

REPORT

## A developmental bottleneck in dispersing larvae: implications for spatial population dynamics

Daniel W. Schneider<sup>1\*</sup>, James A. Stoeckel<sup>2</sup>, Chris R. Rehmann<sup>3</sup>, K. Douglas Blodgett<sup>4</sup>, Richard E. Sparks<sup>5</sup> and Dianna K. Padilla<sup>6</sup>

<sup>1</sup>Department of Urban and Regional Planning, University of Illinois at Urbana-Champaign and Center for Aquatic Ecology, Illinois Natural History Survey, Champaign, IL 61820, USA

<sup>2</sup>Department of Zoology, Miami University, Oxford, OH 45056, USA

<sup>3</sup>Department of Civil and Environmental Engineering, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA

<sup>4</sup>The Nature Conservancy, Lewistown, IL 61543, USA

<sup>5</sup>Environmental Council, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA

<sup>6</sup>Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, NY 11794, USA

\*Correspondence:

Tel.: +1 217 244 7681;

fax: +1 217 244 1717;

E-mail: ddws@uiuc.edu

### Abstract

We found evidence for a critical population bottleneck at a developmental-stage transition in larvae of the zebra mussel *Dreissena polymorpha* Pallas from field estimates of mortality. Identification of this critical period in the field was made possible by closely tracking cohorts of larvae over 5 days of development as they dispersed 128 km in a river system. The presence of a survival bottleneck during development was confirmed in laboratory studies of zebra mussel larvae. Development-specific mortality has important implications for spatial population dynamics of the zebra mussel in particular, and all species with indirect development in general. Marine reserves that do not take development-specific mortality into account may dramatically underestimate reserve size needed to protect rare and/or exploited marine populations. Conversely, for the zebra mussel, the lower contribution of dispersing individuals to population growth downstream of reserves can lead to more feasible control through the blocking of dispersal.

### Keywords

*Dreissena polymorpha*, larvae, marine reserves, metapopulations, mortality.

Ecology Letters (2003) 6: 352–360

### INTRODUCTION

Many aquatic species have indirect development with a significant portion of the life cycle spent as larvae. Because these larvae are a dispersal stage, the dynamics of populations in space as well as time can depend on the number of larvae surviving to settlement and their spatial distribution (Roughgarden *et al.* 1985, 1988). While the importance of larval supply to adult population dynamics has been debated (Caley *et al.* 1996; Shima 1999), recent studies have shown a correlation between the number of recruits and number of settlers in a wide variety of systems (Hunt & Scheibling

1997), suggesting that processes affecting the abundance of larvae can have a significant impact on adult population dynamics. Despite the importance of the larval stage to population dynamics, little is known about processes affecting the abundance of larvae. Because of the difficulty of tracking and identifying larvae in the field (May 1974; Levin 1990; Andre *et al.* 1999), empirical studies have been few. Most studies of mortality compare larval production and settlement but have no information on the intervening period. As a result, research, particularly on aquatic invertebrates, has often assumed constant mortality rates during the larval period (Rumrill 1990; Morgan 1995; Cowen *et al.* 2000).

A number of investigators have hypothesized developmental transitions as periods of high mortality in marine organisms (Gosselin & Qian 1996; Kristiansen *et al.* 1997). While fisheries biologists have explored the effect of these critical periods on annual variability in year class strength (May 1974; Leggett & Deblois 1994), stage-structured mortality may also have important implications in spatially structured populations, such as those contained in marine reserves. The establishment of marine reserves seeks to protect local populations by maintaining adequate populations in source areas that can supply recruits (Halpern & Warner 2002). The successful design of marine reserves depends on identifying source areas and likely settlement locations for recruits produced there. Because the abundance and spatial distribution of recruits depends on the interactions among mortality, developmental time, and patterns of water movement (Eckman 1996; Allison *et al.* 1998), an understanding of larval mortality is critical. However, the impact of developmental-specific mortality on spatial population dynamics has not been explored.

There are numerous obstacles to identification of critical periods and understanding the dynamics of marine larvae in the field (May 1974; Leggett & Deblois 1994). To investigate patterns of growth and mortality, larvae should ideally be tracked in the water column by following the water mass in which larvae are entrained and resampling the same cohort over time frequently enough to capture important variation in mortality and growth during development (Fortier & Leggett 1987). This tracking is difficult in the marine environment because of complex circulation patterns and hydrodynamics. In addition, the lack of taxonomic expertise makes the identification of invertebrate larvae difficult, even impossible for a number of groups (Hare *et al.* 2000). Furthermore, larval concentration within a water mass would be expected to decrease through time through two processes: dispersion and true losses because of mortality and settlement. Even in the few instances in which planktonic stages can be tracked, identified and enumerated (Wieland *et al.* 2000), calculated mortality rates are often confounded by unevaluated declines because of mixing processes alone. Recent successes in using environmental or artificial markers for tracking larvae (Jones *et al.* 1999; Swearer *et al.* 1999; Thorrold *et al.* 2001) have helped reveal spatial patterns of dispersal, but still cannot answer questions concerning dynamics during the intervening larval period.

The zebra mussel in riverine habitats presents a unique opportunity to study larval dynamics (Stoeckel *et al.* 1997). Because the zebra mussel is a species of great environmental and economic importance, an understanding of the factors affecting population dynamics is of great interest (Karateyev *et al.* 1997; O'Neill 1997). Because the zebra mussel is the only riverine mollusc that produces a

planktonic larva,<sup>1</sup> larvae cannot be confused with other species, and the population can be enumerated. The well-understood hydrodynamics of rivers allows an estimate of effects of dispersion on abundance. Thus, cohorts of larvae can be tracked through time by following parcels of water as they travel downstream, and independent effects of mixing and mortality can be evaluated. Furthermore, because the biology of the zebra mussel is similar to that of marine bivalves, an understanding of zebra mussel larval biology may be directly applicable to the study of marine mussels, oysters and clams, as well as other species with similar life histories.

In this study, we measure mortality rates of zebra mussel larvae by tracking and repeatedly sampling a cohort of larvae as it disperses downstream over a substantial portion of larval development. We then confirm with laboratory experiments the pattern of stage-dependent mortality found in the field. We apply these results to a metapopulation model of zebra mussels in the Illinois River to explore the effects of stage-dependent mortality on spatial population dynamics of the zebra mussel, and explore the implications of these results for the spatial population dynamics within marine reserves in general.

## METHODS

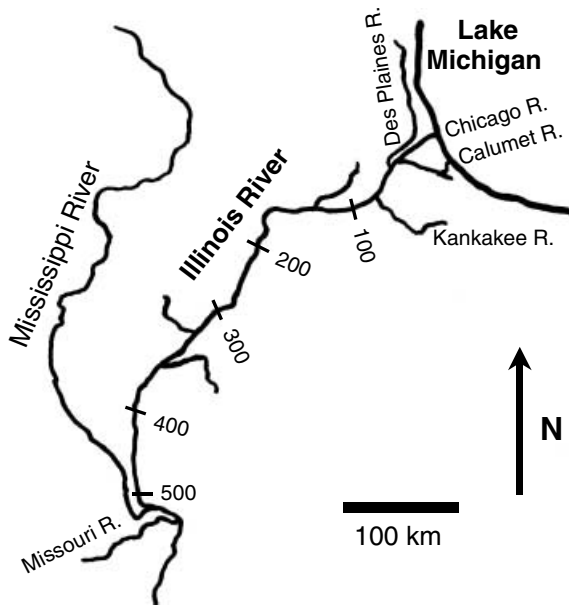
### Study site

We worked in the connected waters of Lake Michigan and the Illinois River System (Fig. 1). Water flows out of Lake Michigan at two points into the Chicago and Calumet Rivers. Canals constructed between 1900 and 1930 carry water into the Des Plaines River, 58 km downstream of the Lake. The Des Plaines and Kankakee Rivers join to form the Illinois River 85 km downstream of Lake Michigan. We sampled in the Illinois River, beginning 137 km downstream of the Lake.

### Veliger tracking and sampling

Zebra mussel developmental stages were determined by examining larvae under a compound microscope for the presence and shape of the larval shell. Zebra mussel larvae first develop from an egg to a trochophore-stage larva. At the end of the trochophore stage, the larva develops the velum, a swimming and feeding structure, and is known as a veliger. At the end of the trochophore stage, at approximately 70 µm, the larva also begins secreting the

<sup>1</sup>Larvae in this study were all *Dreissena polymorpha*; there have been no quagga mussels, *D. bugensis*, reported from the Illinois River. Of approximately 10 000 adult mussels collected in the Illinois River in our research we have never found a quagga mussel.



**Figure 1** Map of the study site. Water flows out of Lake Michigan into the Chicago and Calumet Rivers. Numbers along river indicate river kilometres downstream of Lake Michigan.

larval shell, or Prodissoconch I, at which time it is known as a D-stage larva. The feeding veliger continues development and begins the secretion of the Prodissoconch II. The Prodissoconch II, or umbonal larva, no longer has a straight hinge margin, but rather shows a distinct umbo (Morse & Zardas 1997). The trochophore stage typically lasts 1–2 days. The duration of the planktotrophic stage (D-stage and umbonal stage) depends on temperature, with values in the literature ranging from a minimum of 6 days to up to 5 weeks (Sprung 1992).

Working from a houseboat, we sampled downstream in the Illinois River until we encountered a sharp increase in the concentration of small, D-stage larvae ( $>50 \text{ L}^{-1}$ ). We then followed this parcel of water downriver by tracking a drifter that was placed in the current. The drifter had drogues at 1- and 2-m depth and travelled passively with the parcel of water. Sampling position was later compared (Meade & Stevens 1990) to hydraulic models of this river reach (Zuehls 1987) to assess our ability to sample the same patch of water. Thirty litres of depth-integrated river water (two replicates) were sampled by moving a hose connected to a diaphragm pump vertically through the entire water column in the centre of the channel, and filtering plankton through a 55- $\mu\text{m}$  plankton net. Previous studies showed that veligers were well mixed laterally across the river and that a depth-integrated centre-channel sample represented the abundance across a cross-section of the river (Stoeckel *et al.* 1997). Veligers were rinsed from the plankton net and immediately preserved in buffered formalin. Larvae were

counted under cross-polarized light, allowing us to enumerate all larvae that had secreted a larval shell. The first 100 larvae in each of the two replicate samples were measured along the maximum linear dimension.

Cohorts were identified in the sample by resolving the polymodal size–frequency distribution into normal components using the algorithms of Bhattacharya (1967). A threshold separation index of 2, calculated as the ratio of the difference in mean size of the components to the average of their standard deviations, was used to identify cohorts.

### Calculating mortality

Because our sampling followed a cohort, the peak abundance,  $N_{\text{max}}$ , in a cohort can be expressed as  $N_{\text{max}}(t) = P(t)L(t)$ , where the function  $P(t)$  accounts for declines due to physical transport and the function  $L(t)$  accounts for losses due to mortality and settlement. The effect of longitudinal dispersion, or  $P(t)$ , was estimated from results of dye studies in this reach of the Illinois River (Zuehls 1987). The time response of an instantaneous spawn was estimated as a scalene triangle; at a position  $x$  in the river, the traveltime  $T_p$  of the peak concentration is  $x/V_p$ , where the velocity (in  $\text{m s}^{-1}$ ) is  $V_p = 9.28 \times 10^{-4} Q + 7.13 \times 10^{-2}$  and  $Q$  is discharge in  $\text{m}^3 \text{ s}^{-1}$ . The travel times of the leading edge and the trailing edge are  $0.84T_p$  and  $1.39T_p$ , respectively. The expected peak concentration,  $C_p$ , of larvae undergoing no mortality or settlement is

$$C_p = 4.05 \frac{M}{Q} T_p^{-1}$$

where  $M$  is number of larvae. These coefficients are specific to the reach of the Illinois River where we sampled. We treated the finite duration spawn as the sum of many instantaneous spawns and superimposed the responses to determine the concentration of zebra mussel veligers. Concentration was insensitive to spawn duration for spawns  $>2$  h, which our laboratory experiments showed was a reasonable minimum spawn duration for individual zebra mussels. Concentrations for each sampling point were calculated using the above method and fit with

$$P(t) = C_0 \frac{1 + be^{\alpha_1 t}}{1 + be^{\alpha_2 t}}$$

where  $C_0$  is the initial measured concentration,  $\alpha_1 = 0.962 \text{ day}^{-1}$ ,  $\alpha_2 = 1.033 \text{ day}^{-1}$ , and  $b = 0.194$ . For large time, this equation predicts the exponential decay  $P = C_0 \exp[(\alpha_1 - \alpha_2)t] = \exp(-0.071t)$ .

Describing mortality with a first-order model with a time varying loss rate  $m(t)$ , one can write the function  $L(t)$  as

$$L(t) = \exp\left(-\int_0^t m(\tau) d\tau\right)$$

The mortality rate was then computed with

$$m(t) = -\frac{d}{dt} \{\ln[L(t)]\} = -\frac{d}{dt} \left\{ \ln \left[ \frac{N_{\max}(t)}{P(t)} \right] \right\}$$

by fitting a cubic smoothing spline to the measurements and calculating its derivative. The size-dependent variable  $m$  is analogous to the constant instantaneous rate of population growth from the equation  $N_t = N_0 e^{mt}$ , where  $N_t$  is the population size at time  $t$  and  $N_0$  the initial population size. Parameterizing  $m$  in this way allows for direct comparison to other mortality estimates for marine invertebrate larvae (Rumrill 1990; Morgan 1995).

Because no larvae large enough to settle were found in the samples, we assume that biological losses were principally because of mortality rather than settlement. Mean settlement size  $\pm 1$  SD in the Illinois River ( $235 \pm 21 \mu\text{m}$ ) was determined by bleaching shells of newly settled mussels and measuring the length of the Prodissoconch I region under a dissecting microscope (Martel *et al.* 1995).

### Laboratory culture

Following a modification of established procedures (Wright *et al.* 1996), cultures were maintained in a dedicated, embryologically clean room, and kept at 25 °C. Spawning stock was from the Illinois River. Mussels were spawned by exposure to a 1 mM solution of serotonin. Larvae were cultured in artificial freshwater [990 mL deionized water + 10 mL artificial sea water + 200 mg CaCl + 100mg Na(CO<sub>3</sub>)<sub>2</sub>] and maintained in 1-L beakers with loose fitting lids at an initial density of 200 L<sup>-1</sup>. Larvae were fed a diet of *Isochrysis galbana* (T-ISO) ( $3 \times 10^5$  cells mL<sup>-1</sup>) daily. The culture water was changed daily by gently filtering off 80% of the water through a 55- $\mu\text{m}$  filter, and individually pipetting larvae into new culture water and container. Antibiotics (0.25 mL L<sup>-1</sup> of penicillin/streptomycin/neomycin; Sigma #3664) were added to the culture on days 2, 7, and 11. The number of live larvae was counted daily, and 10 larvae from each of four replicate cultures were measured along the maximum linear dimension and their developmental stage (D-stage, umbral) was determined. We calculated mortality rates of the larvae in the laboratory in an identical manner to the field studies to allow a direct comparison.

### Population modelling

Larval transport and settlement were computed over several spawning seasons. In each season, the larval abundance  $L$  was computed with a one-dimensional, steady-state advection–dispersion–reaction model:

$$U \frac{dL}{dx} = K \frac{d^2L}{dx^2} - m(x)L$$

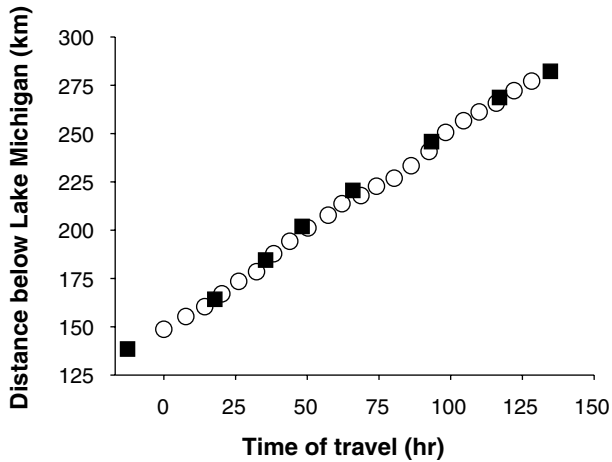
where the mean velocity over the spawning season  $U$  was taken from US Geological Survey measurements in the Illinois River and the dispersion coefficient  $K$  was estimated from dye studies (Zuehls 1987). For the stage-dependent mortality case, the mortality rate  $m$  was derived from our field measurements. For the constant mortality case, a constant exponential rate was calculated that gave the observed total mortality. Shell size and downstream distance  $x$  were related with the growth rate taken from our field measurements and mean velocity. Larvae were assumed to settle as adults when they reached 230  $\mu\text{m}$ . Adult survivorship was 50% in the first year, 80% in the next 2 years, and 0% afterwards. Adults along the river spawned at a rate of  $10^6$  larvae per female per season, producing larvae that entered the water column and settled downstream according to the larval transport equation above. Boundary conditions for the flux and size distribution of larvae leaving Lake Michigan were taken from unpublished data, and dispersion of larvae from the Mississippi River into the Illinois River was assumed to be zero. The transport equation was solved numerically with a standard finite-difference method. To examine the sensitivity of the model to variability in flow and growth rate, we ran 50 pairs of 30-year simulations. Average spawning season velocities were drawn randomly from a lognormal distribution computed from the previous 82 years of record for the Illinois River. Larval growth rate was drawn from a Gaussian distribution centred on 17  $\mu\text{m day}^{-1}$  with SD of 1.9  $\mu\text{m day}^{-1}$ .

### RESULTS

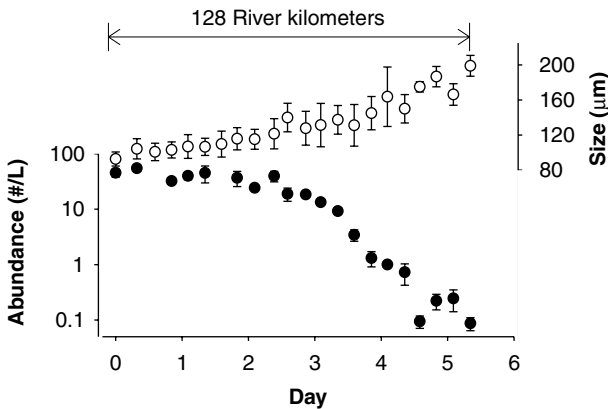
We were able to follow the water mass and its entrained cohort of larvae as it moved 128 km downstream. Comparison of the time required to travel a given distance during our sampling with existing hydrodynamic models of the same reach of river demonstrates that we were able to maintain our position within the water mass as it moved downstream (Fig. 2).

Repeated sampling of the water mass at 6-h intervals revealed fine scale patterns of larval size and abundance (Fig. 3). Larval density declined over time, initially at a relatively slow rate. By day 3, density declined more rapidly, and then by day 4, more slowly again. Larval growth increased with increasing size. Growth rate was best fit with an exponential model [size ( $\mu\text{m}$ ) =  $90.4 e^{0.13(\text{days})}$ ,  $r^2 = 0.92$ ,  $P < 0.0001$ ].

The well-described hydrodynamics of the Illinois River allowed us to separate biological and physical factors causing larval abundance to decline downstream. Apportioning the decreases to dispersion and mortality showed that dispersion accounted for a relatively small proportion of the decline in abundance over time. Approximating the decrease due to dispersion with an exponential function gives a rate



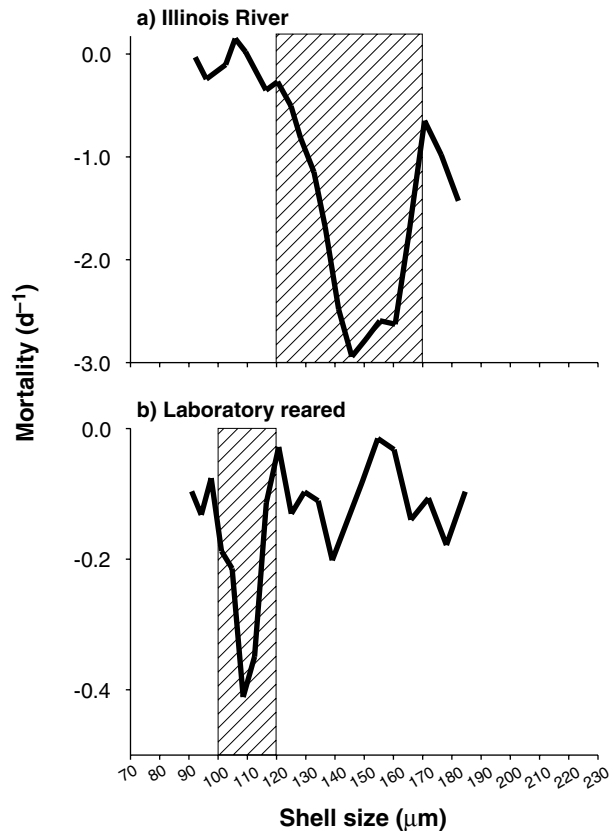
**Figure 2** Comparison between the veliger sampling locations (○) and locations predicted from US Geological Survey dye studies (■) in the study reach. Comparison of slopes suggests no difference between the zebra mussel study and USGS study ( $F = 1.05$ , d.f. = 1,  $P = 0.315$ ), indicating that larvae were sampled from the same patch of water as it moved downstream.



**Figure 3** Abundance (●) and mean size (○) of veligers sampled during study  $\pm$  1 SD. Note log scale of the abundance axis.

of  $-0.071 \text{ day}^{-1}$ . Over the sampling period of 5.3 days, dispersion, in the absence of mortality, would lead to a total decline in abundance of 30.8%. In contrast, over the same period, from early D-stage to a size competent to settle, overall mortality of the zebra mussel larval cohort (not including declines due to dispersion) was 99.8%.

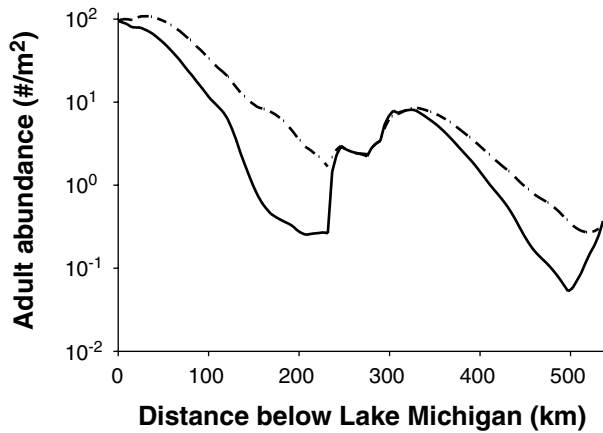
Mortality in the Illinois River was not constant, and we found a striking pattern of mortality with development. There was a marked increase in larval mortality at the transition between the D-stage and umbonal-stage of development (Fig. 4a). Mortality of smaller, D-stage larvae was low, averaging  $-0.093 \text{ day}^{-1}$  (equivalent to  $8.9\% \text{ day}^{-1}$ ). Averaged over the transition between D and umbonal stages, mortality increased to  $-1.69 \text{ day}^{-1}$  (equivalent to



**Figure 4** (a) Size-specific mortality rates  $m$  ( $\text{day}^{-1}$ ) of zebra mussel larvae in the Illinois River. More negative values of  $m$  indicate higher mortality. Hatched area shows the size at transition from D to umbonal stage, defined as the range between the smallest size class with  $\geq 5\%$  of larvae in umbonal stage to the largest size class with  $\geq 5\%$  larvae in D-stage. D-stage or straight-hinged larvae have deposited their first shell following the trochophore stage. In umbonal-stage larvae, the umbo, or rounded portion of the shell near the hinge, has begun to develop. (b) Size-specific mortality rates  $m$  ( $\text{day}^{-1}$ ) of zebra mussel larvae from the laboratory. Categories and shading are as for 'a'.

$81.5\% \text{ day}^{-1}$ ). Following the transition, mortality decreased to an average of  $-1.02 \text{ day}^{-1}$  (equivalent to  $63.9\% \text{ day}^{-1}$ ). At small sizes, declines in concentration due to dispersion were comparable to those due to mortality. For larger larvae, however, mortality produced losses much greater than the reduced concentration due to dispersion.

To narrow down the causes of the developmental bottleneck, we reared zebra mussel larvae in the laboratory. Under conditions of constant temperature and food availability, the laboratory experiments controlled for environmental conditions in the river that could have caused a spurious correlation between development and mortality, such as predation, shift in food availability, or changes in temperature or hydrodynamic environment. The laboratory experiments confirmed the pattern of increased mortality



**Figure 5** Comparison of adult abundance predicted with stage-specific mortality (solid line) and constant mortality (dashed line). The model was run using river velocities for 1971–2000 and a growth rate of  $17 \mu\text{m day}^{-1}$ .

at the developmental transition (Fig. 4b). While overall mortality in the laboratory experiments was lower than in the river (94% over 22 days), mortality peaked during the transition from the D to the umbonal stage. Mortality of smaller, D-stage larvae was low, averaging  $-0.101 \text{ day}^{-1}$  (equivalent to  $9.6\% \text{ day}^{-1}$ ). Once larvae grew to the size of transition between the D and umbonal stages, mortality increased to an average of  $-0.255 \text{ day}^{-1}$  (equivalent to  $22.5\% \text{ day}^{-1}$ ). Following the transition, mortality decreased to an average of  $-1.05 \text{ day}^{-1}$  (equivalent to  $9.9\% \text{ day}^{-1}$ ).

Population modelling showed that the spatial structure of the zebra mussel population in the Illinois River would differ under differing assumptions about the stage-dependence of mortality (Fig. 5). Using the last 30 years of flow data, assuming constant larval mortality for the zebra mussel overestimated adult abundance by a factor of as much as 17 downstream compared to the observed pattern of stage-dependent mortality, even though total mortality during the larval stage was identical in the two cases. Variation in flow or growth rate did not change the overall pattern. On average ( $\pm 1 \text{ SD}$ ), over the 50 runs of the model, assuming constant mortality overestimated downstream adult abundance by a factor of as much as  $14.3 \pm 5.2$ . The position of the peak overestimation factor between the two mortality schedules was  $202 \pm 56 \text{ km}$  downstream of Lake Michigan. In addition to 14-fold differences in the prediction of abundance at a given point, assuming a constant mortality would over-predict the total population of zebra mussels in the Illinois River by  $67 \pm 4\%$ .

## Discussion

By successfully tracking a cohort of zebra mussel larvae over time, we could measure parameters, such as larval growth

and mortality, which are difficult to measure in field populations. By sampling at a fine temporal scale and accounting for changes in density due to physical processes, we showed that mortality is not constant over development; rather, mortality peaked at the developmental transition from D-stage to umbonal stage. The bottleneck in survivorship appears intrinsic to the developmental programme. The developmental transition was uncoupled from age or size, occurring between  $120$  and  $170 \mu\text{m}$  in the field and between  $100$  and  $120 \mu\text{m}$  in the laboratory. Studies of other molluscs, while not addressing mortality, have shown that rearing conditions, such as temperature, salinity or food availability, can uncouple size, growth rate and development (Zimmerman & Pechenik 1991). The development at smaller size in the laboratory experiments may reflect the high-quality food source used in these experiments (Wacker *et al.* 2002). Yet, in the zebra mussel, the period of increased mortality in both the field and laboratory was specific to the D-stage–umbonal transition rather than age or size. Environmental conditions shift the size at which larvae undergo developmental transitions and produce shifts in the size of veligers undergoing the bottleneck in survivorship.

Sources of mortality to larvae may include physiological stress, inadequate food resources, predation, sinking or advection (Morgan 1995). The presence of the survivorship bottleneck in both the field and laboratory suggests that environmental factors unique to the field are not responsible. The shift in shell morphometry that marks the developmental transition corresponds with many changes in larval bivalve biology. The development of the digestive system in the pearl oyster *Pinctada* is associated with the transition from D to umbonal stage (Fujimura *et al.* 1995), and the transition also corresponds to a peak in metabolic activity in *Mytilus* (Sprung & Widdows 1986). These factors may lead to increased nutritional or energetic stress and higher mortality. Further, in high-fecundity organisms like the zebra mussel, genetic load may be high; as development progresses, increasing numbers of lethal genes may be expressed, as demonstrated for the oyster *Crassostrea gigas* (Launey & Hedgecock 2001).

Developmental stage-specific mortality, as we demonstrated for the zebra mussel, has important implications for the spatial population structure of species with a dispersing larval stage. Where metapopulations are structured with a single, large population supplying recruits to many other local populations (e.g. mainland–island metapopulation), the stage-dependent pattern of mortality can make a large difference in spatial population dynamics. In riverine systems, downstream populations of adult zebra mussels depend on settlement of larvae produced upstream. In the Illinois River, the ultimate upstream population is Lake Michigan (Stoeckel *et al.* 1997). This population structure is similar to marine systems in which populations in protected reserves produce recruits to

numerous local populations down-current (Botsford *et al.* 1998). The assumption of constant mortality rate during the larval phase can substantially overestimate the contribution of larvae from such a marine reserve.

Adult abundance in the Illinois River decreased much more rapidly downstream of Lake Michigan in the case of stage-dependent mortality. This decrease in abundance was due to the greater than average mortality suffered by larvae larger than the D–umbonal transition. Larvae of this size leaving the lake undergo greater than average mortality and thus produce smaller adult populations downstream than in the constant mortality case. Only the smallest and largest larvae have identical total mortality for both cases (Fig. 6). Where these larvae settle, then, abundance should be the same in both the constant and stage-dependent mortality cases, and abundance will converge at the point in the river where the smallest larvae leaving the lake eventually settle (Fig. 5). Plans to control the zebra mussel in the Illinois River by interrupting downstream dispersal of larvae from Lake Michigan (Stoeckel *et al.* 1997) appear more feasible when stage-specific mortality is taken into account, as a given reduction in larval flux from Lake Michigan will produce a 1–2 orders of magnitude greater reduction in adult density downstream than with constant mortality.

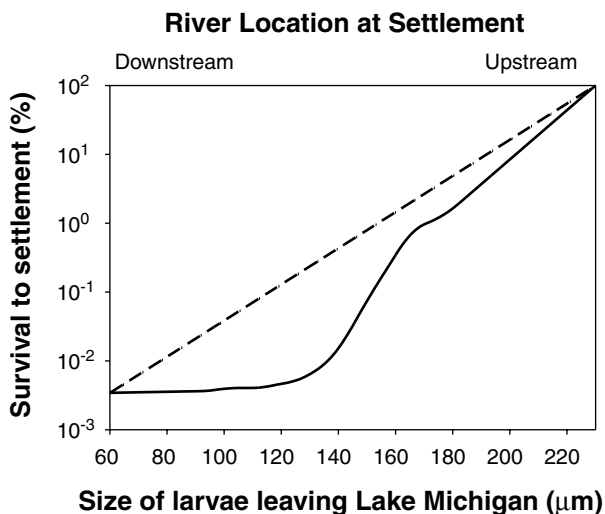
Conversely, marine reserves that do not account for stage-specific mortality during their design can potentially lead to local extinctions, as recruitment rate may be substantially lower than predicted. While total recruitment downstream of a reserve may vary substantially under the two assumptions about mortality schedule, recruitment at particular locations can differ to an even greater extent. Spatial population

structure depends on the specific pattern of stage-specific mortality, the size distribution of larvae leaving the reserve and dispersal distance. In the case of Lake Michigan, a broad size-spectrum of larvae disperses downstream. Peak mortality, occurring at an intermediate size, leads to a deficit in recruitment at the location where these moderate-sized individuals would settle. The spatial location of that recruitment deficit is determined by the interaction of larval growth rate and current velocity. For marine systems, where suitable habitat is often patchily distributed, such as coral reefs, estuaries or rocky headlands, the precise spatial location of habitat in relation to the reserve is an important parameter, given the potential for order of magnitude differences in recruitment to patches depending on the pattern of stage-dependent mortality. For the design of marine reserves, then, information on the developmental pattern of mortality must be considered along with other design parameters such as reserve fraction (Mangel 2000), reserve spacing (Botsford *et al.* 2001) and larval dispersal distance (Botsford *et al.* 1998). Management of multi-species marine resources is one of the challenges facing conservation biologists (Gulland & Garcia 1984). The design of marine reserves is no exception. Species differ in their life history, with consequent differences in larval production and dispersal. Furthermore, different species will have varying patterns of stage-specific mortality. Piecing together the different spatial patterns created by differences in larval supply presents a complicated problem for the optimal design of marine reserves.

Current theory on marine reserves has not considered the implications of developmental bottlenecks in the dispersal phase of target species for spatial population structure. Our results are based on one estimate of stage-dependent mortality in the zebra mussel. It will be important to investigate how stage-dependent mortality may vary annually to understand the implications for spatial population dynamics. Because of the tractability of river hydrodynamics and the low diversity of bivalve larvae in freshwater, the larval stage of the zebra mussel can be empirically studied in great detail in river ecosystems. The zebra mussel in river ecosystems thus represents an ideal system for examining the relationships among hydrodynamics, larval ecology, population dynamics and ecosystem management in general.

#### ACKNOWLEDGMENTS

Supported by the Illinois/Indiana, New York, and National Sea Grant College Program grants R/ANS-07-99, R/ANS-04-97, A/SE (ANS)-07-99, and R/CE-18, the Illinois River Biological Station of the Illinois Natural History Survey and the University of Illinois Campus Research Board. We thank J. Saenz for discussions on the modelling, A. Nealand and M. Lemke for their work in culturing larvae and L. Henne, K. Stevenson and T. Snider for assistance in the field.



**Figure 6** Survival of larvae of different sizes as they leave Lake Michigan under conditions of stage-specific mortality (solid line) and constant mortality (dashed line). Smaller larvae travel further downstream before settlement.

## REFERENCES

- Allison, G.W., Lubchenco, J. & Carr, M.H. (1998). Marine reserves are necessary but not sufficient for marine conservation. *Ecol. Appl.*, 8 (Suppl.), S79–S92.
- Andre, C., Lindegarth, M., Jonsson, P.R. & Sundberg, P. (1999). Species identification of bivalve larvae using random amplified polymorphic DNA (RAPD): differentiation between *Cerastoderma edule* and *C. lamarcki*. *J. Mar. Biol. Assoc. UK*, 79, 563–565.
- Bhattacharya, C.G. (1967). A simple method of resolution of a distribution into gaussian components. *Biometrics*, 23, 115–135.
- Botsford, L.W., Wing, S.R. & Largier, J.L. (1998). Population dynamics and management implications of larval dispersal. *S. Afr. J. Mar. Sci.*, 19, 131–142.
- Botsford, L.W., Hastings, A. & Gaines, S.D. (2001). Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecol. Lett.*, 4, 144–150.
- Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P. & Menge, B.A. (1996). Recruitment and the local dynamics of open marine populations. *Annu. Rev. Ecol. Syst.*, 27, 477–500.
- Cowen, R.K., Lwiza, K.M.M., Sponaugle, S., Paris, C.B. & Olson, D.B. (2000). Connectivity of marine populations: open or closed? *Science*, 287, 857–859.
- Eckman, J.E. (1996). Closing the larval loop: linking larval ecology to the population dynamics of marine benthic invertebrates. *J. Exp. Mar. Biol. Ecol.*, 200, 207–237.
- Fortier, L. & Leggett, W.C. (1987). A drift study of larval fish survival. *Mar. Ecol. Prog. Ser.*, 25, 245–257.
- Fujimura, T., Wada, K. & Iwaki, T. (1995). Development of digestive system of the pearl oyster larvae, *Pinctada fucata*. *Jap. J. Malac.*, 54, 203–223.
- Gosselin, L.A. & Qian, P.Y. (1996). Early post-settlement mortality of an intertidal barnacle: a critical period for survival. *Mar. Ecol. Prog. Ser.*, 135, 69–75.
- Gulland, J.A. & Garcia, S. (1984). Observed patterns in multi-species fisheries. In: *Exploitation of Marine Communities* (ed. May, R.M.). Springer-Verlag, Berlin, pp. 155–190.
- Halpern, B.S. & Warner, R.R. (2002). Marine reserves have rapid and lasting effects. *Ecol. Lett.*, 5, 361–366.
- Hare, M.P., Palumbi, S.R. & Butman, C.A. (2000). Single-step species identification of bivalve larvae using multiplex polymerase chain reaction. *Mar. Biol.*, 137, 953–961.
- Hunt, H.L. & Scheibling, R.E. (1997). Role of early post-settlement mortality in recruitment of benthic marine invertebrates. *Mar. Ecol. Prog. Ser.*, 155, 269–301.
- Jones, G.P., Millicich, M.J., Emslie, M.J. & Lunow, C. (1999). Self-recruitment in a coral reef fish population. *Nature*, 402, 802–804.
- Karatayev, A.Y., Burlakova, L.E. & Padilla, D.K. (1997). The effects of *Dreissena polymorpha* (Pallas) invasion on aquatic communities in eastern Europe. *J. Shellfish Res.*, 16, 187–203.
- Kristiansen, T.S., Jørstad, K.E., Otterå, H., Paulsen, O.I. & Svåsand, T. (1997). Estimates of larval survival of cod by releases of genetically marked yolk-sac larvae. *J. Fish Biol.*, 51 (Suppl. A), 264–283.
- Launey, S. & Hedgecock, D. (2001). High genetic load in the Pacific oyster *Crassostrea gigas*. *Genetics*, 159, 255–265.
- Leggett, W.C. & Deblois, E. (1994). Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? *Neth. J. Sea Res.*, 32, 119–134.
- Levin, L.A. (1990). A review of methods for labeling and tracking marine invertebrate larvae. *Ophelia*, 32, 115–144.
- Mangel, M. (2000). On the fraction of habitat allocated to marine reserves. *Ecol. Lett.*, 3, 15–22.
- Martel, A., Hynes, T.M. & Buckland-Nicks, J. (1995). Prodissoconch morphology, planktonic shell growth, and size at metamorphosis in *Dreissena polymorpha*. *Can. J. Zool.*, 73, 1835–1844.
- May, R.C. (1974). Larval mortality in marine fishes and the critical period concept. In: *The Early Life History of Fish* (ed. Blaxter, J.H.S.). Springer-Verlag, New York, pp. 3–19.
- Meade, R.H. & Stevens, H.H. (1990). Strategies and equipment for sampling suspended sediment and associated toxic chemicals in large rivers – with emphasis on the Mississippi River. *Sci. Total Environ.*, 97/98, 125–135.
- Morgan, S.G. (1995). Life and death in the plankton: larval mortality and adaptation. In: *Ecology of Marine Invertebrate Larvae* (ed. McEdward, L.). CRC Press, Boca Raton, FL, pp. 279–322.
- Morse, M.P. & Zardas, J.D. (1997). In: *Microscopic Anatomy of Invertebrates. Volume 6A: Mollusca II* (eds Harrison, F.W. & Kohn, A.J.). Wiley-Liss, New York, pp. 7–118.
- O'Neill, C.R. (1997). Economic impact of zebra mussels – results of the 1995 National Zebra Mussel Information Clearinghouse study. *Great Lakes Res. Rev.*, 3, 35–44.
- Roughgarden, J.D., Iwasa, Y. & Baxter, C. (1985). Demographic theory for an open marine population with space-limited recruitment. *Ecology*, 66, 54–67.
- Roughgarden, J., Gaines, S. & Possingham, H. (1988). Recruitment dynamics in complex life cycles. *Science*, 241, 1460–1466.
- Rumrill, S.S. (1990). Natural mortality of marine invertebrate larvae. *Ophelia*, 32, 163–198.
- Shima, J.S. (1999). Variability in relative importance of determinants of reef fish recruitment. *Ecol. Lett.*, 2, 304–310.
- Sprung, M. (1992). The other life: an account of present knowledge of the larval phase of *Dreissena polymorpha*. In: *Zebra Mussels: Biology, Impacts, and Control* (eds Nalepa, T.F. & Schloesser, D.W.). Lewis Publishers, Boca Raton, FL, pp. 39–53.
- Sprung, M. & Widdows, J. (1986). Rate of heat dissipation by gametes and larval stages of *Mytilus edulis*. *Mar. Biol.*, 91, 41–45.
- Stoeckel, J.A., Schneider, D.W., Soeken, L.A., Blodgett, K.D. & Sparks, R.E. (1997). Larval dynamics of a riverine metapopulation: implications for zebra mussel recruitment, dispersal, and control in a large-river system. *J. North Am. Benthol. Soc.*, 16, 586–601.
- Swearer, S.E., Caselle, J.E., Lea, D.W. & Warner, R.R. (1999). Larval retention and recruitment in an island population of a coral-reef fish. *Nature*, 402, 799–802.
- Thorrold, S.R., Latkoczy, C., Swart, P.K. & Jones, C.M. (2001). Natal homing in a marine fish metapopulation. *Science*, 291, 297–299.
- Wacker, A., Becher, P. & von Elert, E. (2002). Food quality effects of unsaturated fatty acids on larvae of the zebra mussel *Dreissena polymorpha*. *Limnol. Oceanogr.*, 47, 1242–1248.
- Wieland, K., Hinrichsen, H.H. & Grønkaer, P. (2000). Stage-specific mortality of Baltic cod (*Gadus morhua* L.) eggs. *J. Appl. Ichthyol.*, 16, 266–272.

Wright, D.A., Setzler-Hamilton, E.M., Magee, J.A. & Harvey, H.R. (1996). Laboratory culture of zebra (*Dreissena polymorpha*) and quagga (*D. bugensis*) mussel larvae using estuarine algae. *J. Great Lakes Res.*, 22, 46–54.

Zimmerman, K.M. & Pechenik, J.A. (1991). How do temperature and salinity affect relative rates of growth, morphological differentiation, and time to metamorphic competence in larvae of the marine gastropod *Crepidula plana*? *Biol. Bull.*, 180, 372–386.

Zuehls, E.E. (1987). Traveltime and dispersion in the Illinois River, Marseilles to Peoria, Illinois. U.S. Geological Survey Water Resources Investigations Report 87-4106.

Manuscript received 4 November 2002

First decision made 13 December 2002

Manuscript accepted 17 January 2003