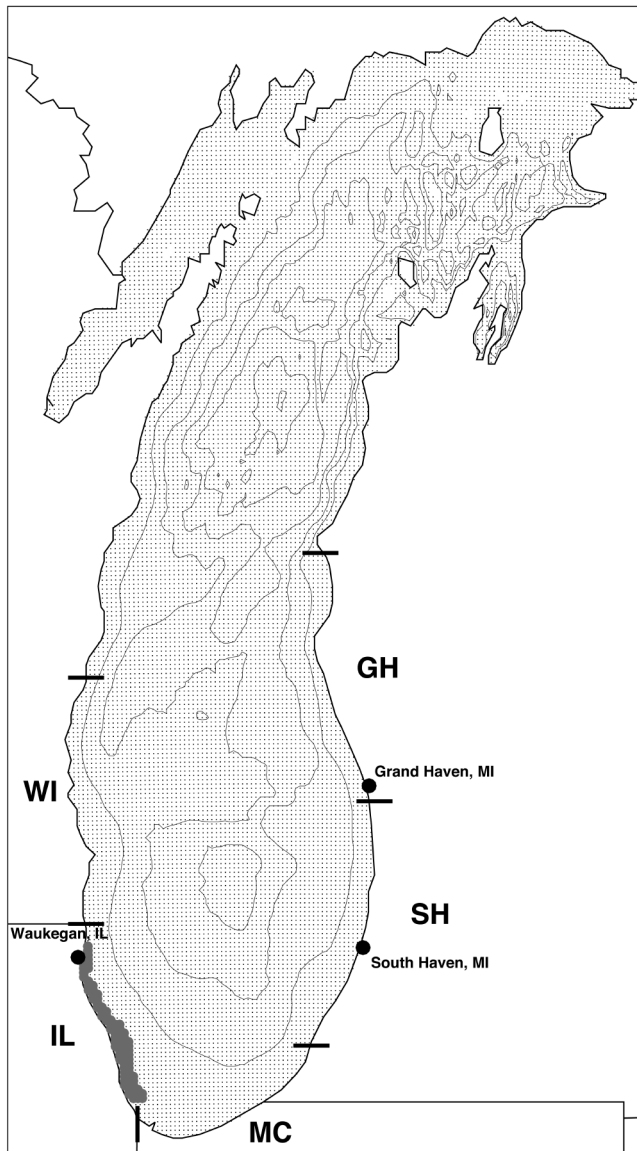
FIG. 1. Lake Michigan 2 km hydrodynamic model grid, bathymetry (isobaths every 50 m), initial particles location, and observation sites (filled circles). Five coastal sectors of the lake (WI, IL, MC, SH, and GH) under study are also shown.

Individual-based Biological Model

An individual-based bioenergetics model was used to grow larval yellow perch (particles) from hatch to settlement size. The hydrodynamic model (Beletsky *et al.* 2006) supplied information on the three-dimensional temperature field along the larval path predicted by the particle transport model. Another critical parameter for larval development is food availability (primarily zooplankton). Unfortu-

nately, there is very little information available on the spatial distribution of zooplankton in southern Lake Michigan in summer. Therefore, in all biological model runs, we assumed that there is no spatial gradient in food (zooplankton) available for larval yellow perch.

The bioenergetics model used was a species-specific, energy-balanced approach that described the flow of energy through an individual fish and how energy obtained (through consumption) was partitioned between growth, and losses (respiration, egestion, excretion, and specific dynamic action) (Kitchell *et al.* 1977). Energy per unit time was related to weight per unit time by a specific energy density for predator and prey (Joules per unit weight). The basic form of the bioenergetics model in terms of weight specific growth rate (g·g·d⁻¹) was,

$$\frac{1}{W}\frac{dW}{dt} = \phi - (R_{resp} + SDA + F + U) \tag{5}$$

where W is weight of the individual, t is time in days, ϕ is feeding rate, R_{resp} is respiration, SDA is specific dynamic action, F is egestion, and U is excretion. Each of the terms in the equation was a function of water temperature, thus both feeding rate, ϕ, and temperature drive growth (Table 1). Parameter values (Table 2) were adapted from previously published bioenergetics models for yellow perch juveniles (Kitchell *et al.* 1977, Hanson *et al.* 1997, Rose *et al.* 1999). We adopted juvenile bioenergetics parameters because they predicted larval consumption rates that were closer to observed rates (Letcher *et al.* 1997). For this exercise, we assumed that ϕ was a constant proportion of maximum consumption C_{max} ($\phi = p*C_{max}$), and growth rate was driven primarily by temperature, which differed across space and time. The *p*-value was fixed at 0.5 (assumed uniform food availability) in the base model run (which represented average growing conditions) and varied from 0.4 to 1.0 in the model sensitivity studies to simulate the likely range of growth conditions encountered in Lake Michigan. These *p*-values were selected based upon prior modeling efforts of yellow perch larvae growth (Letcher *et al.* 1997, Rose *et al.* 1999, Fulford *et al.* 2006a). Larval weight (g) was converted to length (mm) using a length – weight relationship $L = 45.9*W^{0.33}$ (Rose *et al.* 1999).

All larvae were assumed to have an initial length of 6 mm at hatching. Movement and growth of larvae in the model were followed from hatching to

TABLE 1. Bioenergetic equations for yellow perch.

Equation	Description
$C_{\max} = Ca \times wt^{Cb} \times f_c(T)$	Maximum consumption ($gg^{-1}d^{-1}$)
$f_c(T) = V^x e^{x(1-V)}$	Temperature-dependent function (dimensionless)
$V = \dfrac{CTM - T}{CTM - CTO}$	
$x = \left\{ Z^2 \left[1 + \left(1 + \dfrac{40}{Y}\right)^{0.5} \right]^2 \right\} \dfrac{1}{400}$	
$Z = \ln(CQ)(CTM - CTO)$	
$Y = \ln(CQ)(CTM - CTO + 2)$	
$R = Ra \times wt^{Rb} \times f_R(T) \times ACT$	Respiration ($gg^{-1}d^{-1}$)
$f_R(T) = V^x e^{x(1-V)}$	Temperature-dependent function (dimensionless)
$V = \dfrac{RTM - T}{RTM - RTO}$	
$x = \left\{ Z^2 \left[1 + \left(1 + \dfrac{40}{Y}\right)^{0.5} \right]^2 \right\} \dfrac{1}{400}$	
$Z = \ln(RQ)(RTM - RTO)$	
$Y = \ln(RQ)(RTM - RTO + 2)$	
$S = SDA(C - F)$	Specific dynamic action ($gg^{-1}d^{-1}$)
$F = F_a \times T^{F_b} \times e^{(F_g \times p\text{-}val)} \times C$	Egestion ($gg^{-1}d^{-1}$)
$U = U_a \times T^{U_b} \times e^{(U_g \times p\text{-}val)} \times (C - F)$	Excretion ($gg^{-1}d^{-1}$)
$G = E\_ratio \times [C - (R + S + F + U)]$	Growth rate ($gg^{-1}d^{-1}$)

30 mm, the minimum length at which they can set-
tle and become demersal; larvae metamorphose
into juveniles at 20 mm, and by 30 mm take on the
characteristics of adult fish. Whiteside *et al.* (1985)
found that yellow perch from Lake Itasca, Min-
nesota, became demersal at about 25 mm total
length. A similar length, 30 mm, was reported for
Lake St. George, Ontario (Post and McQueen
1988) and Lake Erie (Wu and Culver 1992). In
southwestern Lake Michigan, the mean size of yel-
low perch returning to nearshore Illinois waters has
varied between 32 and 61 mm since 1986, with
40–50 mm being the most common. Generally, the
later yellow perch returned, the larger they were. In
1998, a year of relatively late return (late August)
the mean size of yellow perch was 54 mm. In con-
trast, fish arriving nearshore in late July were about
42 mm long. Generally, age-0 yellow perch which

appeared nearshore before the end of July, were
less than 40 mm long and were over 50 mm long if
they arrived at the end of August or later
(Dettmers, INHS unpublished). In southeastern
Lake Michigan, yellow perch length ranged from
43–71 mm in 1996–2002 (Fitzgerald *et al.* 2004).
Thus, we also used a settlement size of 50 mm in
the model sensitivity studies.

The depth range for settlement is poorly known.
Janssen and Luebke (2004) sampled for age-0 yel-
low perch in about 1.5 m of water, but presumably
the fish became associated with the bottom in
deeper water. In Illinois waters, age-0 yellow perch
are caught between 3 and 10 m deep water. The
maximum depths reported are anecdotal and in-
clude about 25–30 m at Julian's Reef, southwestern
Lake Michigan (Edsall *et al.* 1993), 50–75 m for
southeastern Lake Michigan (Geffen and Nash

TABLE 2.   *Larval yellow perch bioenergetics model parameters*

Symbol	Description	Value	Unit
Ca	Intercept for C_{max}	0.25	$gg^{-1}d^{-1}$
Cb	Exponent for C_{max}	–0.27	dimensionless
CQ	Slope for temperature-dependence of consumption	2.3	dimensionless
CTO	Optimum temperature for consumption	29.0	$°C$
CTM	Maximum temperature for consumption	32.0	$°C$
Ra	Intercept for maximum std respiration	0.0108	$gg^{-1}d^{-1}$
Rb	Exponent for maximum std respiration	-0.2	dimensionless
RQ	Slope for temperature-dependence of std respiration	2.1	dimensionless
RTO	Optimum temperature for std respiration	32.0	$°C$
RTM	Maximum temperature for std respiration	35.0	$°C$
ACT	Activity multiplier	1.0	dimensionless
SDA	Specific dynamic action coefficient	0.172	dimensionless
Fa	Intercept of the proportion of consumed energy egested vs. water temperature and ration	0.158	$gg^{-1}d^{-1}$
Fb	Water temperature dependence of egestion	–0.222	dimensionless
Fg	Feeding level dependence of egestion	0.631	dimensionless
Ua	Intercept of the proportion of consumed energy excreted vs. water temperature and ration	0.0258	$gg^{-1}d^{-1}$
Ub	Water temperature dependence of excretion	0.58	dimensionless
Ug	Feeding level dependence of excretion	–0.299	dimensionless
ED_{prey}	Energy density of prey	1675	Joules g^{-1}
ED_{pred}	Energy density of predator	2100	Joules g^{-1}
E_ratio	Ratio of prey energy density to predator energy density	ED_{prey}/ED_{pred}	dimensionless

1992), and about 20 m for eastern Lake Michigan (Clapp, MDNR unpublished). We developed a relatively simple settlement model in this study: any particle reaching 30 mm and finding itself in waters less than 20 m is considered settled (its position is fixed). A similar simplifying assumption was used for studies of larval fish settlement in the Caribbean by Cowen *et al.* (2005).

Observations

To evaluate model predictions, we used age-0 yellow perch observations collected by trawls in Illinois and Michigan waters. In Illinois, age-0 yellow perch were collected nearshore using an otter trawl with a 4.9-m head rope, 38-mm stretched mesh body, and 13-mm mesh cod-end. All trawls occurred during daylight and were taken along the bottom at approximately weekly intervals from mid-July through late October at four depth stations (3, 5, 8, and 10 m). All

sampling occurred north of Waukegan Harbor (Fig. 1) at a speed of about 2 m s^{-1}. Fish were identified to species, counted, and measured to the nearest mm total length. In Michigan, samples near the ports of South Haven and Grand Haven were collected with multiple bottom trawls (4.9-m head rope, body and cod end composed of 19-mm and 16-mm bar mesh, respectively, and with a 6-mm stretched-mesh inner liner) in nearshore areas with water depths ≤ 7 m. Trawling was completed in both daylight and dark periods, once a month, during mid-summer (late July to early August) and late summer (late August to early September).

RESULTS

Temperature and Circulation Patterns

Detailed description of Eulerian model results and comparison with observations is presented in
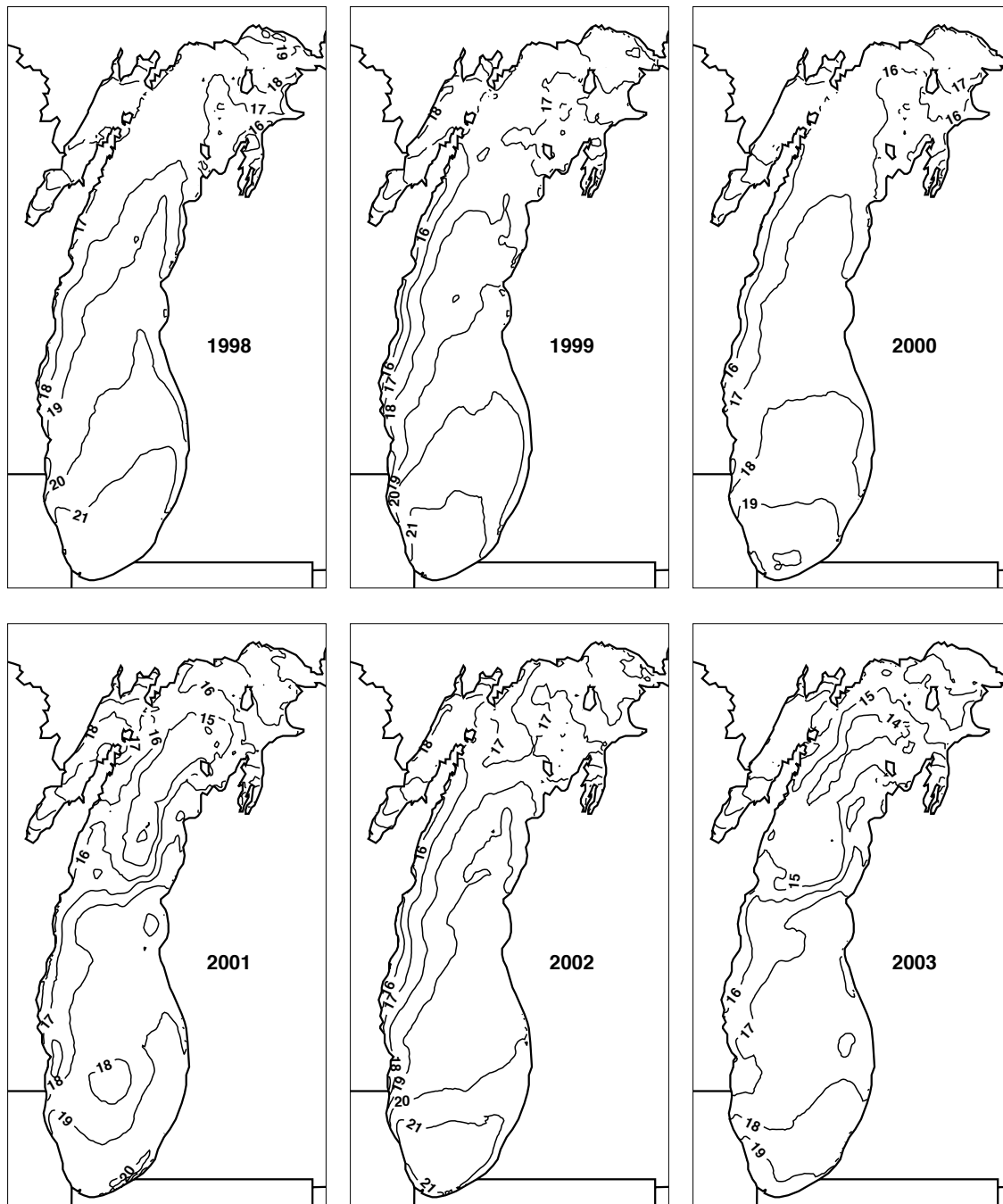
FIG. 2. Mean lake surface temperature in June–August, 1998–2003.

Beletsky *et al*. (2006), so here we only give a brief summary of results essential for biophysical modeling. Because temperature plays a crucial role in larval yellow perch growth, we present average surface temperature patterns for each summer in 1998–2003 (Fig. 2). There was a general north-south temperature gradient seen in all years.

Another prominent feature of lake temperature patterns was a wind-driven upwelling at the west coast typical of summer conditions in Lake Michigan (Beletsky and Schwab 2001, Plattner *et al*. 2006). In southern Lake Michigan, mean surface temperature varied between 18 and 19°C in 2000, 2001, and 2003. In 1998, 1999, and 2002, mean surface tem-

1998   **1999**   **2000**

2001   **2002**   **2003**
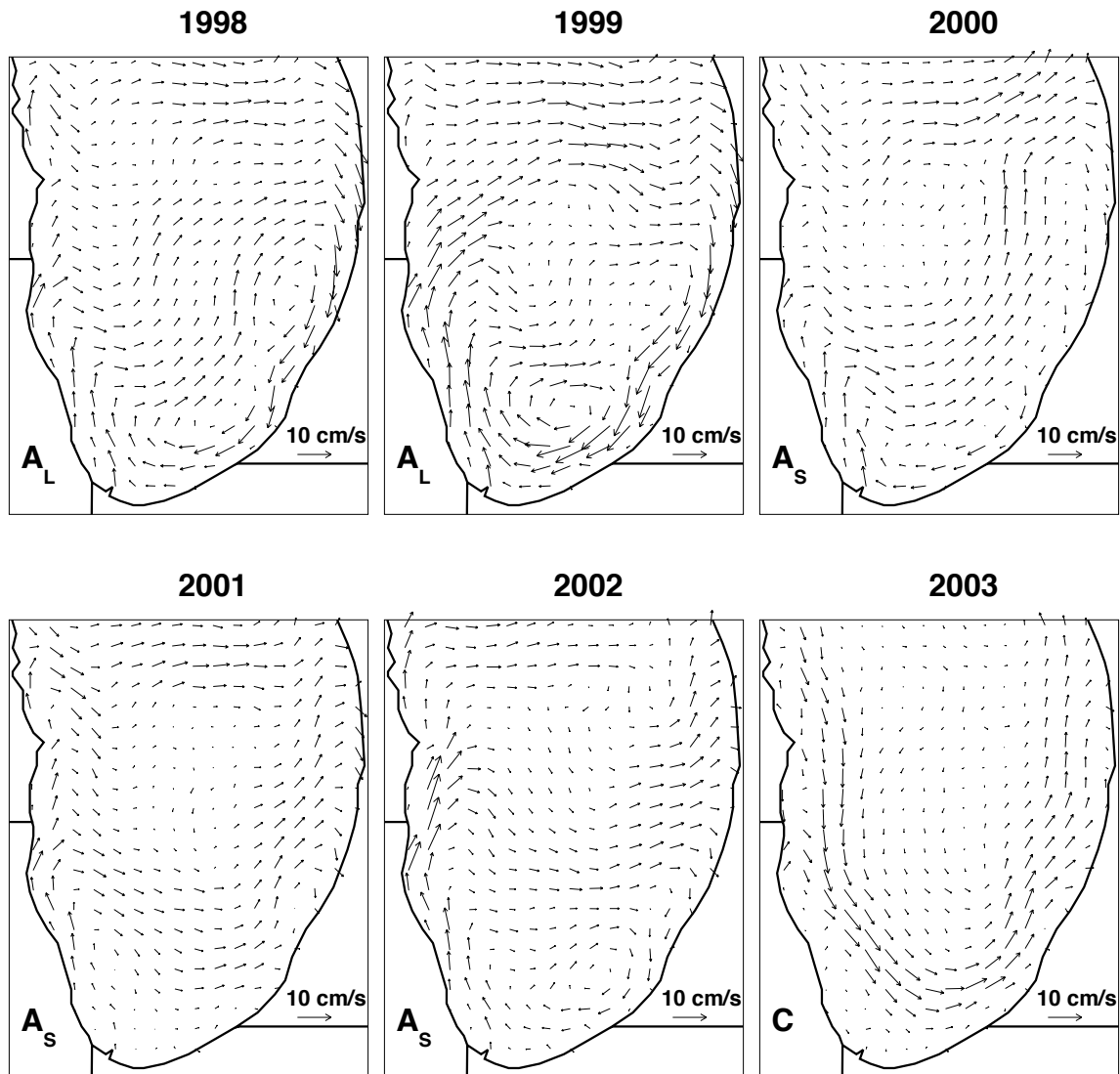
FIG. 3. *Mean surface currents in southern Lake Michigan in June–August, 1998–2003. Every 4-th vector is shown. Circulation type is also shown (A_L - anticyclonic-large, A_S - anticyclonic-small, C - cyclonic).*

perature was about 1–2°C higher (20–21°C) due to warmer than normal preceding winters.

Summer circulation patterns also varied significantly in Lake Michigan between years, especially in the southern basin, as a result of interannual variability in wind and water temperature fields. In southern Lake Michigan, circulation patterns tended to be cyclonic in the deep area but anticyclonic in the shallow southernmost area (Fig. 3). In some years, anticyclonic circulation covered the whole southern basin (circulation type "A_L" in 1998 and 1999), whereas in some years it was confined to a smaller southernmost area (circulation type "A_S" in 2000, 2001, and 2002). In other years (i.e., 2003), cyclonic circulation (circulation type "C") was

dominant. We also note that in average (in a climatological sense) years, circulation tended to be cyclonic, whereas in warmer years, an anticyclonic circulation (also supported by relevant horizontal temperature distribution) was more likely. The typical speed of surface currents was about 10 cm s^{-1}.

Physical Transport

Particle locations at the end of each month (June–August) are shown in Figure 4. Because all particles were released in very shallow waters, they tended to stay relatively close to the surface (0–20 m). Movement of particles released near the surface did not differ from particles that were released closer to the bottom. Overall, particle movement

Jun 1998

Length > 6 mm

Mean = 16.4 mm
Min = 14.2 mm
Max = 17.6 mm

Jul 1998

Length > 6 mm

Mean = 32.0 mm
Min = 23.2 mm
Max = 35.4 mm

Aug 1998

Length > 6 mm

Mean = 49.4 mm
Min = 32.5 mm
Max = 55.0 mm

Jun 1999

Length > 6 mm

Mean = 16.4 mm
Min = 13.4 mm
Max = 17.8 mm

Jul 1999

Length > 6 mm

Mean = 30.2 mm
Min = 21.3 mm
Max = 33.8 mm

Aug 1999

Length > 6 mm

Mean = 45.9 mm
Min = 29.7 mm
Max = 51.9 mm

Jun 2000

Length > 6 mm

Mean = 15.3 mm
Min = 13.2 mm
Max = 16.1 mm

Jul 2000

Length > 6 mm

Mean = 28.4 mm
Min = 24.1 mm
Max = 30.7 mm

Aug 2000

Length > 6 mm

Mean = 44.1 mm
Min = 32.6 mm
Max = 48.1 mm

FIG. 4. Larval transport and growth in 1998–2003. Total number of particles shown. The histogram shows distribution of larvae with length.
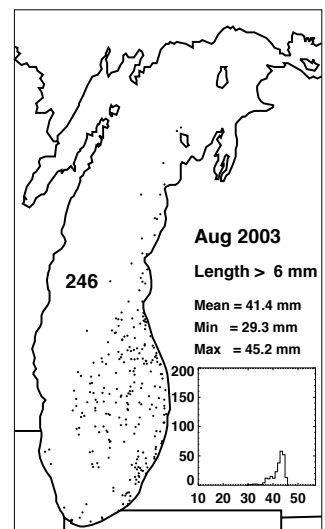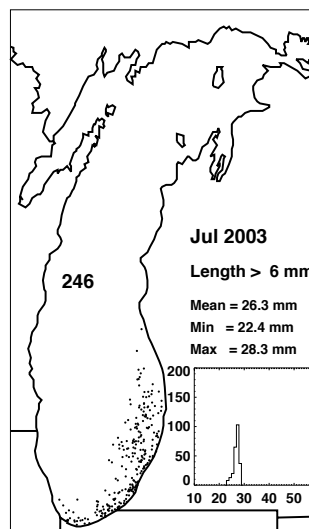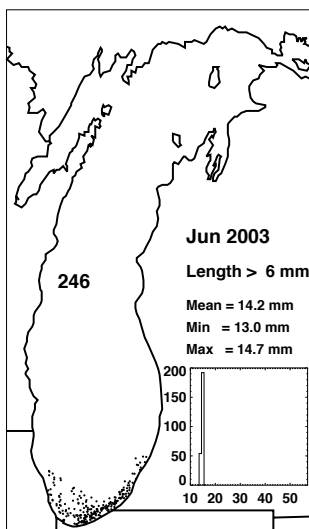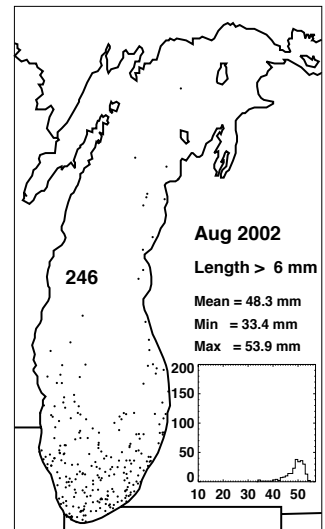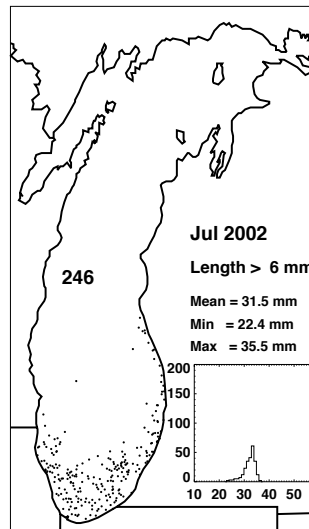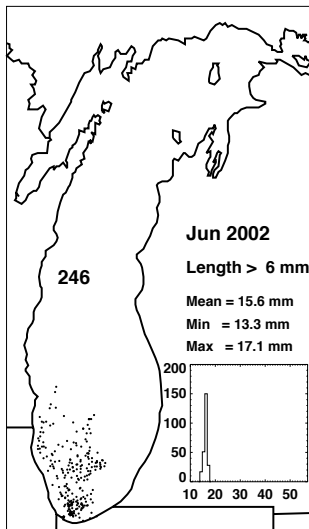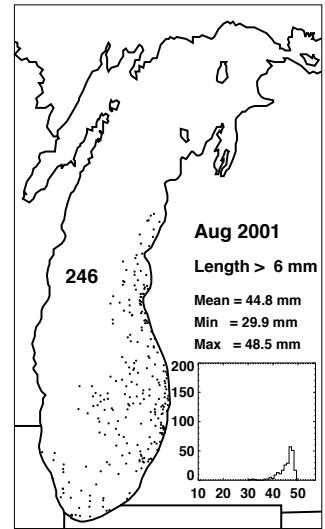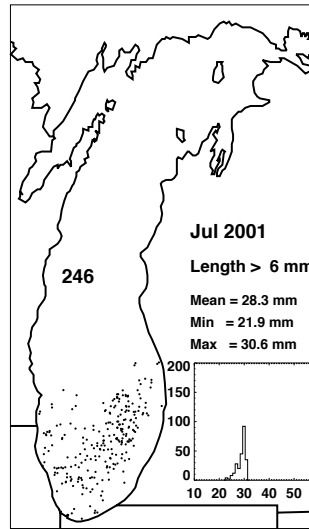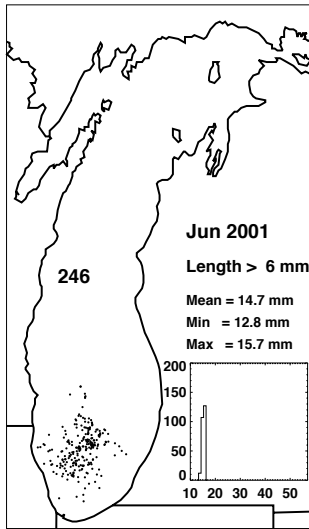
TABLE 3. *Modeled larval growth and settlement characteristics in 1998–2003*
(A_L – anticyclonic large; A_S – anticyclonic small; C – cyclonic circulation).

Year	1998	1999	2000	2001	2002	2003
Circulation type	A_L	A_L	A_S	A_S	A_S	C
Number of settled larvae (%)	35	46	52	58	85	52
Average time to 30 mm (days)	57	60	64	64	58	69
Average time to settlement (days)	77	63	68	71	65	69
Average settlement size (mm)	44	32	33	35	35	31

matched the monthly mean surface current pattern. Particles initially were transported offshore and then continued to circulate in southern Lake Michigan in an anticyclonic fashion in most years (with 2003 being the most notable exception when strong cyclonic circulation prevailed). Under certain conditions, e.g., particularly strong northward currents along the east coast in August 1998, 2001, and 2003 (see also Fig. 3 in Beletsky *et al.* 2006) some particles escaped the southern basin and penetrated the northern basin of Lake Michigan.

Larval Growth

Given that all larvae were assumed to be the same initial length (6 mm), the original length frequency distribution exhibited a distinct peak that gradually diffused as larvae experience different temperature regimes in the lake (Fig. 4). Larvae did not obtain a critical length of 30 mm, minimum length for settlement, by the end of June (30 days post hatch). By the end of June 2000–2002, most larvae were more than 10 km offshore with sizes ranging between 13 and 17 mm. Lengths were consistent (although the model tended to overestimate length) with data from early July 2000–2002 presented in Figure 4 of Dettmers *et al.* (2005). Dettmers *et al.* (2005) observed that yellow perch larvae increased in size from nearshore to offshore with the largest larvae being 8–10 mm 12 km offshore. Larval length at the end of June between years showed consistent patterns between model results and the field observation of Dettmers *et al.* (2005) where largest mean length occurred in 2002 (15.6 mm), smallest mean length was in 2001 (14.7 mm), and intermediate length in 2000 (15.3 mm).

By the end of July, only a few larvae (less than 13%) reached 30 mm in 2000, 2001, and 2003 whereas in 1998, 1999, and 2002, more than 60% of larvae grew to their settlement length (Fig. 5). The variability in annual growth is undoubtedly the result of much cooler water temperatures in 2000,

2001, and 2003 (Fig. 2). On average, it takes about 62 days for yellow perch larvae to reach 30 mm (Table 3). About 99% of all particles reached 30 mm by the end of August.

Settlement, Connectivity, and Self-recruitment

For a given settlement length, settlement pattern is a result of a complex interplay between circulation and temperature patterns. In case of a base model run ($p = 0.5$, settlement at 30 mm), most larvae settled in southern Lake Michigan (Fig. 6), and most settle east of the site of original release in Illinois. By the end of July, more larvae settled in 1999 (24%) and 2002 (38%) than in other years. By the end of August, 54% of all larvae settled, with 2002 being again the best year (85% settled) (Table 3). The average size at settlement increases with time as larvae continue to grow, from 30–32 mm by the end of July to 31–44 mm by the end of August. The largest average settlement size occurred in August 1998, which was one of the warmest years on record.

Strong interannual variability in total number of settled larvae (Table 3) is largely attributed to varying circulation patterns, some of which promote settlement (A_S and C), whereas some reduced it (A_L). The difference between 1998 and 2002 is especially striking, when settlement varied from 35% to 85% for practically the same time to settlement size (57–58 days). This is further reflected in the time lag between reaching settlement size and settlement time. This time lag was about 20 days in 1998 whereas in 2002 and in other years it was only 1 week or less.

Distribution of settled larvae by geographic sector WI, IL, MC, SH, and GH (see Fig. 1 for details) aids our understanding of the connectivity of different areas in Lake Michigan (Fig. 7). Sectors were selected to be roughly the same length (average sector length is about 140 km) and to cover the area that contains 99% of all settled larvae by the end of

August. In all years except 1998 and 2002, larval export was highest to the MC-SH sector which is consistent with prevailing circulation patterns. In 1998, settlement shifted north to SH-GH sector, while in 2002 settlement area expanded west from MC-SH sector to include the IL sector. Settlement time also varied by sector. The 1998–2003 mean settlement time gradually increased from 65–66 days at IL and MC sectors (closest to the source of larvae) to 75 days at GH sector (farthest away from the source of larvae). Settlement time varied by 8–10 days between years at IL and MC sectors and by 14–16 days at SH and GH sectors.

Biophysical model results can be used further to address a question of self-recruitment in Lake Michigan (to sector IL). We define self-recruitment as the process by which fish settle in the area where they originated, in our case southwest Lake Michigan. In all years except 2002, the number of modeled larvae settled in Illinois was low, less than 2% of all released particles that settled in Lake Michigan. In 2002, at least 10 times more larvae (20%) settled in Illinois waters. Favorable circulation patterns along with higher than normal temperatures were among the factors causing high numbers of settled yellow perch in Illinois.

Model Sensitivity Studies

We tested model sensitivity to two parameters: consumption rate and settlement length. In the first test, we varied consumption rate (always constant within each model run) by varying p-value from 0.4 to 1.0 (Fig. 8). In the base model run case, it took larvae 62 days on average to reach 30 mm and over 90 days to reach 50 mm. The growth was fastest in 1998 (57 days) and slowest in 2003 (69 days) which reflects interannual variability in water temperature. Increased consumption gradually accelerates larval growth. In particular, in the two-fold increased consumption scenario ($p = 1$), all larvae reached 30 mm by early July, indicating that doubling consumption reduces the time for particles to reach the 30 mm settlement size by about 1 month.

The impact of p on settlement is shown in Figure 9. Consistent with model results shown in Figure 8, increase in p lead to acceleration of settlement, again by about one month for $p = 1$. It also lead to an overall increase in the number of settled larvae. That increase was highly variable between years; the change was less than 10% in 1998 and almost 100% in 2003. Settlement expanded on the fringes of main settlement areas (Fig. 7) to the WI sector in

1998–1999 and to the IL sector in 2003, while remaining unchanged in 2000–2002.

Some research indicates that the timing for yellow perch to become demersal may be delayed for yellow perch in Lake Michigan (Dettmers *et al.* 2005). Therefore, we performed additional model runs to demonstrate the impact of increase in settlement size on settlement by gradually varying settlement size from 30 mm to 50 mm (Fig. 9). As expected, increasing settlement size caused a delay in settlement and reduced the numbers of settled larvae. In particular, increasing settlement size to 50 mm caused a delay in settlement by one month or longer and also a sharp decrease in numbers of settled larvae. In 3 out of 6 years the number of settled larvae decreased to zero. Two years, 1998 and 2002, stand out with approximately 20% of all larvae settled by the end of August. In addition to the reduced numbers, settlement area shrank in both years by cutting the fringes of main settlement areas (Fig. 7) and limiting settlement to the SH-GH sector in 1998 and to the IL-MC-SH sector in 2002.

Results presented in Figure 9 show complex relationships among temperature, feeding rate, circulation patterns, and settlement even in a simple biophysical model. Thus, in the base model run, in 1998 (which was a warm year) settlement was lower than in other years and practically insensitive to consumption rate, being primarily driven by the unfavorable circulation type (A_L). On the other hand, in the model run with extended pelagic phase (settlement at 50 mm), the 1998 circulation type *was* favorable for settlement bringing more larvae nearshore than in any other year, including 2002.

Model Validation

In 1998–2003, age-0 yellow perch samples were collected at several sites in southern Lake Michigan. The most complete observation time-series at a site in Illinois and two sites in Michigan are presented in Figure 10 along with model results for IL, SH, and GH sectors. The 2003 observations at Grand Haven are missing. Although all samples were collected within 5 kilometers or so from each port, analysis of additional data showed that they are representative of larger areas, comparable in size with defined model sectors. Thus, available in some years (1998–2003) are observations at St. Joseph (near the southern end of SH sector) and at Pentwater (near the northern end of GH sector) which were considered consistent with respective observations at South Haven and Grand Haven.
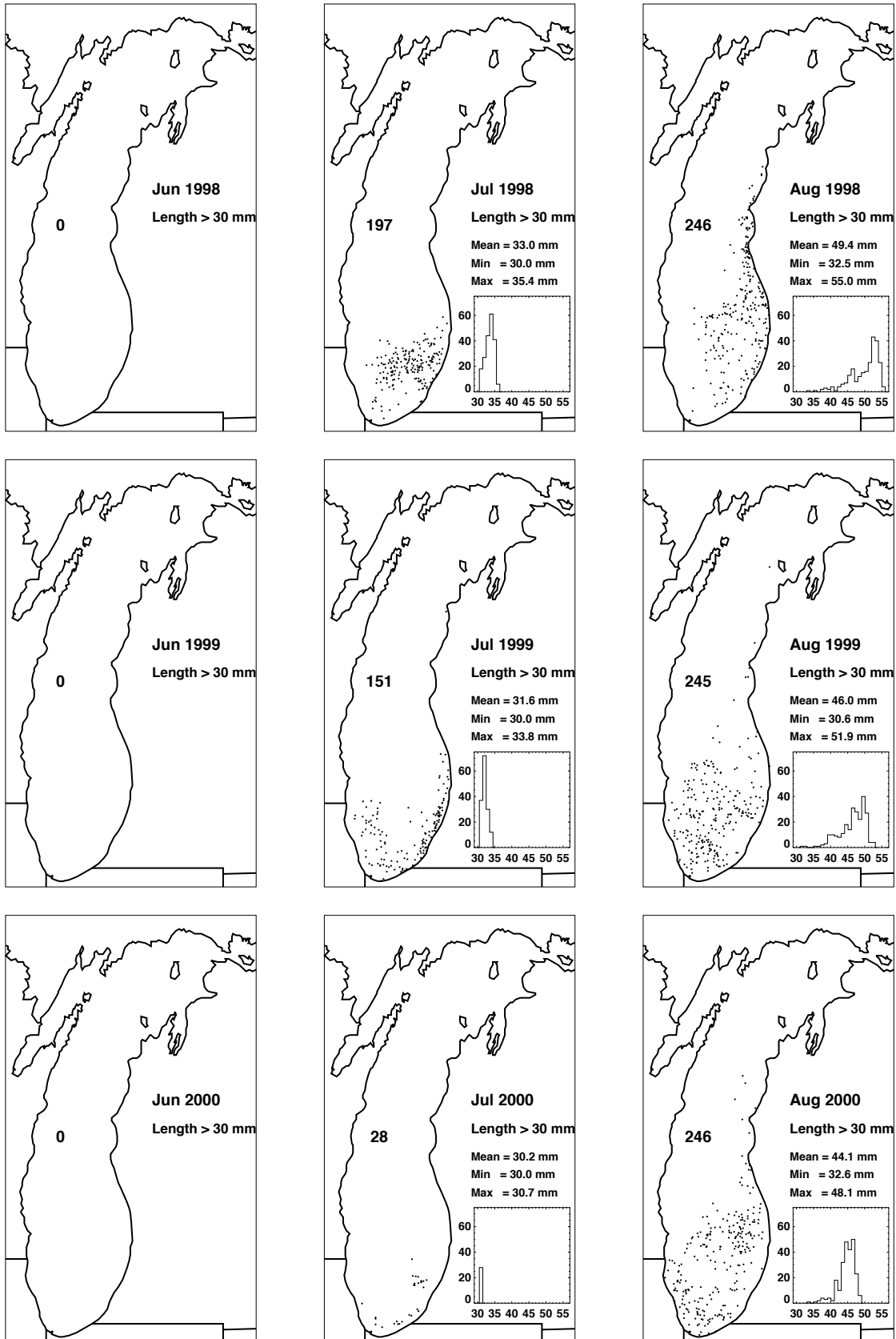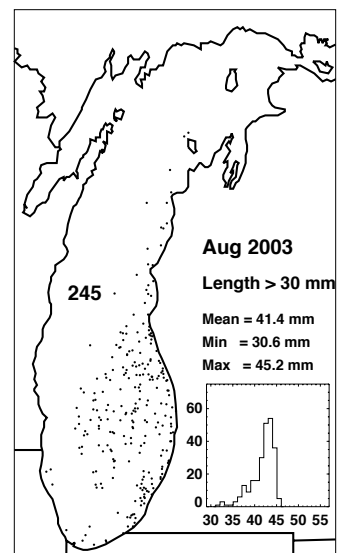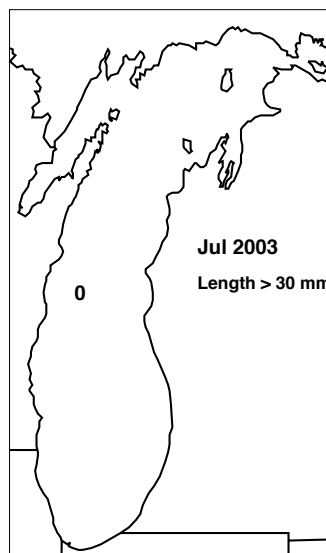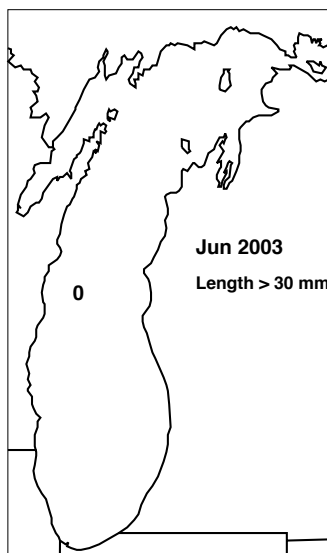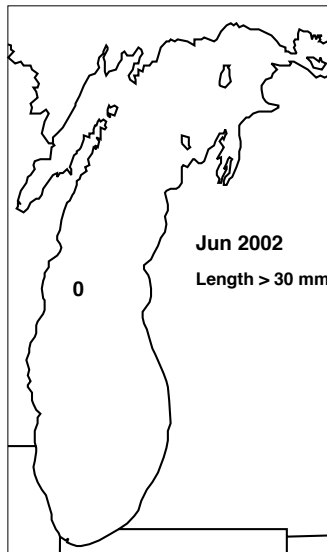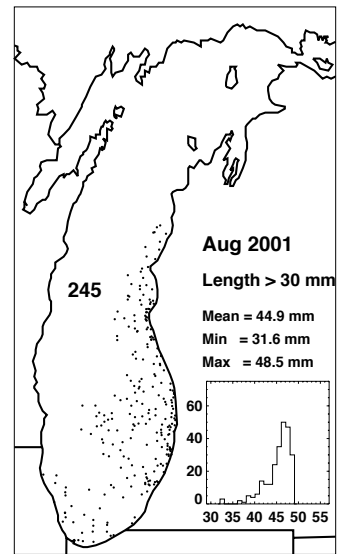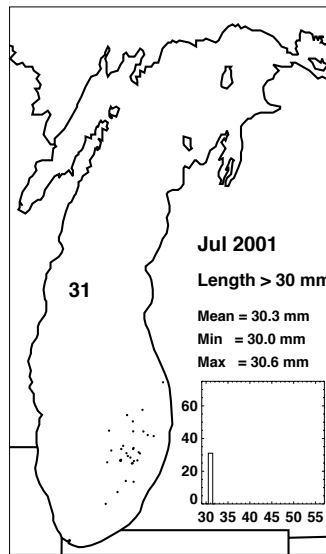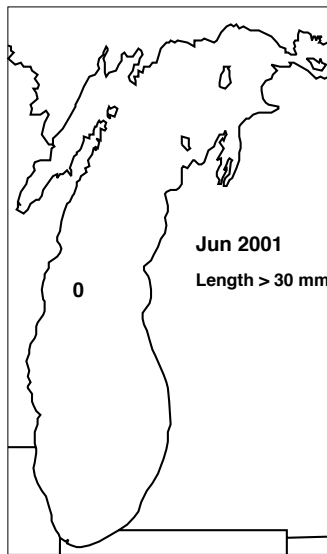
FIG. 5. *Distribution of larvae reaching 30 mm in June–August, 1998–2003. Number of larvae shown. The histogram shows distribution of larval length.*
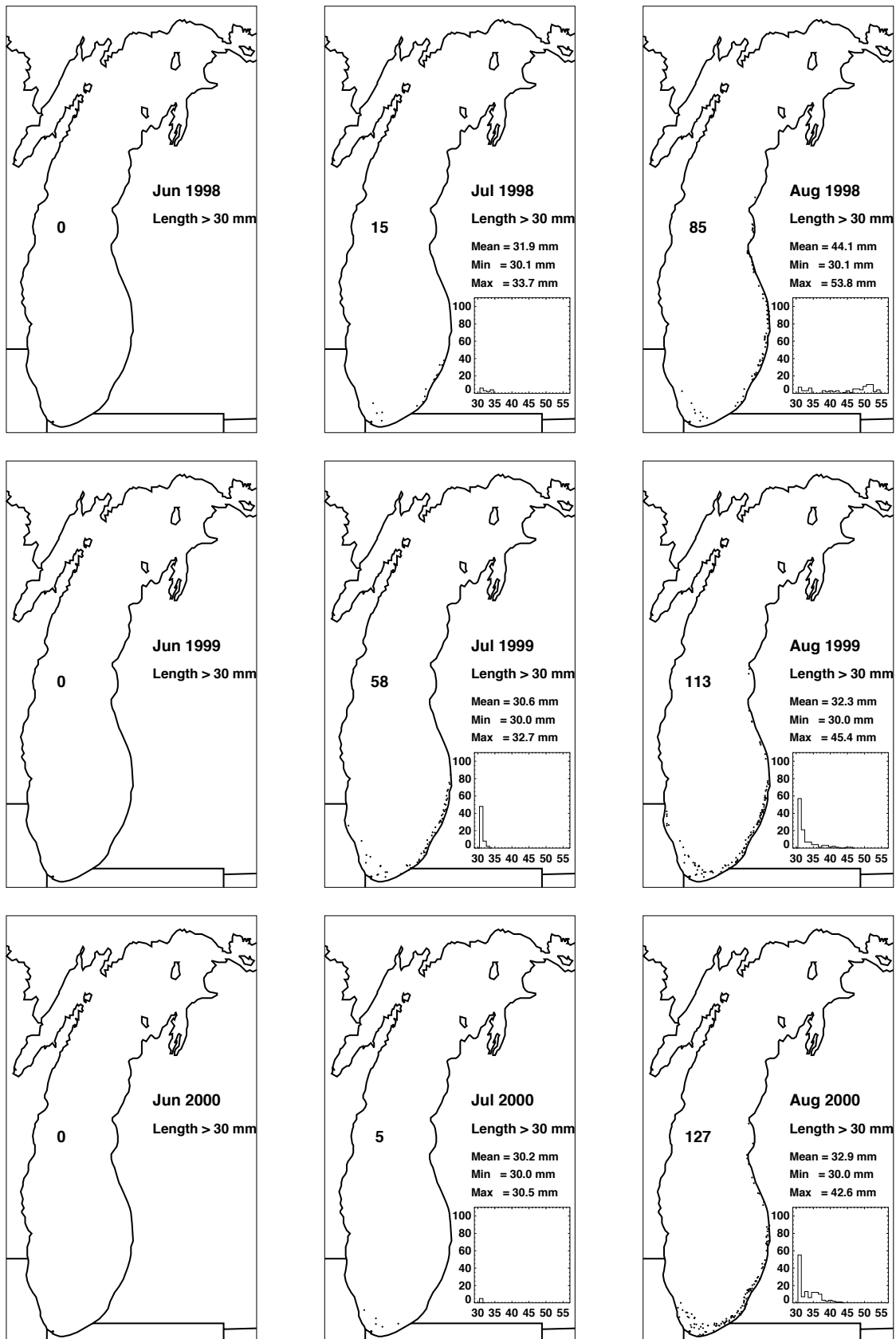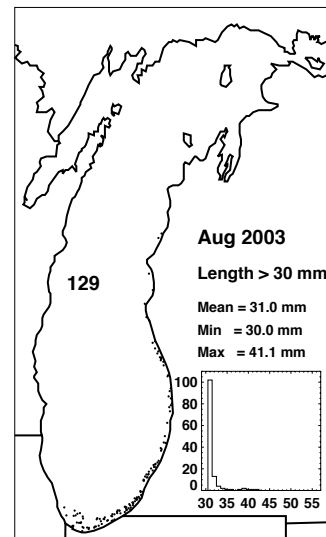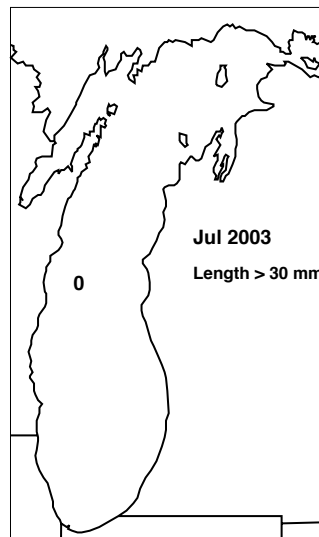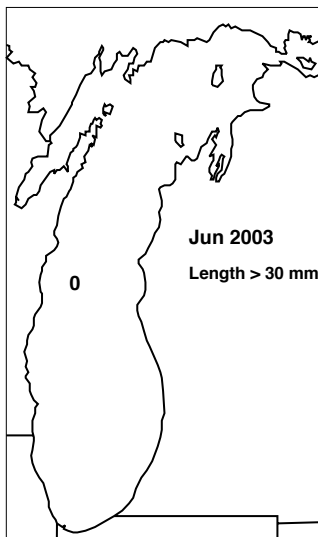
Jun 2001

0

Length > 30 mm

Jul 2001

31

Length > 30 mm

Mean = 30.3 mm
Min = 30.0 mm
Max = 30.6 mm

Aug 2001

245

Length > 30 mm

Mean = 44.9 mm
Min = 31.6 mm
Max = 48.5 mm

Jun 2002

0

Length > 30 mm

Jul 2002

193

Length > 30 mm

Mean = 32.5 mm
Min = 30.2 mm
Max = 35.5 mm

Aug 2002

246

Length > 30 mm

Mean = 48.3 mm
Min = 33.4 mm
Max = 53.9 mm

Jun 2003

0

Length > 30 mm

Jul 2003

0

Length > 30 mm

Aug 2003

245

Length > 30 mm

Mean = 41.4 mm
Min = 30.6 mm
Max = 45.2 mm
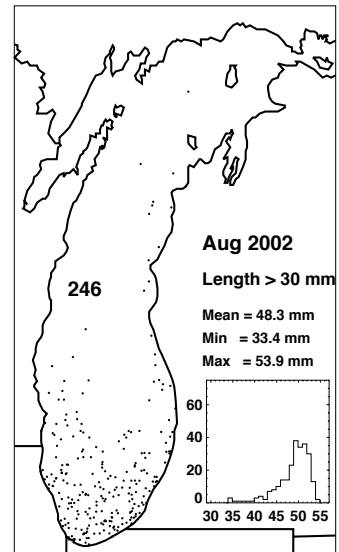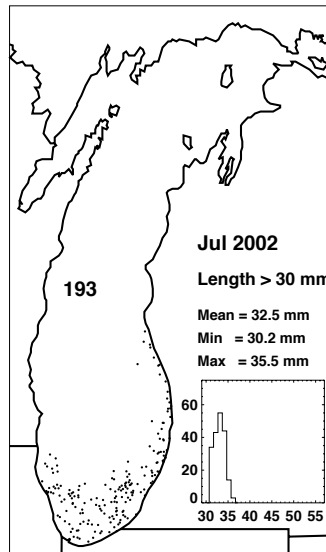
FIG. 6. *Larval settlement in 1998–2003. Total number of larvae settled is also shown. The histogram shows distribution of larvae with length.*
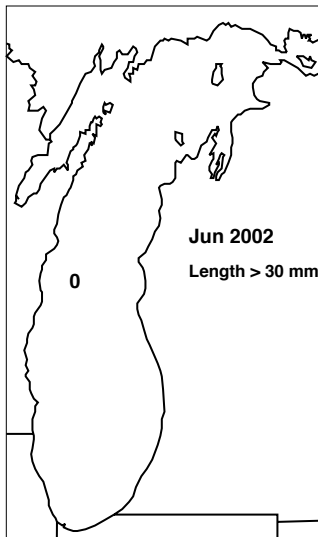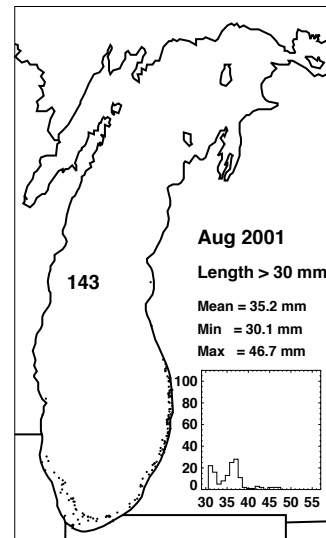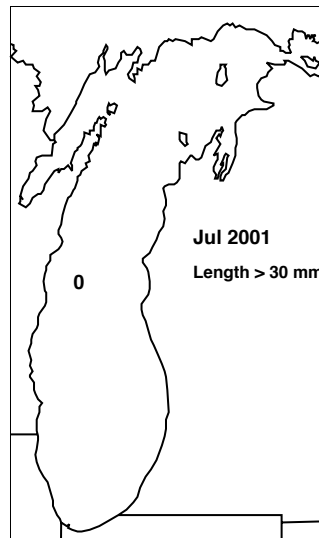
Jun 2001

Length > 30 mm

0

Jul 2001

Length > 30 mm

0

Aug 2001

Length > 30 mm

143

Mean = 35.2 mm
Min = 30.1 mm
Max = 46.7 mm

Jun 2002

Length > 30 mm

0

Jul 2002

Length > 30 mm

94

Mean = 31.1 mm
Min = 30.0 mm
Max = 34.1 mm

Aug 2002

Length > 30 mm

208

Mean = 34.6 mm
Min = 30.0 mm
Max = 49.1 mm

Jun 2003

Length > 30 mm

0

Jul 2003

Length > 30 mm

0

Aug 2003

Length > 30 mm

129

Mean = 31.0 mm
Min = 30.0 mm
Max = 41.1 mm
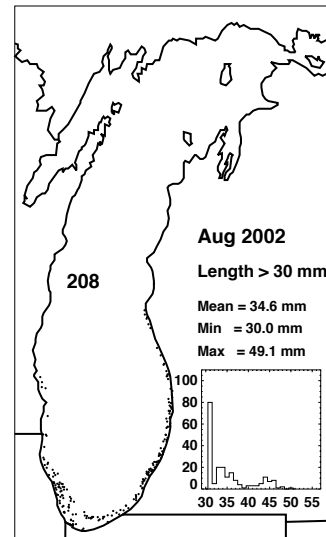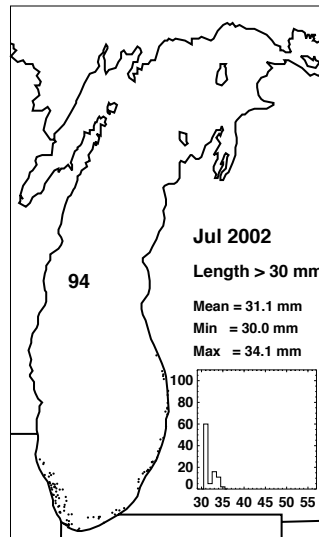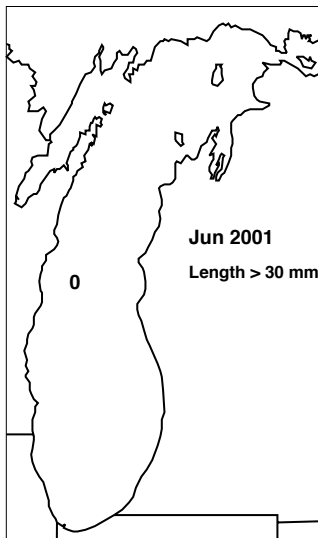
FIG. 7. Number of settled larvae in August 1998–2003 by sector (defined in Fig. 1). Numbers above sector names indicate average days to settlement.
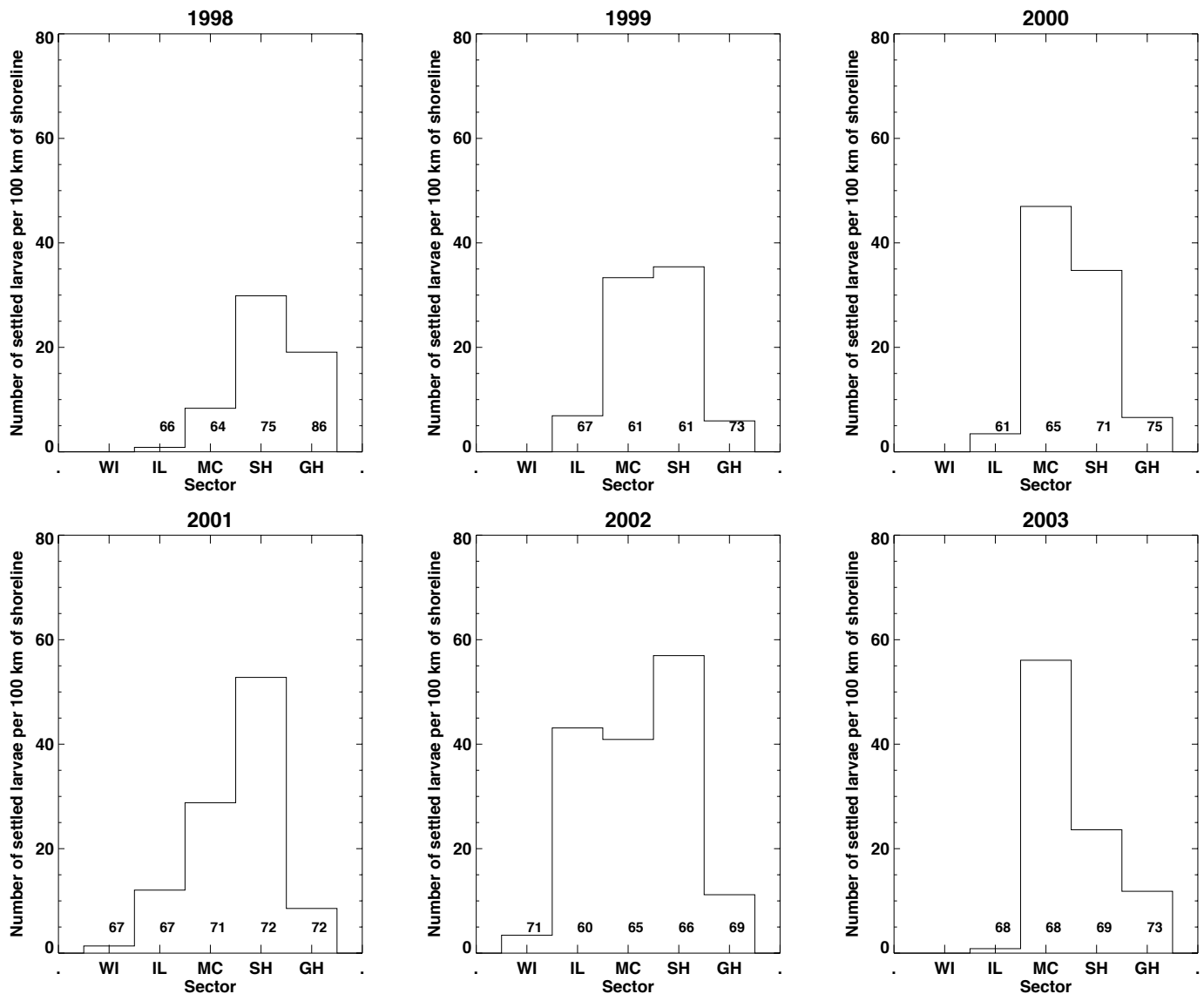
During the years of the model exercise (1998–2003), age-0 yellow perch abundance was generally low, but the 1998 and 2002 year classes stand out. Unlike observations at the Illinois site where both 1998 and 2002 peaks were pronounced (with 2002 peak being three times larger), observations at Michigan sites showed just a single peak (although in different years and with the magnitude of the northern site 2002 peak being six times smaller than the southern site peak in 1998).

The model matched observations best at the Illinois site where the correlation coefficient was 0.89 in the base model run (although based on only six data points or five data points for Grand Haven). The model reproduced the 2002 peak but missed the 1998 peak. The correlation was negative (–0.31) at South Haven, where the model reproduced only a small 2002 peak and missed a strong 1998 peak, and slightly positive (0.11) at Grand Haven, where the model exhibited a small peak in 1998, contrary to observations. The comparison improved dramatically (especially at Michigan sites) when 1998 data were removed from consideration (1998 was an unusual year for the lower food web in Lake Michigan as will be shown below).

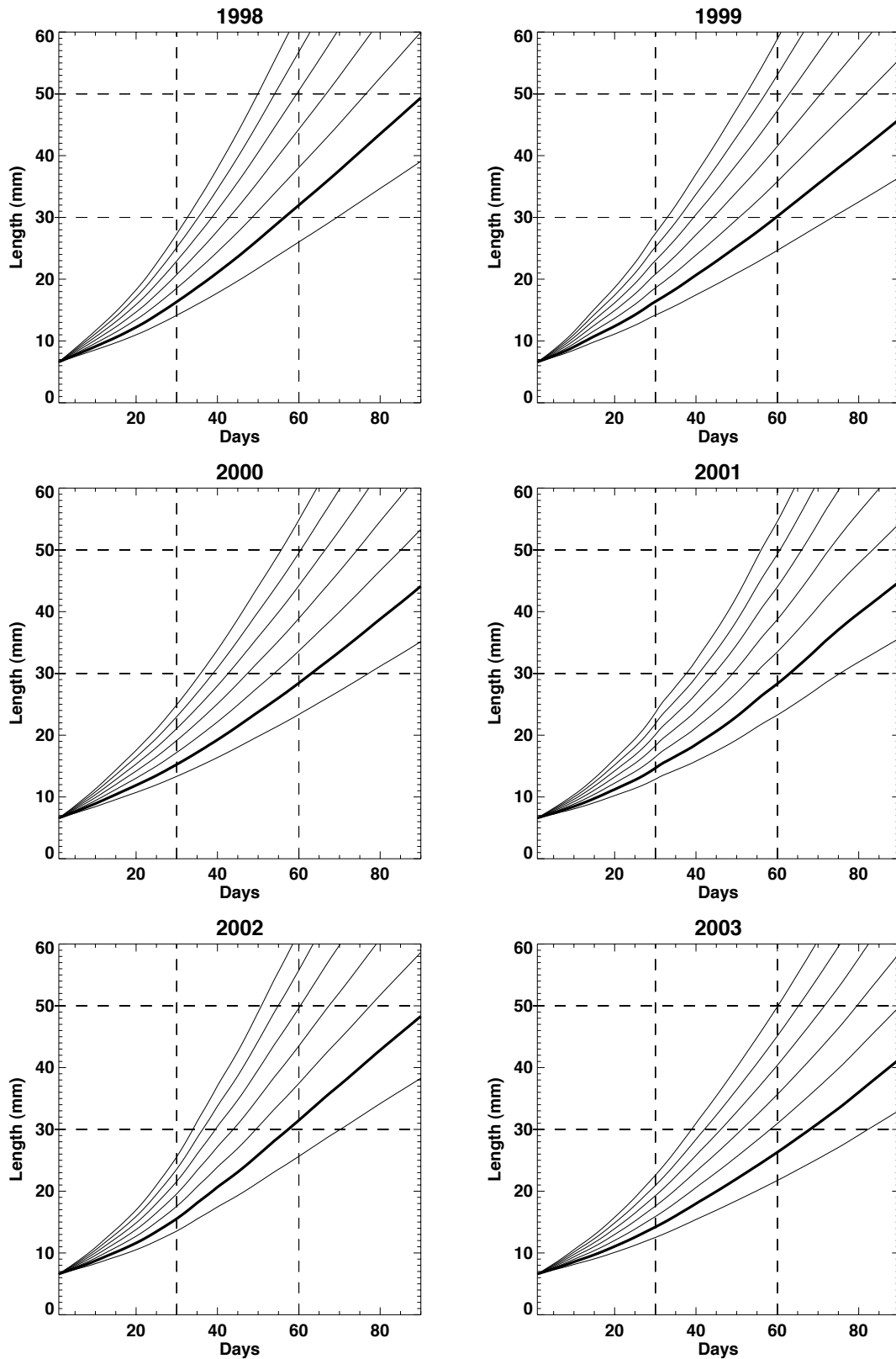For experiments with higher consumption rate (p

FIG. 8. *Modeled average larval yellow perch growth for different foraging scenarios. Thick curve represents base model run, p = 0.5. The curve to the right represents model run with p = 0.4, curves to the left represent model runs with increasing p = 0.6–1.0 (right to left), 0.1 increment.*

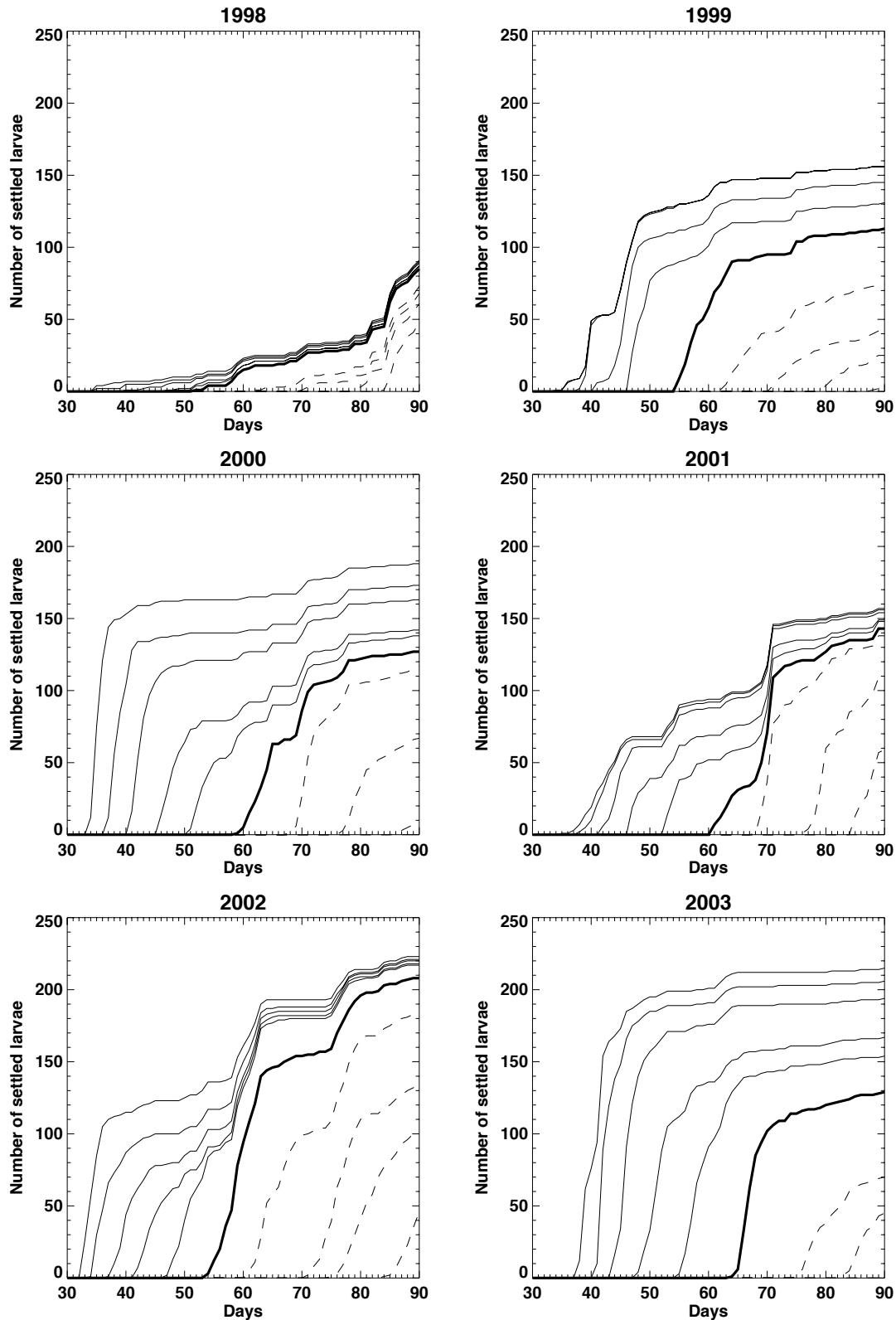**FIG. 9.** *Modeled larval settlement variations due to variations in settlement length (dashed curves) and foraging (solid curves). Thick solid curve represents base model run, p = 0.5, settlement at 30 mm. Dashed curves represent settlement length increase (left to right) from 35 to 50 mm (5 mm increments). Solid curves represent "p" increase (right to left) from 0.6 to 1.0 (0.1 increments).*
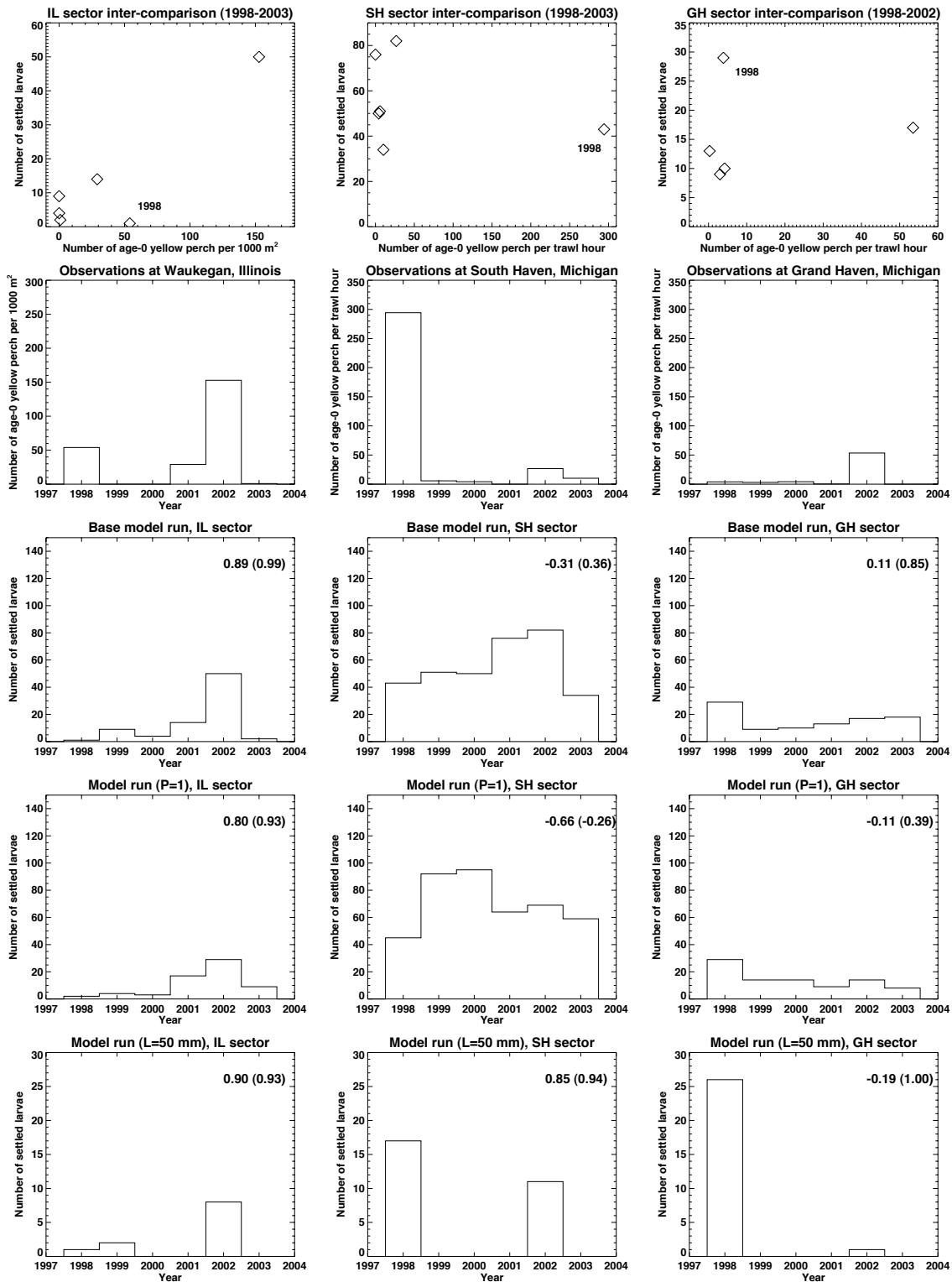
FIG. 10. *Model-data comparison for 1998–2003 for IL, SH, and GH sectors. Observed data are from summer and fall bottom trawls off Waukegan, Illinois, and from late summer bottom trawls off South Haven, Michigan and Grand Haven, Michigan (note that Illinois and Michigan units are different). Correlation coefficient (number of settled yellow perch versus survey catch-per-unit effort) is shown in the upper right corner of each of the nine bottom panels (without 1998 data shown in parenthesis). Comparison for GH sector is done without 2003 data due to a lack of observations.*

= 1), number of settled larvae increased in some sectors (SH) and overall (consistent with results shown in Fig. 9) but decreased in others (IL and GH). Decreases at IL and GH happened because larvae grew faster and settled in other sectors (primarily MC and SH) due to variable circulation patterns. In both IL and GH sectors, abundance peaks in 2002 and 1998, respectively were retained with increased consumption rates, while the 2002 peak in SH sector shifted to 1999–2000. Correlation of model predictions with observed abundances deteriorated for all sectors when *p*-value was changed from 0.5 to 1.0. As in the base model run, removal of 1998 data improved model-data correlation.

In the case of increased settlement size (50 mm), the respective 2002 and 1998 peaks were retained in IL and GH sectors. The 2002 peak in IL sector was five times smaller than in the base model run case while the 1998 peak decreased only slightly in the GH sector, and settlement numbers dropped to zero in most other years. The SH results changed most dramatically with settlement numbers dropping to zero in most years except 1998 and 2002, and these two new distinct peaks matched observations quite well. Correlation coefficients at both IL and SH sectors increased to 0.90 and 0.85, respectively, but deteriorated at GH sector (–0.19). Correlation with observations improved again when 1998 data were removed.

Based on comparison with a limited number of observations, we conclude that the base model run and especially the simulation with extended pelagic stage matched observations best. Still, missing strong IL and SH sector peaks in 1998 in the base model run results need to be explained. We believe that one reason the model failed to predict 1998 peaks was the exclusion of larval mortality from the bioenergetics model component. In 1998, productivity of lower trophic levels was stimulated by strong winds and a large resuspension event in southern Lake Michigan (Lesht *et al.* 2002), that occurred a few days prior to larval yellow perch emergence in IL. Lesht *et al.* (2002) estimated that this single event increased annual pelagic primary production by 20%. We demonstrated (Fig. 9) that increased consumption had little effect on settlement in 1998, but the related decrease in mortality may have been important (Houde 1987), and could have produced missing peaks in the base model run in 1998. In particular, the 1998 settlement numbers should have been reduced less by mortality than settlement numbers in other years when mortality was higher because less food was available. Other potential reasons for model/observation discrepancies are inaccuracy in modeled advection fields or lack of swimming ability causing errors in larval transport or contribution from sources of larvae other than Illinois, not included in the model. All these factors, as well as potential undersampling problem at Michigan sites (which only sampled monthly versus weekly sampling at Illinois) can also be responsible for mismatch of 1998 and 2002 modeled and observed peaks in GH sector.

DISCUSSION

This is the first 3D physical-biological model of larval fish developed for the Great Lakes. The model shows strong interannual variability in larval transport during 6 years of study with implications for larval yellow perch growth and settlement. The tendency for warmer years to exhibit anticyclonic currents versus colder years to exhibit cyclonic currents confounds the growth model in that, if warmer years correlate with improved recruitment, the mechanism may be currents rather than temperature. Currently, we have not included mortality and zooplankton fields (larval fish food) in our model. Future efforts will focus on these areas. Yet another issue to resolve is the assumption that fish larvae are passive particles. Swimming ability of fish larvae increases with size (Houde 1969, Miller *et al.* 1988), and swimming competence along with other behavioral patterns can influence their horizontal and vertical distributions, but are not captured in our model. For example, observed growth rates may be greater than model results if yellow perch larvae will increase their ability to locate zooplankton patches as their swimming ability increases. Despite these apparent shortcomings, our model results are consistent with many recent observations in Lake Michigan. In particular, model results indicate that the hydrodynamic dispersal of young yellow perch provides a mechanism for the genetic homogeneity of the Lake Michigan yellow perch population. Miller (2003) reported that collections from southern basin collection sites in Michigan, Wisconsin, and Indiana were homogenous and not much different from those from Lake Michigan's northern basin.

If we assume that self-recruitment is important for maintenance of the southern basin yellow perch population, it appears that the hydrodynamic conditions may produce a "source and sink" recruitment dynamic. The rocky habitat, preferred for spawning (Dorr 1982, Robillard and Marsden 2001) and pre-

sumably for feeding (Wells 1977, 1980; Janssen and Luebke 2004; Janssen *et al.* 2005) is primarily on the western side of Lake Michigan, and is perhaps most extensive in Illinois (Powers and Robertson 1968, Fucciolo 1993, Janssen *et al.* 2005). The present modeling effort suggests that larvae originating from this preferred habitat would be mostly transported to the sandier and generally unconsolidated substrate along the eastern side of Lake Michigan. Much of the habitat along eastern Lake Michigan is now depauperate of potential forage for newly settled juvenile yellow perch (Nalepa *et al.* 1998), which may impact survival in later life stages.

The model presented here assumes that "settlement" by juveniles occurs as a consequence of passive transport of individuals to suitably shallow water, in this case water less than 20 m deep. This assumption is almost certainly oversimplified and may give inaccurate predictions of settlement/recruitment. Further research on settlement dynamics would be useful to better understand yellow perch recruitment. We highlight several issues that should be resolved.

1. The extent to which juvenile yellow perch large enough to feed on benthos can orient towards shore and become demersal is an important factor affecting the length of time they may remain pelagic. As young yellow perch grow and become stronger swimmers (Houde 1969), they will be increasingly capable of directed swimming rather than passive drift. Our model shows that directed swimming is not necessary for a high percentage of juveniles to reach shallow water. Some of the results of Dettmers *et al.* (2005) also indicate that passive movement can bring fish closer to shore; free-swimming sac-fry tended to be closer to shore during downwelling events compared to upwelling events.

Appropriate directed swimming would increase the fraction of juveniles that successfully become demersal, but directed swimming requires some cue for orientation. Terrestrial features create an asymmetry in the polarized light distribution viewed through Snell's window which is a sufficient cue for *Daphnia* orientation (Schwind 1999). Whether yellow perch can detect light polarization appears untested, but the ability is found in diverse fishes (Hawryshyn 1992). Offshore, such cues are not available. A signal that appears useful for at least some marine coastal fishes is sound from reefs (Simpson *et al.* 2004, 2005). Additionally, Gerlach *et al.* (2007) have demonstrated use of odor for spa-

tial orientation by coral reef fish larvae. It would be interesting if yellow perch can use such cues, because they have scarcely diverged genetically from inland populations (Miller 2003) where dispersal distance from the shore is much less and have had only ca 10,000 years to evolve such an orientation method.

2. The relative costs and benefits of being pelagic versus benthic are likely unique for Lake Michigan. For Lake Erie yellow perch, Wu and Culver (1992) argued that yellow perch became demersal as the spring *Daphnia* bloom crashed, perhaps forcing the juvenile fish to seek alternative prey. The zooplankton phenology for Lake Michigan is very different in that there is no spring *Daphnia* bloom, and the peak for this prey is in August or September (Torke 1975, Lehman and Carceres 1993), when yellow perch are transitioning to the demersal stage. Thus the energetic benefits of becoming benthic in Lake Michigan may not be as great. Wu and Culver's (1992) experiments suggested that the juvenile yellow perch required several days to make a transition from benthivory to planktivory suggesting the switch may be in response to a food crisis. Such a crisis may not occur in Lake Michigan. Janssen and Luebke's (2004) diet analysis of juvenile yellow perch in shallow water included some individuals that were feeding on zooplankton, and others that were feeding on benthos. The zooplankton feeders may not yet have made the transition to feeding on benthic prey. If an upwelling carried their prey offshore, it is not clear whether they would move with the warm water mass, retaining their pelagic habit, or stay on the bottom as hypolimnetic water moves into shallow water.

3. The relative importance for supply of yellow perch larvae by different sections of Lake Michigan is unknown. The model presented here focused only on deposition of eggs in Illinois; in reality egg deposition occurs throughout the coastal areas (Goodyear *et al.* 1982). It is likely that the spatial distribution of eggs is not uniform, but rather concentrated in rocky spawning habitat (Janssen *et al.* 2005) or coastal wetland areas (Chubb and Liston 1986, Jude and Pappas 1992). Our focus on Illinois was based on two observations: (1) there is an abundance of the rocky habitat preferred for egg deposition and (2) a single cross-lake transect collecting larval yellow perch produced no larvae on the Michigan side (Dettmers *et al.* 2005). Nonetheless, larval yellow perch production along the Michigan coast has been well-documented in the past (e.g., Perrone *et al.* 1983) and by recent (unpublished)

sampling. A more ambitious sampling effort would help resolve where larvae are produced in the greatest abundance. Such a sampling effort would be most effective when informed by a hydrodynamics model. For example, Dettmers *et al.* (2005) found that upwelling and downwelling events affected the relative offshore/nearshore abundance of larval yellow perch on the scale of a few km. Given variable hydrodynamic patterns at this scale, there are certain to be impacts on larval yellow perch distribution offshore. Perhaps the most effective initial approach would be to hindcast where larval fishes likely originated based on hydrodynamic modeling, and increase sampling efforts in these areas.

4. The relative value of offshore versus nearshore water for feeding is not well known. Advection by lake currents may have a positive influence on feeding by yellow perch larvae by transporting them away from areas of low zooplankton density to more favorable feeding environments. Yellow perch larvae emerge from eggs attached to rocky habitats that are covered with zebra mussels which have a profound negative impact on phytoplankton and zooplankton (Dettmers *et al.* 2003). Although it may take a while for the young fish to encounter more abundant prey, microzooplankton densities are likely higher away from coastal areas infested by zebra mussels.

Our modeling results suggest that recruitment to the benthic stage will vary across spatial and temporal scales. Assessing whether this is true will require modifications in sampling strategies for demersal yellow perch. At present, sampling varies by state due to differences in available bottom type. Michigan and Indiana DNRs conduct bottom trawl surveys because of predominantly unconsolidated bottom types in their waters. Until recently, Wisconsin sampled by beach seines at sandy beaches; in the past few years Wisconsin has added sampling by micro-mesh gill nets used by Janssen and Luebke (2004). Illinois sampling has been primarily by beach seines and bottom trawling where the bottom is not rocky north of Waukegan, IL. To determine whether the eastern side of Lake Michigan tends to get greater numbers of recruits, the same type of sampling gear will have to be used at all stations. Although rocky habitat is scarce along the eastern coast, it will also need to be sampled to determine whether the preference for rocky habitat for adults (Wells 1977) begins in the juvenile yellow perch.

Our modeling effort represents a first step in integrating lake physics for understanding fish recruitment in the Great Lakes. Moreover, the modeling exercises presented here have shed light on how lake physics may modify and impact larval fish growth and survival in Lake Michigan. In addition, it has also exposed new questions in understanding the behavior (as the larvae become less passive "particles") and ecology (size at which fish go demersal, mortality, feeding relative to water movements, and prey availability influencing growth and settlement) of larval yellow perch, which may differ from inland lakes.

Modeling and field work are both improved when they inform each other. A combined modeling-sampling effort that refines the model while improving the efficiency of sampling would ultimately change the present model from a heuristic tool to an adaptive tool that improves prediction and assessment. An example of this is the recruitment model for Baltic herring produced by Axenrot and Hansson (2003). This statistical model combined information about climate with assessments of larvae and spawner abundance to make accurate predictions of herring recruitment. It is likely that an integration of hydrodynamic modeling, updated in near real time by targeted sampling, could produce a model that predicts yellow perch recruitment and its spatial variation.

ACKNOWLEDGMENTS

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