Long-term demography of a zebra mussel (*Dreissena polymorpha*) population

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SUMMARY

1. We used long-term data and a simulation model to investigate temporal fluctuations in zebra mussel populations, which govern the ecological and economic impacts of this pest species.
2. The size of the zebra mussel (*Dreissena polymorpha*) population in the Hudson River estuary fluctuated approximately 11-fold across a 13-year period, following a cycle with a 2–4 year period.
3. This cycling was caused by low recruitment during years of high adult population size, rapid somatic growth of settled animals, and adult survivorship of 50% per year.
4. Adult growth and body condition were weakly correlated with phytoplankton biomass.
5. The habitat distribution of the Hudson's population changed over the 13-year period, with an increasing proportion of the population spreading onto soft sediments over time. The character of soft-sediment habitats in the Hudson changed because of large amounts (mean = 34 g DM m^{-2}) of empty zebra mussel shells now in the sediments.
6. Simulation models show that zebra mussel populations can show a range of long-term trajectories, depending on the balance between adult space limitation, larval food limitation, and disturbance.
7. Effective understanding and management of the effects of zebra mussels and other alien species depend on understanding of their long-term demography, which may vary across ecosystems.

Keywords: bivalve, ecological engineering, invasive species, long-term study, population cycles

Introduction

Like many alien species, the zebra mussel [*Dreissena polymorpha* (Pallas)] has had strong economic and ecological effects in the ecosystems it has invaded. Since 1800, this species has spread over most of western Europe and eastern North America, and continues to expand its range (Kinzelbach, 1992; Drake & Bossenbroek, 2004). Zebra mussels have reduced plankton populations by >75% (MacIsaac, Lonnee & Leach, 1995; Caraco *et al.*, 1997; Pace, Findlay & Fischer, 1998), increased water transpar-

ency and nutrient concentrations (Fahnenstiel *et al.*, 1995; Effler *et al.*, 1996; Caraco *et al.*, 1997), allowed submersed vegetation and macroalgae to proliferate (Skubinna, Coon & Batterson, 1995; Hecky *et al.*, 2004), changed benthic animal communities, including the extirpation of populations of native bivalves (Strayer, 1999; Nalepa *et al.*, 2001), led to large changes in fish populations (Karatayev, Burlakova & Padilla, 1997; Strayer, Hattala & Kahnle, 2004), and caused millions of dollars of damage each year to water intakes and other structures (O'Neill, 1996; Leung *et al.*, 2002).

One of the key factors that determine the effects of any alien species is its population size, which may vary across space and time. The spatial variation in zebra mussel population density has been modelled using the probability of colonisation, substratum

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particle size, and water chemistry as independent variables (e.g. Mellina & Rasmussen, 1994; Karatayev, Burlakova & Padilla, 1998; Bossenbroek, Kraft & Nekola, 2001; Lewandowski, 2001). Much less attention has been devoted to describing or predicting how zebra mussel populations might vary over time at a single site, although the temporal range in zebra mussel populations may be 10- to 100-fold (e.g. Stanczykowska, 1977; Strayer *et al.*, 1996; Lewandowski, 2001). Likewise, although the spatial distribution of zebra mussel populations may change dramatically over time (e.g. Berkman *et al.*, 1998), this problem has received limited attention.

Five kinds of long-term trajectories for populations of zebra mussels and other aliens have been assumed (Fig. 1). Perhaps most commonly, it is assumed that zebra mussel populations follow a boom-bust cycle, with very high population densities for a few years after colonisation, followed by much lower densities over the long-term (e.g. Stanczykowska, 1977). Neither the length of the 'boom' phase nor the magnitude of population decline after the boom phase is usually specified. This scenario provides some hope for the survival of native communities, if they can survive the boom phase, and underlies programmes such as the temporary relocation of native mussels to refuge sites, with the hope that they can be returned to their native habitats once the initial outbreak of zebra mussels has passed (e.g. Newton *et al.*, 2001). 'Boom-bust' dynamics have been reported for zebra mussel populations in alpine lakes (Walz, 1974; Burla & Lubini-Ferlin, 1976; Burla & Ribi, 1998) and Long Point Bay, Lake Erie (Petrie & Knapton, 1999), as a result of predation following the arrival of large flocks of migratory waterfowl in the first decade after the zebra mussel invasion. Second, zebra mussel populations might show stable cycles driven by dominance of strong year-classes. An early model of zebra mussel demography (Deutschman, 1993) showed such strongly cyclic behaviour, which faded out only over decades and was easily restarted by environmental perturbations. The period of cycling is determined by the life-span of dominant year-classes. Data from a few populations suggest cycling (Stanczykowska, 1977; Strayer *et al.*, 1996; Burla & Ribi, 1998). Third, populations of zebra mussels might be more or less equilibrial after their initial establishment, fluctuating from year to year but showing no long-term pattern in population density. Stanczykowska (1977) suggested
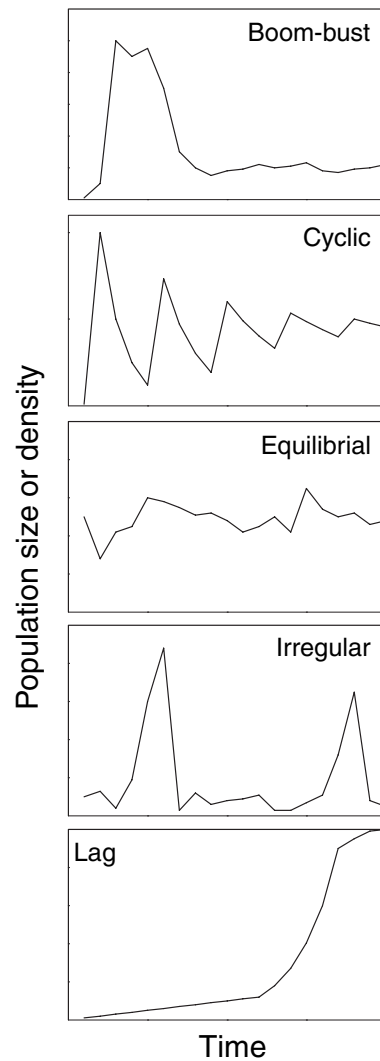

Fig. 1 Five possible long-term trajectories for populations of zebra mussels and other alien species.

that such stable populations occur, but are not common. In this case, it might be possible to extrapolate from studies done early in the invasion to predict the long-term behaviour and impacts of the population. Fourth, the population might show no long-term trends, but show large, irregular fluctuations in population density. Such widely fluctuating populations appear to be common in Polish lakes, although the mechanisms driving the fluctuations are unclear (Stanczykowska, 1977; Lewandowski, 2001). Finally, zebra mussel populations might expand only after a long lag phase, as has been described for other alien species (Crooks & Soulé, 1999). This idea has not been discussed in the zebra mussel literature, probably because zebra mussel populations seem to

expand so rapidly after initial establishment. Nevertheless, there are examples of zebra mussels gradually converting soft sediments into shell-gravels or continuous mats over a period of years (e.g. Burla & Lubini-Ferlin, 1976; Berkman *et al.*, 1998). Thus, it appears that zebra mussel populations may follow several kinds of long-term trajectories, but there are not enough long-term data on zebra mussel populations to know how common each kind of trajectory is, or describe the conditions under which it occurs.

The goals of this paper are to describe the long-term behaviour of a zebra mussel population from a 13-year data record, and to explore the sorts of long-term dynamics that zebra mussel populations might exhibit. This study should assist in the management of zebra mussel populations and the interpretation of short-term studies of zebra mussels and their impacts. It also provides insight into the processes that control zebra mussel populations.

Methods

The study area is the freshwater, tidal part of the Hudson River, extending from Troy at RKM 248 (i.e. river kilometre 248, measured from The Battery in Manhattan) to Newburgh at RKM 100. Sea salt typically is present at least part of the year downriver from RKM 100 (Cooper, Cantelmo & Newton, 1988), where zebra mussels and other freshwater animals are gradually replaced by a brackish-water fauna (Strayer, 2005). The freshwater tidal reach of the Hudson is 900 m wide and 8.3 m deep, on average. The water is turbid (Secchi disk transparency = 0.5–1.5 m; N. F. Caraco, J. J. Cole & S. E. Hazzard, unpublished data), moderately hard (calcium approximately 27 mg L^{-1}), and nutrient-rich. Summer water temperatures usually reach 25–28 °C (Wells & Young, 1992).

Our goal was to describe the characteristics of the zebra mussel population throughout the freshwater tidal reach of the Hudson. Two methods were used to sample this population (additional methods used in 1991–92 were described by Strayer *et al.*, 1996). For soft sediments (sand and mud), samples were taken with a standard (23 × 23 cm) PONAR grab (Wildlife Supply Company, Buffalo, NY, U.S.A.), then sieved in the field through a 2.8-mm mesh screen. The residue remaining on the sieve was placed on ice, frozen, then thawed and sorted in the laboratory to recover all zebra mussels (including those attached to the shells of unionid

mussels). In 2002–2003, we also picked out and weighed all zebra mussel shells, whole or fragmented. These PONAR samples were taken in late June to July 1993–2003 at 48 sites arrayed in a stratified random design covering the entire freshwater tidal Hudson (Strayer *et al.*, 1996; Strayer & Smith, 1996).

Rocky sediments too hard or coarse to collect with a PONAR grab were sampled in 1993–2003 using a diver, who collected 10 rocks (15–40 cm in maximum dimension) from each sampling point. These rocks were placed into a cooler and returned to the laboratory, where all zebra mussels >2 mm long were counted and removed. The area of each rock was estimated by tracing its outline and weighing the tracing. Subsamples of zebra mussels were saved for measurements of shell length (approximately 300 mussels per site, if possible) and length–dry mass regressions (30–50 mussels per site, if possible). We usually took these diver samples at six or seven sites throughout the estuary in August, and often took samples in June as well. The area of rocky bottom in the study area was estimated by trying to take samples with a petite PONAR grab (15 × 15 cm) at 253 sites throughout the estuary. A site was classified as rocky if we failed to retrieve a sample in five attempts. We estimate that 93% of the sediments in the study area are soft.

Demographic analyses were restricted to samples taken from rocky sediments in the middle part of the estuary (RKM 151–213). These were the only samples that consistently contained the large numbers of mussels needed for cohort analyses. Further, rocky areas in the middle estuary represent >75% of the entire population in the estuary. Zebra mussels were placed into 1-mm-wide classes by shell length. Then, we used finite mixture analysis (using the software package Rmix – Du, 2002, http://www.math.mcmaster.ca/peter/mix/mix.html) to estimate the mean shell length and percentage composition of each age-class. We ran one- through four-component models, with and without constrained variances, and chose the model with the lowest value of chi-square that was consistent with other samples (e.g. we rejected models that suggested rapid negative shell growth between one sampling time and the next). These estimates of shell length and cohort size were used to calculate growth and mortality rates of cohorts.

We regressed recruitment, survivorship, somatic growth, and body condition against the estimated filtration rate of the settled zebra mussel population,

phytoplankton biomass, and freshwater flow during 1 May to 30 September of each year. The aggregate filtration rate of Hudson River zebra mussels was estimated by applying the regression of Kryger & Riisgard (1988) to the measured population densities and body sizes of Hudson River zebra mussels. Filtration rates estimated from Kryger and Riisgard's regression agreed well with measurements of filtration rates of Hudson River zebra mussels made in the laboratory (Roditi *et al.*, 1996) and the field (Roditi, Strayer & Findlay, 1997). Estimates of filtration rates assume a water temperature of 20 °C. Phytoplankton biomass (as chlorophyll *a*) was estimated from weekly samples taken at Kingston-Rhinecliff (RKM 144–149) by Caraco *et al.* (1997) and Caraco, Cole & Strayer (in press). Freshwater flow was taken from the United States Geological Survey gage station at Green Island (the head of the Hudson River estuary; USGS, 2004). We chose not to use water temperature as a predictive variable because zebra mussel growth declines at both high and low temperatures, and the temperature-dependency of growth appears to depend on season and food availability (Jantz & Neumann, 1998; Allen, Thompson & Ramcharan, 1999).

Simulation models

We constructed simple simulation models to explore the likely long-term dynamics of zebra mussel populations. These models are not intended to provide accurate predictions of zebra mussel population densities in specific lakes or rivers, but rather to expose the range of dynamics that zebra mussel populations are likely to exhibit and to identify the conditions under which each kind of dynamic will occur. We explored the effects of space limitation, larval food limitation, and disturbance on zebra mussel populations. For the basic space-limited run, model populations consisted of five age-classes (1–5 years old), censused in August. Simulations were started with a population of age 1 animals at a density of 1 m^{-2}, and run for 100 years. Shell lengths were 13, 18, 20.5, 22, and 24 mm for all 1–5 year olds, respectively (Smit, bij de Vaate & Fioole, 1992; Chase & Bailey, 1999, see also Fig. 6). Females were assumed to constitute half of the population, and have a fecundity of $0.4 \times$ (shell length)$^{4.39}$ (Walz, 1978). We assumed that 0.1% of veligers successfully completed development and settled (Sprung, 1989). We allowed enough animals to recruit to age 1 to allow the population to cover the bottom to a thickness of two zebra mussels (the area covered by an individual animal was assumed to be $0.5 \times$ (shell length)^2). Mortality of adults was set at 50% per year (see Fig. 5).

We simulated food-limitation of larvae in three ways. First, we assumed that no larvae would recruit if the adult population exceeded some critical threshold (set at 5%, 15%, 25%, 50%, 75%, 85%, and 95% of the carrying capacity in various runs). Second, we assumed that the proportion of larvae reaching settlement was a declining linear function of adult population size (such that recruitment reached zero at 50% or 100% of the carrying capacity in different runs). Third, we assumed that the proportion of larvae reaching settlement was a negative exponential function of adult population size (such that recruitment was half of the maximum when the adult population was 10% and 25% of carrying capacity in different runs). This third class of runs could also be interpreted as simulating the effects of adult cannibalism on larvae. Disturbance was simulated by increasing adult mortality to 80 or 90% per year in different runs, and proportionately decreasing recruitment of age 1 animals.

Results

Temporal dynamics of the zebra mussel population

The Hudson's zebra mussel population cycled in 1992–2003, fluctuating from 48–550 billion animals (Fig. 2a). These fluctuations were underlain by a strong year-class structure, in which strong year-classes in 1992, 1996, and 2001 (and a moderately strong year-class in 1998) were separated by weak to undetectable year-classes (Fig. 3). Growth of animals in these dominant cohorts caused cycles in mean body size that were out of phase with the cycle in population size (Fig. 2b). The aggregate filtration rate of the population, probably the best measure of its impacts on the ecosystem, also cycled in 1992–2003 (Fig. 2c), but its cycle was muted because of the antagonistic influences of the out-of-phase cycles of population size and body size.

Three variables determine the behaviour of the Hudson River zebra mussel population: recruitment, survivorship of postrecruits, and somatic growth (which determines fecundity – e.g. Walz, 1978). Somatic growth can be further broken down into growth in shell length and body condition; i.e., the
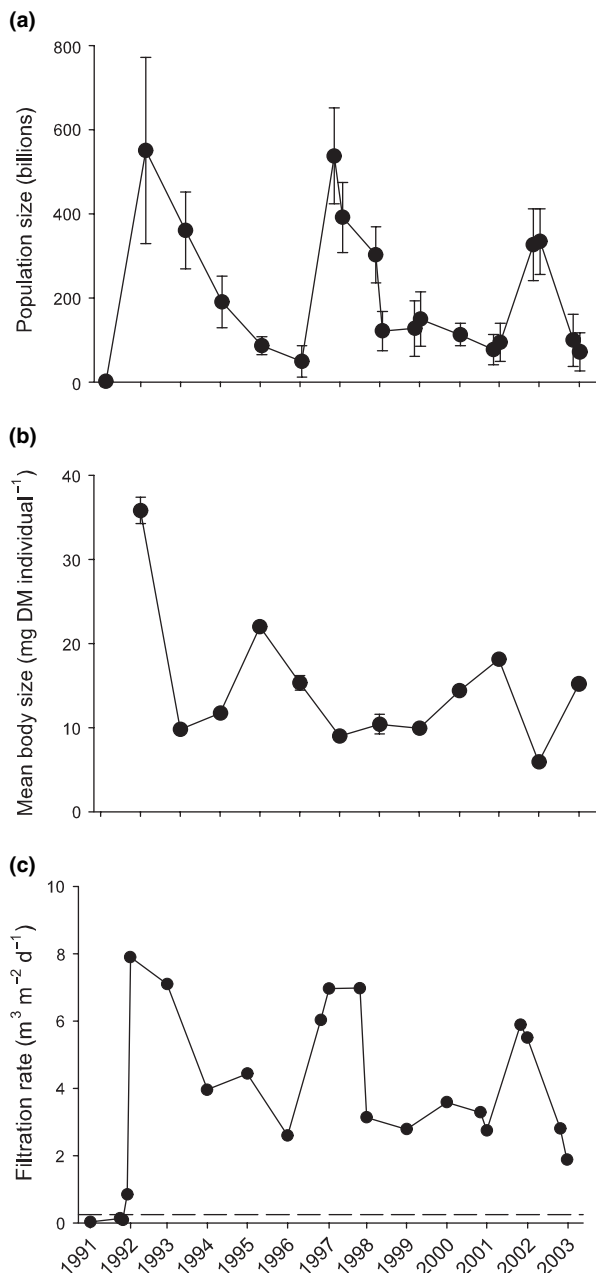
Fig. 2 (a) Number of zebra mussels (±1 SE) in the Hudson River estuary between RKM 100–248. (b) Areally weighted riverwide mean shell-free body mass (±1 SE) of zebra mussels from rock samples in August 1992–2003. Data for 1992 exclude newly settled young-of-year, which were rare or absent in other years. (c) Areally weighted riverwide filtration rate of the zebra mussel population in the Hudson River. Dashed line shows the aggregate mean filtration rate of all suspension-feeders in the river before the zebra mussel invasion (Strayer *et al.*, 1999). Error bars in A and B were estimated by bootstrapping with 1000 runs (Efron & Tibshirani, 1993).

amount of body tissue associated with a given shell length. Recruitment in the river (measured as the number of animals reaching age 1) was highly variable from year to year (Fig. 4), and was strongly associated with the size of the adult population. Recruitment was high when adult filtration rates were approximately <2.8 m^3 m^{-2} day^{-1}, and low when adult populations were above this threshold (Fig. 4).

Interannual survivorship averaged 49% per year, and was not related to the filtration rate of the zebra mussel population, phytoplankton biomass, or age or body condition of the zebra mussels ($P > 0.2$ for all variables). Nevertheless, survivorship of the 1992 cohort was markedly higher than that of the 1996 and 2001 cohorts (Fig. 5).

Shell growth was highly variable across years and mussel sizes (Fig. 6a). When all years were considered, we found a highly significant positive relationship between growth rates and phytoplankton biomass (Fig. 6b) or the filtration rate of the adult zebra mussel population. This effect was largely a result of the rapid growth of the 1991 cohort during the time before zebra mussel grazing reduced phytoplankton biomass, and nearly disappeared when the 1991 cohort was eliminated from the analysis (Fig. 6c).

Body condition (i.e. the residual from the log-log regression of dry tissue mass on shell length) was highly variable among years (Fig. 7a), but this variation was not well correlated with filtration rate of the adult population, freshwater flow, or phytoplankton biomass. The strongest relationship was between body condition and phytoplankton biomass (Fig. 7b); body condition was high during years of highest phytoplankton biomass but variable when phytoplankton biomass was low.

Temporal changes in the spatial distribution of zebra mussels

When zebra mussels first invaded the Hudson (1991–95), nearly the entire zebra mussel population was associated with rocky sediments (Fig. 8). Since 1995, zebra mussels have spread out onto the soft sediments of the river, which now support 10–25% of the river's population. The mechanism behind this spread is not known. It does not appear that zebra mussels are progressively converting the bottom of the river to shell gravels suitable for their own recruitment. The mass of zebra mussel shells at the river's bottom is
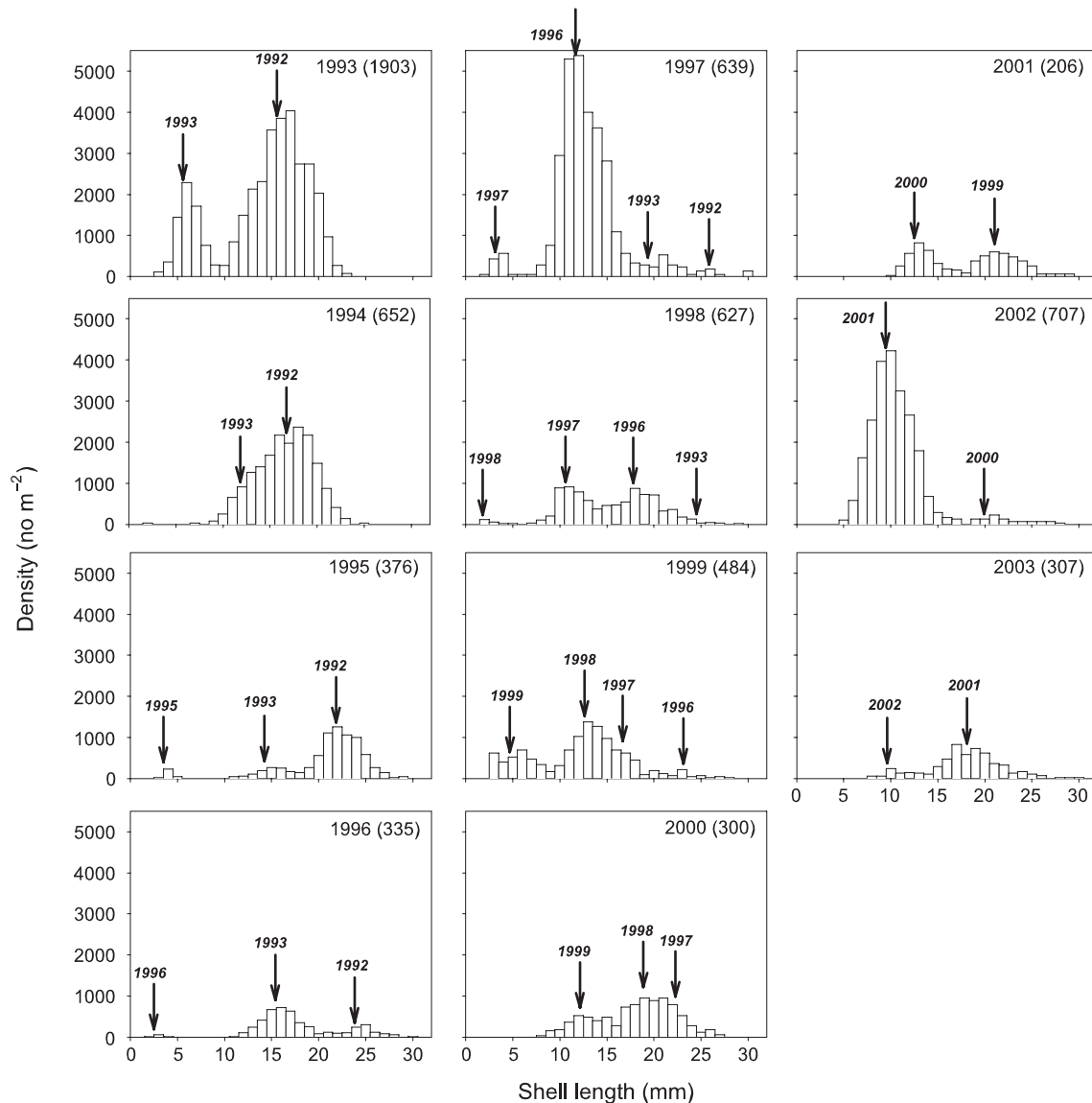
Fig. 3 Size-frequency histograms for zebra mussels collected in August (early September in 1993) from rocks in the mid-Hudson estuary (RKM 151–213). This habitat contains most of the zebra mussels in the river, and is the only habitat for which we consistently have large collections of mussels. The mean shell length of each year-class is indicated, and the number of specimens measured is given in parentheses following the year of collection.

33.9 g DM m^{-2}, substantially less than annual shell production by the zebra mussel population.

Simulation models

The space-limited zebra mussel population was stable over the long-term, following rapid growth and damped oscillations in the first decade after establishment (Fig. 9). Populations subjected to moderate larval food limitation (or moderate adult-larval can-

nibalism) showed similar dynamics. Population dynamics changed as populations were subjected to increasingly severe larval food limitation (or canni-balism), whether expressed as a step-function, a linear decline, or an exponential decline. Populations subjected to moderately severe larval food limitation showed strong, persistent cycles with a period of 3–5 years (i.e. the life-span; Fig. 9b,c). As larval food limitation decreased, populations showed damped cycles that stabilised after a few generations (examples
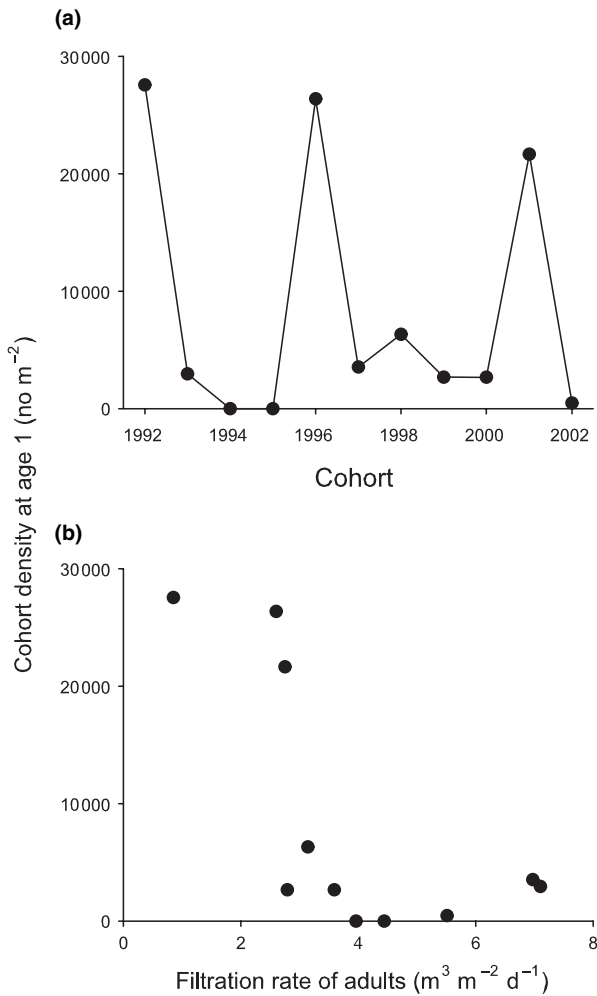
(a)

(b)

Fig. 4 (a) Time-course of recruitment of zebra mussels to age 1 in the mid-Hudson estuary (RKM 151–213). (b) Recruitment of zebra mussel cohorts to age 1 in the mid-Hudson estuary in 1993–2003 as a function of the filtration rate of the adult zebra mussel population. The relationship between filtration rate and recruitment is significant, whether expressed by a linear ($r^2 = 0.43$, $P = 0.015$) or a logistic ($r^2 = 0.94$, $P < 0.001$) function.

Fig. 5 Survivorship curves for three zebra mussel cohorts on rocks in the mid-Hudson River estuary. Data were too sparse to produce survivorship curves for other cohorts. Note that the *y*-axis is logarithmic.

not shown). Finally, as larval food limitation became very severe, cycling became so pronounced that the population went extinct after one to a few generations (Fig. 9d). Increasing disturbance in the space-limited population simply reduced population size and increased the proportion of young animals in the population (Fig. 9e). In severely food-limited populations, disturbance kept the population from reaching the threshold of larval food limitation as often, and stabilised the population, converting cycling populations to stable populations, and unviable populations to cycling populations (Fig. 9f–h).
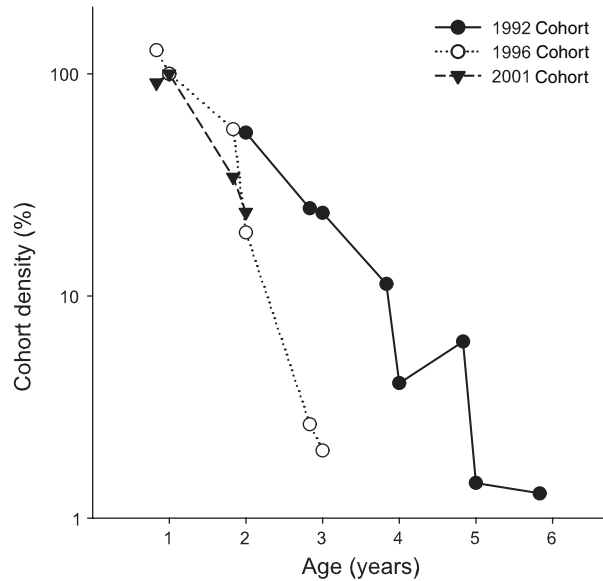
Based on these model explorations, we can identify the domains in which different kinds of population dynamics may occur (Fig. 10). Space-limited or annually disturbed populations ought to be stable over the long-term, whereas those subject to stringent larval food-limitation ought to cycle with a period of about 3–5 years. If larvae are very severely food-limited, the population may not be viable over the long-term. Of course, if populations are subjected to irregular disturbances (instead of the annual disturbances simulated here) or outbreaks of disease, then population dynamics may be irregular. Likewise, if populations of pathogens or predators build up over the long-term, then the zebra mussel population may decline after an initial outbreak phase.

Discussion

The Hudson River population

The size of the zebra mussel population in the Hudson has varied over about an order of magnitude since its initial outbreak in 1992. It appears that most of this variation has been associated with a 2–4 year cycle driven by huge interannual variation in recruitment. Recruitment is negatively correlated with the size of the adult population, as described by its
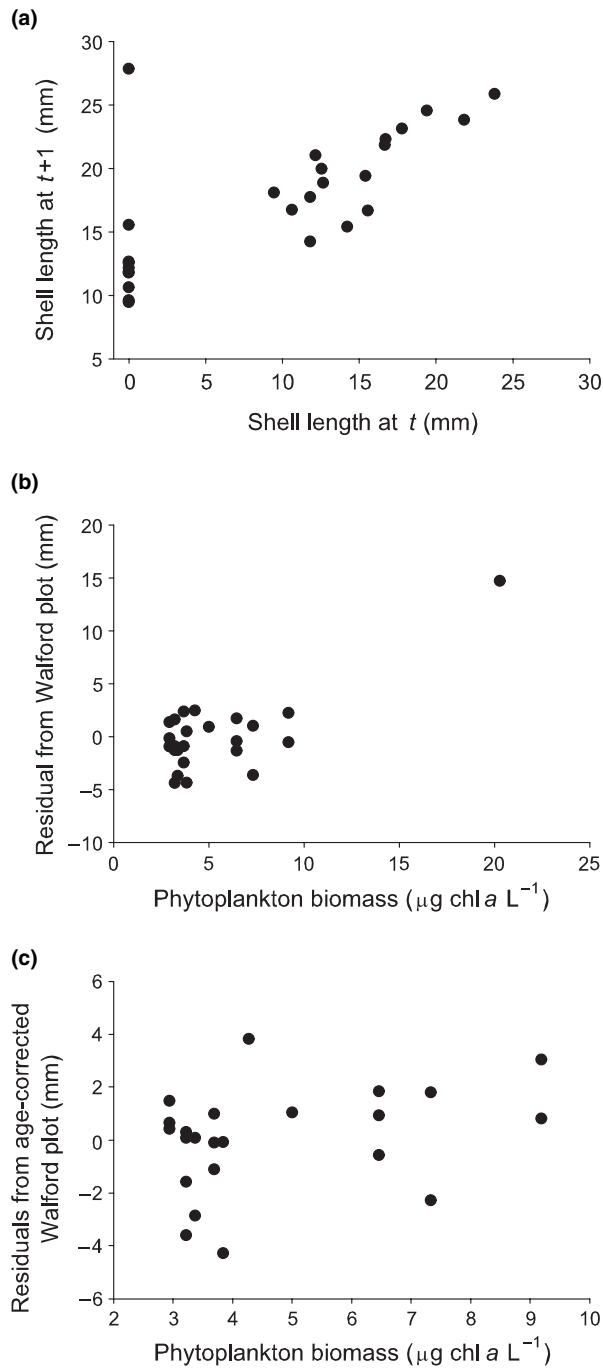
(a)

(b)

(c)

Fig. 6 Shell growth of Hudson River zebra mussels in 1991–2003. (a) Walford plot based on the mean shell length of each cohort in August. (b) Relationship between shell growth (residual from the Walford plot) and mean phytoplankton biomass in May to July ($r^2_{adj} = 0.52$, $P < 0.001$). (c) Relationship between shell growth (residual from the age-corrected Walford plot) and mean phytoplankton biomass in May to July, excluding the 1991 cohort in 1992 (the outlier in panel b; $r^2 = 0.09$, $P = 0.075$).
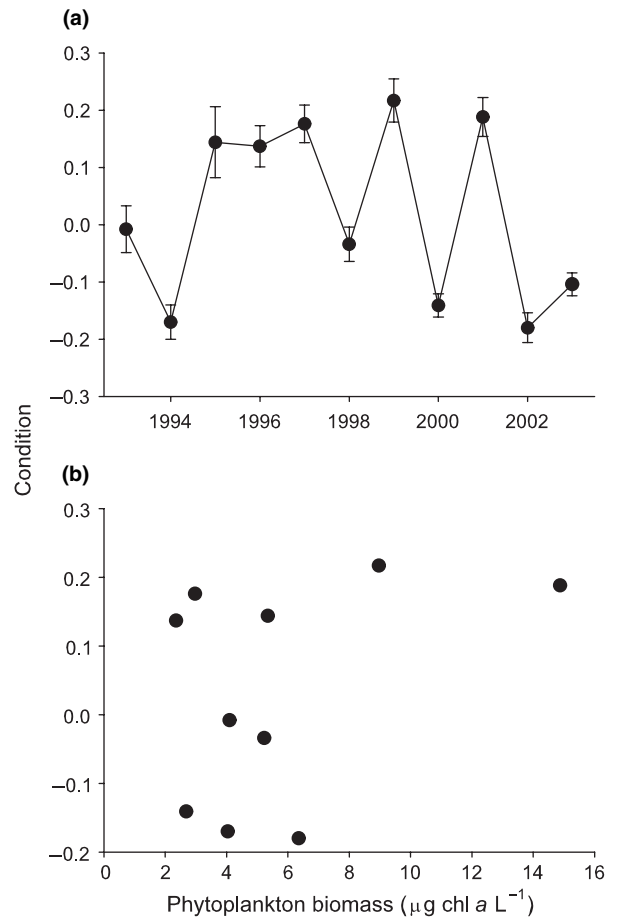
(a)

(b)

Fig. 7 Body condition of Hudson River zebra mussels. Condition is the residual from the log (shell length) – log (dry body mass) regression. (a) Interannual variation in body condition. Error bars are 1 SE. (b) Condition as a function of mean phytoplankton biomass in May to July 1993–2002 ($r^2 = 0.15$, $P = 0.14$).

filtration rate. The functional relationship between filtration rate and recruitment appears to be a step-function rather than a linear or exponential decline, although data are too few to be sure about the shape of this function (Fig. 4). A threshold relationship is consistent with larval food limitation, but not with cannibalism of larvae by adults, which ought to produce a negative exponential relationship between filtration rate and recruitment.

This strong cycling appears to be a result of three essential characteristics of the zebra mussel population. First, there is a time lag between larval settlement and the attainment of high adult filtration rates 1–5 years later, which allows the zebra mussel population to overshoot its carrying capacity as defined by
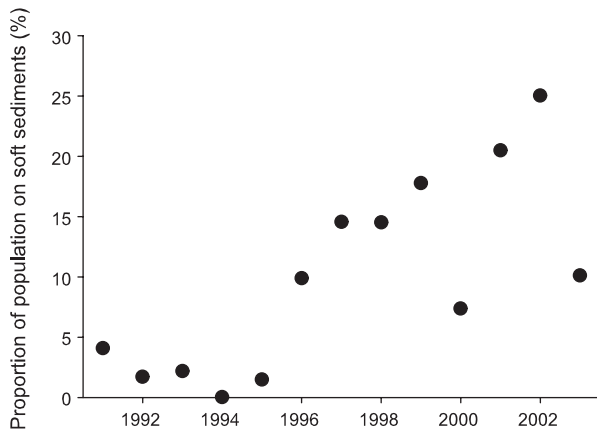
Fig. 8 Proportion of the Hudson River zebra mussel population living on soft sediments. The rising proportion of zebra mussels living on soft sediments is significant ($r^2 = 0.57$, $P = 0.003$).

the amount of food needed to support successful larval development and postlarval growth. It is possible for the resources in an ecosystem to support the recruitment of a strong year-class that can suppress recruitment for several years. Second, somatic growth is rapid, so that a dominant year-class can attain a high enough biomass to suppress resources before the next year-class is recruited. Third, the larvae and their planktonic food resources live in a relatively well-mixed milieu, which means that they (and the adults) are likely to be engaged in a scramble competition for a nearly homogeneous resource. As a result, larval recruitment in food-limited zebra mussel populations may be the all-or-none phenomenon suggested by Fig. 4, rather than a graded response. Our simulation models suggest that population cycling driven by these characteristics can persist indefinitely. Note that these mechanisms are different from those thought to be responsible for most cyclic populations, in which controlling resources or predators have generation times about as long as or longer than those of the cycling species (Turchin, 2003).

Other controls on the Hudson's population are less clear. Growth rates and body condition of postlarvae were correlated only weakly with phytoplankton biomass in the postinvasion period, possibly because phytoplankton biomass has not varied much since the zebra mussel invasion. Considerable interannual variation in growth rates, body condition, and survivorship is not accounted for by phytoplankton biomass or the size of the zebra mussel population. Factors not considered in this study, including water temperature

(Jantz & Neumann, 1998; Allen *et al.*, 1999), food quality (Schneider *et al.*, 1998), and spatial variation in phytoplankton biomass within the Hudson (Caraco *et al.*, 2005), may be responsible for this variation.

The spatial distribution of zebra mussels in the Hudson also has changed over time, with a gradual but large colonisation of soft sediments in the river. This colonisation is associated with, but perhaps not caused by, a large-scale conversion of muddy and sandy sediments to shell-gravels. We do not know how far this colonisation of soft sediments will proceed. Because the Hudson's zebra mussel population is probably limited by food rather than space (see above), this colonisation of soft sediments may affect the spatial distribution of the zebra mussel population but not its overall size.

The long-term behaviour of zebra mussel populations

Environment–organism interactions may induce a wide range of population behaviours in a single species. The limited empirical evidence and our simulation model both suggest that zebra mussel populations in particular may follow any of several long-term trajectories. Although long runs of data on zebra mussel populations are rare, researchers have suggested that zebra mussel populations follow different long-term trajectories, including boom-bust (Burla & Lubini-Ferlin, 1976; Stanczykowska, 1977; Petrie & Knapton, 1999), cycling (Burla & Ribi, 1998; this study), stability (Stanczykowska, 1977), and irregular fluctuations (Stanczykowska, 1977). Such a range of population behaviours is consistent with the model results presented here, which show that zebra mussel populations are capable of qualitatively different behaviours.

We suggest that the long-term trajectory of a zebra mussel population depends on the extent to which each of several factors limit the population. Populations that are simply space-limited may be relatively stable, unless the population is so dense that large areas of zebra mussel beds die and slough off synchronously as a result of overcrowding (Chase & Bailey, 1999). Space-limited populations are perhaps most likely to occur in small lakes, where hard substrata typically are scarce and phytoplankton is abundant.

Populations in which larval development is limited by inadequate food are likely to cycle persistently. Larvae need a diet of small algae high in long-chain
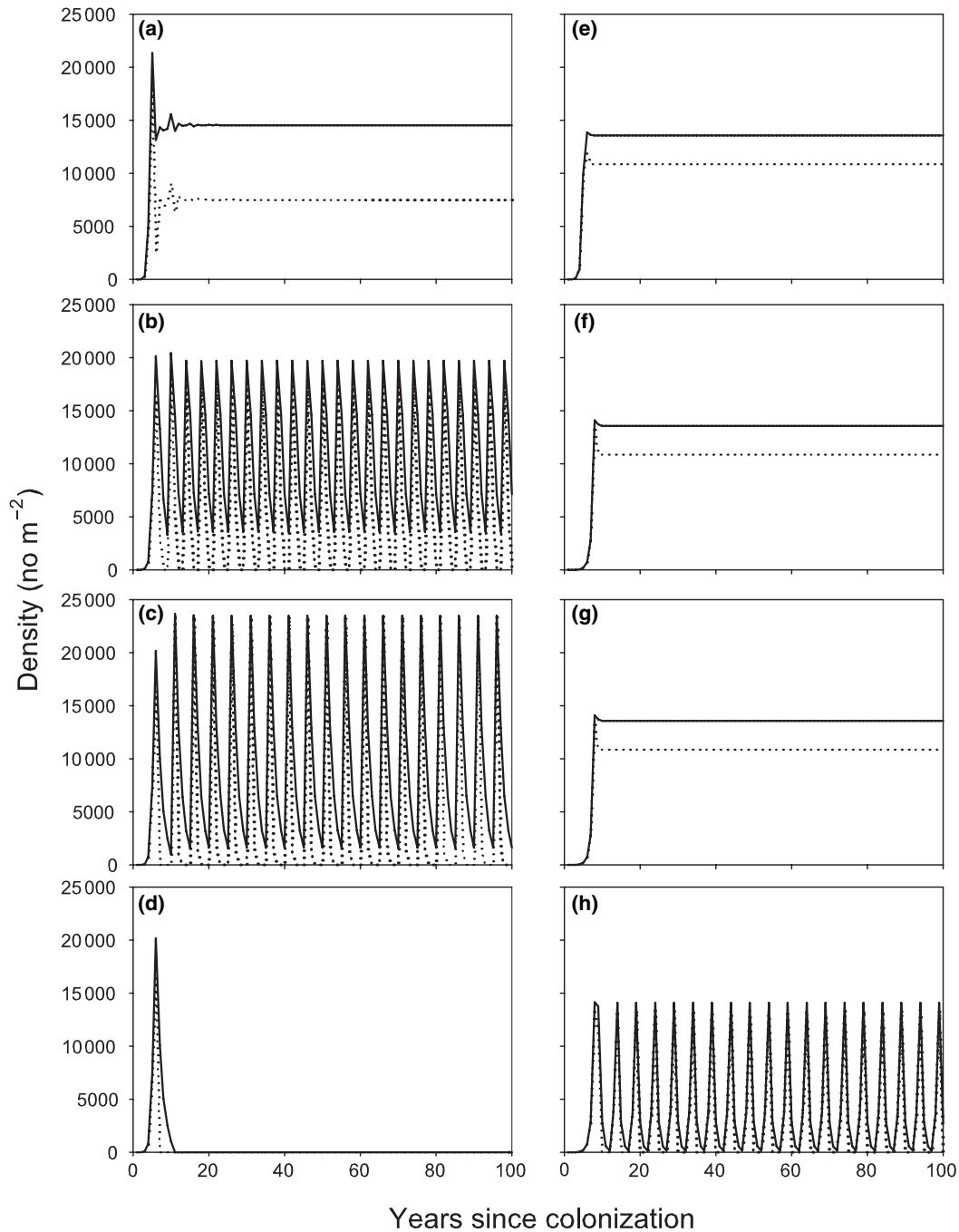
Fig. 9 Selected results from simulation models of zebra mussel populations. The sequence from (a) to (d) represents increasingly severe food limitation of larvae; (e–h) represent the same model runs but with adult mortality increased from 50% to 80% per year (as in a high-disturbance habitat). Solid lines show population density and dotted lines show density of age 1 animals. (a) Space-limited population with adult mortality of 50% per year; (b) food-limited population where no larvae are recruited if adult population is more than 50% of carrying capacity and adult mortality = 50% per year; (c) food-limited population where no larvae are recruited if adult population is more 25% of carrying capacity and adult mortality = 50% per year; (d) food-limited population where no larvae are recruited if adult population is more than 5% of carrying capacity and adult mortality = 50% per year; (e) space-limited population with adult mortality of 80% per year; (f) food-limited population where no larvae are recruited if adult population is more than 50% of carrying capacity and adult mortality = 80% per year; (g) food-limited population where no larvae are recruited if adult population is more then 25% of carrying capacity and adult mortality = 80% per year; (h) food-limited population where no larvae are recruited if adult population is more than 5% of carrying capacity and adult mortality = 80% per year.
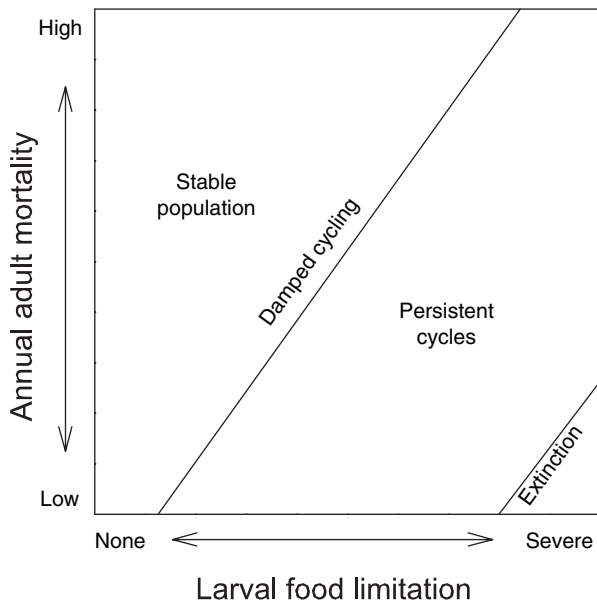
Fig. 10 Suggested domains of different modes of population dynamics of zebra mussel populations, based on results of simulation models.

polyunsaturated fatty acids (Vanderploeg, Liebig & Gluck, 1996; Wacker, Becher & von Elert, 2002), and larval mortality is very high in nature, perhaps as a result of food-limitation (Sprung, 1989; Schneider *et al.*, 2003). Larval food limitation is most likely to occur where hard substrata are abundant and food is scarce and depletable, as in the Hudson and some other rivers, reservoirs, lakes, and estuaries.

If disturbance is regular and severe, our models suggest that it will stabilise the population and increase the proportion of young animals in the population. Disturbances that are severe but irregular will contribute to irregular population dynamics. Disturbance may be an important factor in rivers that are subject to flood scour and in shallow lakes and rivers in cold climates, where waves and ice scour may be important (MacIsaac, 1996; Chase & Bailey, 1999; Bially & MacIsaac, 2000).

Predators, parasites, and diseases may influence zebra mussel population dynamics in at least two distinct ways. First, predation rates may rise once the predator population finds or grows to take advantage of the zebra mussels. This will produce boom-bust dynamics as the predator suppresses the zebra mussel population. Such dynamics have been described as a result of waterfowl altering their migration patterns (Petrie & Knapton, 1999). For this mechanism to be

effective, the predator must be capable of a strong numerical response to zebra mussels. Probably relatively few zebra mussel predators (reviewed by Molloy *et al.*, 1997) are capable of such strong population growth or movement. Second, outbreaks of disease may decimate populations of zebra mussels. Such disease outbreaks are most likely to affect dense populations, and may cause irregular population fluctuations like those described for some lakes (Stanczykowska, 1977; Lewandowski, 2001). Unfortunately, very little is known about the ecological role of zebra mussel diseases in nature (Molloy *et al.*, 1997).

Finally, if the zebra mussel population is able to tailor the environment to its own liking by converting soft sediments into colonisable shell-gravels, the population may grow after a lag phase. Such colonisation has been described for Lake Erie (Berkman *et al.*, 1998) and the Hudson River (this study), but neither study demonstrated that a habitat shift increased the size of the overall population.

Two points are clear from this brief review: zebra mussel populations are capable of a range of dynamics; and we do not fully understand how real zebra mussel populations behave over the long-term. It would be helpful to have good, long-term data on zebra mussel populations and possible controlling factors from a wide range of habitats.

Consequences of different kinds of population trajectories

Different demographic patterns of zebra mussel populations will lead to different ecological and economic impacts. Stable zebra mussel populations will have stable impacts, to the extent that parts of the ecosystem do not adapt or evolve in response to the zebra mussel population. The impacts of such populations are predictable from short-term studies, and are relatively easy to plan for. The long-term behaviour of zebra mussel populations is different from their short-term behaviour for all other population trajectories, so impacts cannot simply be extrapolated from short-term studies.

The boom-bust dynamic gives some hope for ecosystem recovery from the initially high impacts of a zebra mussel invasion, and has been used to justify the temporary relocation of unionid mussels (which are killed by heavy zebra mussel infestations – Strayer, 1999) to off-site refuges until the 'boom' phase

passes. Apart from the technical difficulties with such programmes (Cope & Waller, 1995; Newton *et al.*, 2001), these programmes require that the decline of the ''bust'' phase occur soon enough and be severe enough to allow unionids to be returned to their original location. Although boom-bust dynamics have been observed at some sites, it is not clear whether declines are severe enough to allow ecosystem recovery, or whether such boom-bust dynamics are general or restricted to a few local areas where waterfowl densities are especially high.

If lag effects are important, then the impacts of zebra mussel populations may rise or shift in location over time. There is good evidence of lag effects in the colonisation of soft sediments by zebra mussels (Berkman *et al.*, 1998; this study). The ultimate extent, time-course, and effects of such lag effects are not known for any population.

Finally, the effects of populations that fluctuate widely, whether cyclic or irregular, may be the most difficult to manage. The effects of such populations may depend on the long-term average population density (e.g. production of shell-gravels), the maximum population density (e.g. economic costs of control measures, which probably will have to be designed to deal with maximum populations), or the minimum population density. Further, if fluctuations are irregular, then it will be difficult to plan for or forecast impacts. Unfortunately, it appears that widely fluctuating zebra mussel populations are common.

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