

Modelling the local dynamics of the zebra mussel (*Dreissena polymorpha*)

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SUMMARY

1. The bivalve *Dreissena polymorpha* has invaded many freshwater ecosystems worldwide in recent decades. Because of their high fecundity and ability to settle on almost any solid substratum, zebra mussels usually outcompete the resident species and cause severe damage to waterworks. Time series of *D. polymorpha* densities display a variety of dynamical patterns, including very irregular behaviours. Unfortunately, there is a lack of mathematical modelling that could explain these patterns.

2. Here, we propose a very simple discrete-time population model with age structure and density dependence that can generate realistic dynamics. Most of the model parameters can be derived from existing data on *D. polymorpha*. Some of them are quite variable: with respect to these we perform a sensitivity analysis of the model behaviour and verify that non-equilibrial regimes (either periodic or chaotic) are the rule rather than the exception.

3. Even in circumstances where the model dynamics are aperiodic it is possible to predict total density peaks from previous peaks. This turns out to be true also in the presence of environmental stochasticity.

4. Using the stochastic model we explore the effects of age-selective predation. Quite surprisingly, larger removal rates of adults do not always result in smaller population densities and mussel biomasses. Moreover, non-selective predation can result in skewed size-frequency distributions which, therefore, are not necessarily the footprint of predators' preference for larger or smaller zebra mussels.

Keywords: age-structured models, density dependence, invasive species, peak-to-peak dynamics, selective predation

Introduction

The zebra mussel (*Dreissena polymorpha*, Pallas) is considered to be one of the most invasive freshwater animals in the world. In addition to the biofouling of intake pipes, which can severely impair water delivery to human services (Jenner & Janssen-Mommen 1993; MacIsaac 1996), the functioning of the entire ecosystem may be altered after zebra mussel colonisation and population growth. The species usually outcompetes native bivalves (Ricciardi *et al.* 1996), causes large reductions in phytoplankton (Bastviken

et al. 1998) and zooplankton abundances (Garton & Haag 1993), and greatly modifies the cycling of nutrients (Arnott & Vanni 1996). Despite the extremely high mortality rate at the veliger (the larval life stage) and postveliger stages, adults anchored to the substratum can reach densities in the order of tens of thousands per square metre (Stańczykowska, Schenker & Fafara, 1975; Ramcharan *et al.* 1992; Nalepa & Schloesser 1993). The main reason is that under a broad range of abiotic circumstances – essentially whenever the water temperature exceeds a site-dependent threshold (Garton & Haag 1993; Neumann *et al.* 1993) – every adult female can produce eggs in huge numbers, in the order of millions every year (Mackie 1993). Because adult zebra mussels can adapt to a wide range of environmental conditions and

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because of the high dispersal rate of veligers and postveligers, *D. polymorpha* has spread to most European inland waters during the past two centuries. In light of this, the rate at which zebra mussels spread around the North American continent was unexpectedly fast, reaching Louisiana along the Mississippi river in 1993 from the Great Lakes (Michigan, U.S.A.), where they were first sighted in 1988 (Griffiths *et al.* 1989; Hebert *et al.* 1989; McMahon 1989; Roberts 1990).

Although great attention has been devoted to the invasive characteristics of the species, our understanding of population dynamics at the local scale remains very limited. Various qualitatively different temporal patterns of *D. polymorpha* have been documented in the literature (Fig. 1). In the leading article of the most important monograph on zebra mussels to date, Stańczykowska & Lewandowski (1993) divided long-term population trends into three categories: 'decreasing', 'stable' and 'unstable'. While it is clear what the authors meant for decreasing or stable populations (i.e. the disappearance of the species or its persistence at a positive and approximately constant population density), the term used for the third category is technically ambiguous – by definition, no 'unstable' regime can be reached. Data from Lakes Sniardwy, Boczne and Tattowisko in Poland (see Fig. 1a) are examples of the patterns that were termed

'unstable' by the authors. These patterns are irregular in both the timing and the intensity of zebra mussel outbreaks. In fact, according also to Ramcharan *et al.* (1992), 'the type of dynamics most often observed [in zebra mussel time series] is an irregular pattern of population increases and decreases'. Fig. 1a also reports data from Lake Michigan, U.S.A., by Nalepa *et al.* (2006) where no regular temporal patterns of *D. polymorpha* abundances were observed. In less frequent, yet documented, case studies (see a personal communication by Breitig to Stańczykowska 1977 and one study by Lewandowski, 1982, cited in Ramcharan *et al.* 1992) population dynamics are cyclical with a period comparable with the lifespan of individuals (i.e. a few years). An example of periodic dynamics in *D. polymorpha* emerges from data from Lake Zürich, Switzerland (Burla & Ribi 1998), where both adult and juvenile densities were observed to fluctuate regularly with a 5-year cycle in eight out of nine sampling sites (see Fig. 1b). A slightly more complex dynamics than the pure periodic oscillation of densities has been found in a 30-year study of zebra mussels in Lake Mikolajskie, Poland (see Fig. 1c, reprinted from Stańczykowska & Lewandowski 1993). First, two distinct 'booms' occurred 16 years apart, suggesting periodic dynamics because in both cases the population reached very similar densities in the peak year, as

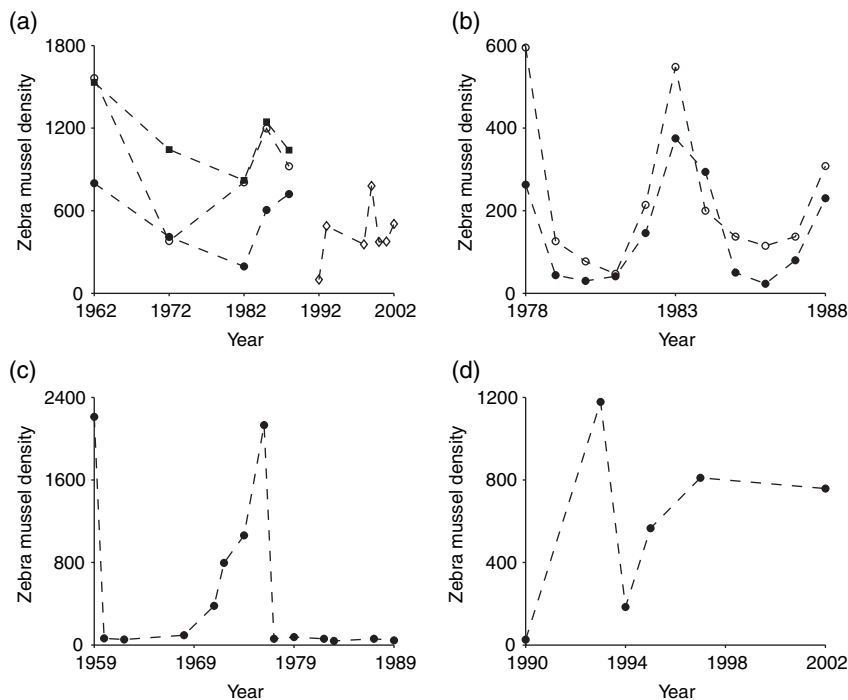


Fig. 1 Temporal patterns of *Dreissena polymorpha* abundances (ind. m⁻²) in different lakes or reservoirs in Europe and North America. See text for a discussion. (a) Filled circles, empty circles and filled squares are for Lake Sniardwy, Tattowisko and Boczne, respectively (from Stańczykowska & Lewandowski 1993), empty diamonds are for Lake Michigan (from Nalepa *et al.* 2006); (b) filled circles and empty circles are for two stations in Lake Zürich (from Burla & Ribi 1998); (c) Lake Mikolajskie (from Stańczykowska & Lewandowski 1993); (d) Lake Naroch (from Burlakova *et al.* 2006).

high as 2000 individuals per square metre. After the collapse of 1975, zebra mussels were rather stable in numbers at much lower abundances in the lake (Stańczykowska & Lewandowski 1993). As for 'stable' populations, it is interesting to notice that in many cases the equilibrium value is reached after a peak of population density. This damped transient toward an equilibrium has been called boom-and-bust dynamics (Walz, 1974, as cited in Strayer & Malcom 2006) and has been recorded in European Alpine lakes, in Lake Erie, U.S.A. (see Strayer & Malcom 2006, and references therein), in Poland (Stańczykowska *et al.* 1975) and in Lake Naroch, Belarus (Burlakova *et al.* 2006; see Fig. 1d).

Very few of these examples can be used to rigorously validate a demographic model, because abundance data have not been regularly collected over time. Although precise information on what happened between two subsequent samples is lost, we can reasonably assume that the populations were sampled without missing the most important events of dynamics, like booms or crashes. Under this hypothesis, the examples in Fig. 1 are representative of the rich variety of demographies exhibited by *D. polymorpha*. Investigating the causes of this variety is crucial to understand the dynamics of this invasive species. In particular, both the problem of prediction and control of the irregular temporal changes in zebra mussel densities remain unsolved. To our knowledge, only two mechanistic models have been used in the literature so far to describe the local dynamics of zebra mussels (MacIsaac *et al.* 1991; Strayer & Malcom 2006). Both were presented as simulation models. The aim of this paper is to propose and analyse a simple demographic model, able to qualitatively capture the core characteristics of the zebra mussel temporal regimes in closed aquatic systems. The model is time-discrete and its explicit mathematical form makes it amenable to a thorough analysis via advanced nonlinear techniques.

In the Methods we introduce the age-structured model of the zebra mussel and analyse its behaviour under different ecological conditions. Almost all the model parameters are drawn from data with the exception of a few uncertain parameters for which we perform a sensitivity analysis. In the Results we use the model in order to (i) predict the abundance of forthcoming population outbreaks under aperiodic

temporal regimes; and (ii) consider the effects of age-selective predation on the mussel bed.

Methods

Life history

The zebra mussel life cycle (Garton & Haag 1993) can be roughly subdivided into three: the larval, juvenile and adult stages. The life of *D. polymorpha* individuals begins with a mature oocyte being externally fertilised by sperm in the water column. Larvae (also known as veligers) are planktonic and swim by means of a ciliated organelle, the velum. This planktonic stage is relatively short (a few weeks) compared with the zebra mussel lifespan (a few years). During the last part of the veliger stage, *D. polymorpha* individuals develop the byssum, the organ which allows attachment to a solid substrate. The juvenile stage begins after settlement and ends when mussels become sexually mature and produce eggs and sperm. The lifespan of *D. polymorpha* is dependent on local conditions, being generally shorter in warmer waters (Stańczykowska 1977). According to some estimates (Stańczykowska 1977; Mackie 1991; Chase & Bailey 1999) *D. polymorpha*'s lifespan usually does not exceed 2–4 years in the Great Lakes, as well as in some central European lakes, like the Neusiedler (Austria) or the Balaton Lake (Hungary); in the Mazurian Lakes (Poland) it reaches 5–6 years; in the Swiss lakes it is as long as 6–7 years while in some Russian reservoirs it reaches 9 years. Some authors (Karpevich 1964; Stańczykowska 1964) have previously reported even higher values for the lifespan of zebra mussels, in the range of 12–19 years, mainly on the basis of the count of annual growth rings. More recent studies, (reviewed in Karatayev *et al.* 2006) revealed that this method can often lead to overestimating the maximum age of mussels. The analysis of size-frequency distributions and the study of growth in experimental cages actually shows that the zebra mussel's lifespan may vary from a minimum of 2 years to a maximum of 8 years (Karatayev *et al.* 2006).

In this paper, we will consider the most frequent case of water bodies in which the lifespan does not exceed 6–7 years so that we can include in the model no more than four age classes. In the oldest class we group individuals aging 4 years or more. The yearly survival of individuals in this last class is a partic-

ularly important parameter because it can account for the differences in site-specific lifespans.

The model

In accordance with the above description of the life cycle, we model the dynamics of *D. polymorpha* at the local scale by considering four age classes. More precisely, we denote by $n_i(t)$ ($1 \leq i \leq 3$) the density of individuals of both sexes that age i years during year t , while we group into a single class $n_4(t)$ all adults aged four or more years during the same year t . Development of a model with a larger number of classes would be easy, but the main results would not change qualitatively (see Discussion).

As zebra mussels can reach very high densities in relatively short-time intervals, it is necessary to account for density-dependent regulatory mechanisms to study the long-term population dynamics. Based on data of Shevtsova *et al.* (1986) and their own experiments, MacIsaac *et al.* (1991) have already shown that, during their intense feeding activities, the adults of zebra mussels filter a wide variety of planktonic invertebrates, including their own veligers. A negative relationship between the adult population and the recruitment of zebra mussel cohorts to age 1 has been found to be significant in long-term data from the mid-Hudson estuary (Strayer & Malcom 2006). Coherently, here we assume that the veligers' survival is a decreasing function of the total adult density

$$N(t) = \sum_{i=1}^4 n_i(t).$$

As first shown by Ricker (1954) with reference to fish populations, when cannibalism is exerted by adults on their own eggs or juveniles, an exponentially decreasing function of the adult density like

$$\sigma(N) = \sigma_0 \exp[-\beta N(t)]$$

is most appropriate to describe juvenile survivorship. More precisely, in the present case we indicate by σ_E the average fraction of released eggs that during a reproductive period are externally fertilised by males, hatch and reach the veliger stage, and by σ_V the survival, at low adult densities, of veligers from the time of hatching to the adult stage, so that $\sigma_0 = \sigma_E \sigma_V$. The parameter β is a filtration rate accounting for the intensity of veliger removal by adults. More sophis-

ticated assumptions could be made at this point, like, e.g. imagining that the filtration rate of adults differs according to their age, but we did not find reliable data to justify such a differentiation.

It is easy to translate the life cycle features illustrated above into a simple nonlinear mathematical model which takes the following form

$$\begin{aligned} n_1(t+1) &= \sigma_0 \exp[-\beta N(t)] \left[\frac{f_2 n_2(t)}{2} + \frac{f_3 n_3(t)}{2} + \frac{f_4 n_4(t)}{2} \right] \\ n_2(t+1) &= \sigma_1 n_1(t) \\ n_3(t+1) &= \sigma_2 n_2(t) \\ n_4(t+1) &= \sigma_3 n_3(t) + \sigma_4 n_4(t) \end{aligned}$$

where the σ_i values (with $1 \leq i \leq 3$) represent the yearly individual survivorships from age i to age $i+1$, σ_4 the yearly survival within the age class 4+ and the f_i values (with $2 \leq i \leq 4$) are the numbers of eggs released by one adult female of age i . As females do not reproduce during their first year and the sex ratio is typically balanced (Stańczykowska 1977; Thorp *et al.* 1994), the yearly offspring production of the entire population amounts to $[f_2 n_2(t)/2 + f_3 n_3(t)/2 + f_4 n_4(t)/2]$. The ranges of variation of fertilities and survivals in the first three adult age classes can be estimated from available data. Their values are summarised in Table 1. By contrast, empirical evidence (Shevtsova *et al.* 1986; MacIsaac *et al.* 1991; Strayer & Malcom 2006) is still too scarce to allow any statistically significant estimation of β . Furthermore, the values to be attributed to the two remaining parameters $\sigma_0 = \sigma_E \sigma_V$ and σ_4 are much more uncertain than those of the other survival fractions.

As for β , it is easy to see that it does not influence the qualitative dynamics of the model. In fact, let $\tilde{n}_i(t) = \beta n_i(t)$, with $i = 1, \dots, 4$, and $\tilde{N}(t) = \beta N(t)$. The model can then be restated in terms of the new variables with no explicit dependence on β . Technically,

Table 1 Biological ranges for the parameter values of our model for *Dreissena polymorpha* as estimated from field data. The f_i values are expressed in millions.

Parameter	Min–Max	References
σ_1	0.3–1	Wiktor (1963); Annoni <i>et al.</i> (1978);
σ_2	0.2–0.8	Smit <i>et al.</i> (1993)
σ_3	0.1–0.4	
f_2	0.1–0.5	Borcherding (1991); Neumann <i>et al.</i> (1993)
f_3	0.15–0.8	
f_4	0.3–1.7	

β is called a scale parameter because it only determines the order of magnitude of the zebra mussel density. Therefore, in the model analysis we will choose values for β so as to provide realistic values of mussel abundances (measured in ind. m⁻²).

As for σ_0 , it is well known (Stańczykowska 1977; Annoni *et al.* 1978; Sprung 1989, 1993; Bij de Vaate 1991; MacIsaac *et al.* 1991) that just a small proportion of the large number of released eggs are fertilised and settle to become established adults in the subsequent year. Just to give an idea of the orders of magnitude, some researchers (see Stańczykowska 1977, for details) have found that in northern European lakes the mortality from the postveliger stage to the first month of adult life was greater than 99%. Sprung (1989) suggested even higher fractions (like 99.9%). Therefore, σ_0 is highly variable although its maximum value cannot exceed a few percentage points (Annoni *et al.* 1978; Sprung 1989; Bij de Vaate 1991; MacIsaac *et al.* 1991). We will consider values of σ_0 up to 2%.

As for σ_4 (the average probability that a 4+ individual remains alive during 1 year), this can be quite variable as shown by the large variation in recorded lifespans (see above). For example, Annoni *et al.* (1978) found that only 9% of individuals aged 4 years survived to age five in Lake Garda (Italy), where the lifespan does not generally exceed 5–6 years. But σ_4 is obviously smaller in environments where the lifespan is shorter. For this reason, we

constrain our analysis to values of σ_4 no larger than 10%.

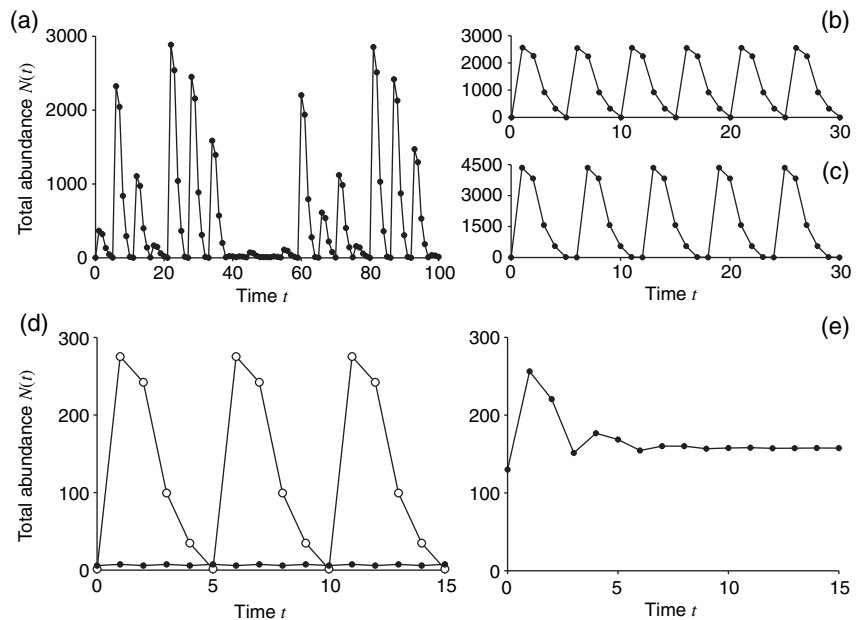
Results

Model dynamics

Fig. 2 shows simulated time series obtained with our model in which parameters have been set to values suggested by Annoni *et al.* (1978). Varying only over three of the model parameters (σ_0 , σ_4 and β), we can qualitatively obtain realistic densities and all the behaviours described in the Introduction and recorded in different freshwater ecosystems (see again Fig. 1). Because of the discontinuous nature of many time series in Fig. 1, it should be emphasised that those data cannot serve the purpose of validating our model in a rigorous sense. However, contrasting the panels in Fig. 2 with those in Fig. 1 shows that the outcomes of the model are more realistic than those obtained via previous demographic models (see, e.g. Fig. 7 in MacIsaac *et al.* 1991 and Fig. 9 in Strayer & Malcom 2006).

First of all, the model can exhibit chaotic dynamics: the zebra mussel time series of panel (a) fluctuates very irregularly, with some years characterised by large population densities shortly followed by remarkable declines. It is interesting to note that the population can remain at low densities for relatively

Fig. 2 Examples of the temporal patterns that can be generated by the model. Abundance $N(t)$ in year t is measured as ind. m⁻². Unless otherwise specified, parameters are set to the values reported by Annoni *et al.* (1978) for Lake Garda (Italy): $f_2 = 0.24 \times 10^6$, $f_3 = 0.465 \times 10^6$, $f_4 = 0.795 \times 10^6$, $\sigma_0 = 0.01$, $\sigma_1 = 0.88$, $\sigma_2 = 0.41$, $\sigma_3 = 0.35$, $\sigma_4 = 0.04$, $\beta = 1$. (a) Chaotic regime; (b) 5-year stable cycle ($\sigma_4 = 0.005$); (c) 6-year stable cycle ($\sigma_0 = 0.015$); (d) bistable periodic behaviour in which a 5-year stable cycle (empty circles) coexists with a 2-year stable cycle (filled circles, $\sigma_0 = 0.005$); (e) damped transient toward equilibrium (see text for details, $\sigma_0 = 0.00001$, $\beta = 0.01$).



long periods (a few decades in our example) before blooming again. Panels (b) and (c) have been obtained for parameter settings where the model predicts a strictly cyclic dynamics with a period of either five (panel b) or 6 years (panel c). Panel (d) in Fig. 2 shows a more complex behaviour: for some parameter settings, the model can indeed display alternative long-term dynamics. In the example, simulations starting from different initial conditions (abundance and age structure at time zero) converge to a 5-year cycle with wide density variations or to a 2-year cycle with tiny fluctuations – namely an almost stationary time series. Situations like this are referred to as ‘bistable behaviours’ in nonlinear dynamical theory (Guckenheimer & Holmes 1983; Strogatz 1994): one attractor or the other is reached in the long-run depending exclusively upon initial conditions. Patterns such as that of Lake Mikolajskie (see Fig. 1c) might thus be explained as a switch from one ecological regime to another because of an unexpected perturbation – for example, a sudden environmental change, a rapid deterioration of feeding conditions or the invasion of some parasite. Catastrophic shifts of this kind are not rare phenomena in either aquatic or terrestrial ecosystems, as well documented in the ecological literature (Holling 1973; May 1976; Scheffer *et al.* 2001; Classen & de Roos 2003; Schröder *et al.* 2005). Finally, for very small values of veliger survival σ_0 , as in panel (e), total population density can also reach an equilibrial value (the so-called ‘stable populations’ cited by Stańczykowska & Lewandowski 1993) after a damped transient, where the overshoot becomes more pronounced when the strength β of density dependence is reduced.

As the model can display a rich variety of behaviours under different parameter settings, it is important to systematically classify them through a *bifurcation analysis* (Kuznetsov 1995). This analysis partitions a biologically relevant parameter space into regions where the functioning modes of the system are qualitatively the same (more technically, the attractors of the system are topologically equivalent). These regions are bounded by the bifurcation curves, namely the geometric loci in parameter space along which the system undergoes a structural change in its functioning. Numerically, such an analysis can be easily performed with specific software packages that implement suitable continuation techniques (Khibnik *et al.* 1993; Doedel & Kernévez 2000; Dhooge *et al.*

2003; Govaerts *et al.* 2005). The two parameters σ_0 , the annual survival of veligers at low adult densities, and σ_4 , the survival of mature individuals in the population, are particularly appropriate for the study, because their values are usually more variable than the others (see above). A simplified synthesis of our numerical investigation is shown in Fig. 3, while a more detailed analysis of the bifurcation structure of the model is reported in the Appendix. It is important to note that the main outcomes of our bifurcation analysis are largely independent of the pair of survival parameters we focus on. This means that the variety of behaviours displayed by our model in parameter space (σ_0, σ_4) are found even if we replace σ_4 with one of the other survival parameters.

For extremely low values of either σ_0 or σ_4 or both – that is the region of the parameter space under the dashed magenta curve in Fig. 3 – model dynamics generally converge towards attractors characterised by low *D. polymorpha* densities (in the order of few tens of zebra mussels per square metre). Actually, in this region there are also attractors characterised by

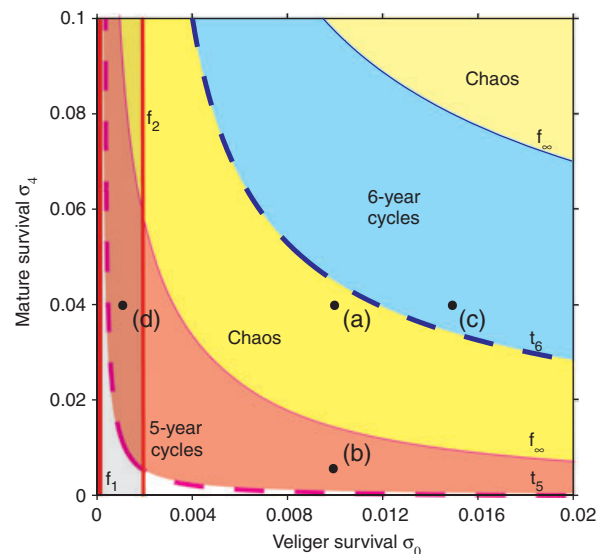


Fig. 3 Simplified bifurcation diagram of our model in the parameter space (σ_0, σ_4) . The stability regions of the 5-year cycle (or its multiples) and 6-year cycle (or its multiples) are coloured orange and cyan, respectively. The yellow colour marks the region of the parameter space where the dynamics is chaotic. The grey-shaded region in between the curves corresponds to a low-density 2-year cycle. Letters in brackets refer to the parametric conditions used to obtain the simulated time series shown in Fig. 2. Parameters other than σ_0 and σ_4 as those for Lake Garda (Fig. 2a). See the Appendix and Fig. A1 for a legend of the bifurcation curves.

higher densities; however, these attractors are not very important from an ecological viewpoint, as the corresponding regions in the parameter space (σ_0, σ_4) are typically very small (see Appendix). By contrast, coloured portions of the parameter space correspond to attractors with average total densities in the order of 1000 ind. m^{-2} and outbreaks as high as 5000 ind. m^{-2} , as found in many field datasets. As the bifurcations originating the high-density attractors do not involve the low-density ones, it is possible to have coexistence of multiple alternative stable modes of behaviour, as already shown in Fig. 2d. To clarify this point, in Fig. 3 we also draw the stability region of the low-density 2-year cycle (the grey-shaded region between curves f_1 and f_2 – see Appendix for details). The intersection between this region and the coloured ones is characterised by bistability. Actually, this represents an underestimation of the bistability region, whose boundaries are difficult to estimate (see Appendix).

Equilibrium population densities can be reached only if veliger survival σ_0 is very low (the tiny region left of f_1). Otherwise, oscillatory behaviours are generated and larger values of σ_0 and of the product $\sigma_0\sigma_4$ (which corresponds to a larger average lifetime of mussels) give rise to larger cycle periods or larger return times of population outbreaks in chaotic regimes. Note that the parametric conditions for which the model predicts time-series qualitatively similar to those shown in Fig. 2 are not exceptional, in the sense that each of the parameter settings used there belongs to a large enough region of the parameter space of Fig. 3. Therefore, we can say that our previously simulated temporal patterns were not fortuitous. In addition, if we assume that the values of survivals σ_0 and σ_4 of most zebra mussel populations are more or less uniformly distributed within the bounds of Fig. 3, we find that the parametric combinations under which the simulated time series are cyclical or chaotic (coloured regions) are the most common. We can thus conclude that the proposed model is quite effective at describing the dynamics of real populations of *D. polymorpha*, in which widely fluctuating densities represent the rule rather than the exception.

Having developed an age-structured model that can realistically mimic the irregular dynamics of *D. polymorpha*, we next investigate if it can be used to predict mussel outbreaks and to study the effects of age-selective predation on mussel bed dynamics.

Prediction

The most important test for the predictive ability of a zebra mussel model is its ability to predict outbreaks. In particular, we would like to forecast the timing and intensity of a forthcoming mussel peak knowing the intensity of the present and/or the previous simulated peaks. If there were no or little stochasticity, such a prediction via the model would be trivial in all circumstances other than chaotic behaviour, which is, however, a very typical regime in both reality and the model. In fact, unpredictability is a typical feature of chaos. Fortunately, it has been shown (e.g. by Rinaldi *et al.* 2001a) that in many cases there exists a simple relationship linking subsequent peaks even in chaotic models or data. This happens to be true for our zebra mussel model, as shown in Fig. 4. The black dots constitute the so-called peak-to-peak plot (PPP, see Rinaldi *et al.* 2001b, for details) of total abundance $N(t)$. It is obtained with the model for parameter values like those of point (a) in Fig. 3, which corresponds to a chaotic temporal pattern. Remember that to obtain a PPP from a generated time series [here the series is that of $N(t)$] it is sufficient to simulate the system over an arbitrarily long-time interval and systematically extract all the local maxima, (i.e. the peaks N_k , with $k = 1, 2, \dots$). Then the PPP is simply the set of points (N_k, N_{k+1}) . As the PPP shown in Fig. 4 has a filiform geometry, we can say that the intensity of

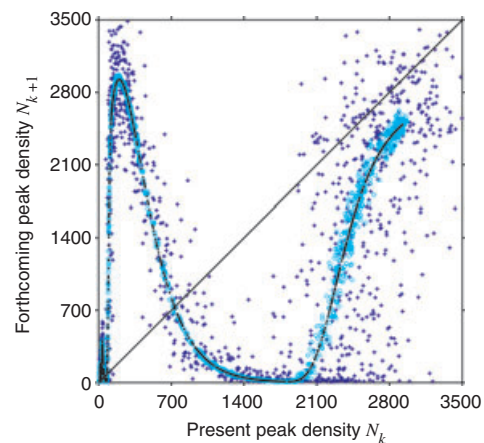


Fig. 4 Peak-to-peak plots (PPP) of zebra mussel abundances as predicted by the model. Black dots: PPP of the deterministic time series in Fig. 2a. Cyan circles: stochastic model with small environmental noise (logvariance $\xi^2 = 0.0001$). Blue crosses: stochastic model with large noise (logvariance $\xi^2 = 0.01$). All parameters as in Fig. 2a.

the forthcoming peak $k + 1$ can be simply predicted from the PPP 'curve' on the basis of the intensity of the present peak k . It is worth noting that the most intense forthcoming outbreaks originate from either small or large present peaks, while intermediate peaks are followed by relatively small zebra mussel booms.

No real population has a behaviour that can be entirely captured by a simple deterministic model. A little stochasticity might break the regular geometry of the PPP, thus destroying the peak-to-peak dynamics. Fortunately, this is not the case for our model. The two other PPPs shown in Fig. 4 are obtained with a stochastic version of the model in which we assume that the yearly survival parameters σ_i ($0 \leq i \leq 4$) are all affected by the same environmental stochasticity with low or high variance. In each of the two cases, the survival parameters are multiplied by a random number extracted from a lognormal distribution with median 1 and logvariance given by either $\xi^2 = 0.0001$ (cyan circles), which corresponds to a coefficient of variation (CV) of about 1%, or $\xi^2 = 0.01$ (blue crosses, CV approximately 10%).

Compared with the deterministic case, although the PPP is no longer filiform in the presence of environmental stochasticity, the qualitative features of the peak-to-peak dynamics are preserved. More general assumptions could be made on how the environmental fluctuations perturb the dynamics of the population. For example, one can imagine that individuals in the planktonic life stage are more prone to unusual seasonal conditions than settled adults. From a modelling viewpoint, this would imply age-differential noise variances (ξ_i^2 , with i being the age class). We have explored this extension of the model (not shown) but found that the scenario depicted in Fig. 4 is substantially unaltered.

The effects of predators on mussel populations

One of the most important sources of *D. polymorpha* mortality caused by natural causes is predation. Fishes in particular are the most active predators of settled mussels (McMahon 1991). In some ecosystems crayfish and waterfowl can also be important molluscivores. For instance, Smit *et al.* (1993) estimated that diving ducks consumed 14–63% of a European dreissenid population during 1 year. The size-dependent nature of predation on mussels is a controversial topic. Some authors found that fishes

prefer small mussels (McMahon 1991; Tucker *et al.* 1996), some showed that they prefer large individuals (Prejs *et al.* 1990), while others reported little (Bartsch *et al.* 2005) or no evidence of fish selectivity (Perry *et al.* 1997). One study (Thorp *et al.* 1998) found that size-selective predation by fishes is significant in the Mississippi River, while it is not in its largest tributary, the Ohio River, thus suggesting that no univocal conclusion can be easily drawn on this matter. The situation is quite similar for waterfowl, because either small (De Leeuw 1999; Werner *et al.* 2005) or large mussels (Draulans 1984; Hamilton *et al.* 1994; MacIsaac 1996; Petrie & Knapton 1999) are preferred in different cases.

The proposed model allows us to explore the consequences of predation on the population dynamics of *D. polymorpha*. The intensity of predators' activity can be incorporated into the model by assuming that the yearly survival of mussels in each class i is reduced by a mortality factor ρ_i . The yearly survival parameters become then

$$\tilde{\sigma}_i(\rho_i) = \sigma_i(1 - \rho_i)$$

with $i = 1, 2, 3, 4$. In order to keep our analysis as general as possible, we study two alternative scenarios describing both non-selective and age (size)-selective predation. In the first case we simply set $\rho_1 = \rho_2 = \rho_3 = \rho_4 = \rho$. In the second we assume that the ρ_i values are linear functions of age, increasing if the preference is for larger mussels or decreasing if small mussels are preferred, i.e.

$$\rho_i = \rho_1 + \frac{\rho_4 - \rho_1}{3}(i - 1)$$

To synthesise the results of the analysis we use two important demographic indicators of zebra mussel abundance in the ecosystem, namely the population density averaged over time, i.e.

$$\bar{N} = \frac{1}{T} \sum_{t=1}^T N(t)$$

and the CV of population density, defined as

$$CV_N = \frac{1}{\bar{N}} \sqrt{\frac{\sum_{t=1}^T [N(t) - \bar{N}]^2}{T}}$$

where T is a sufficiently long time horizon.

As for non-selective predation, panel (a) of Fig. 5 shows the \bar{N} and CV_N as functions of the (constant) additional predation mortality ρ . With increasing

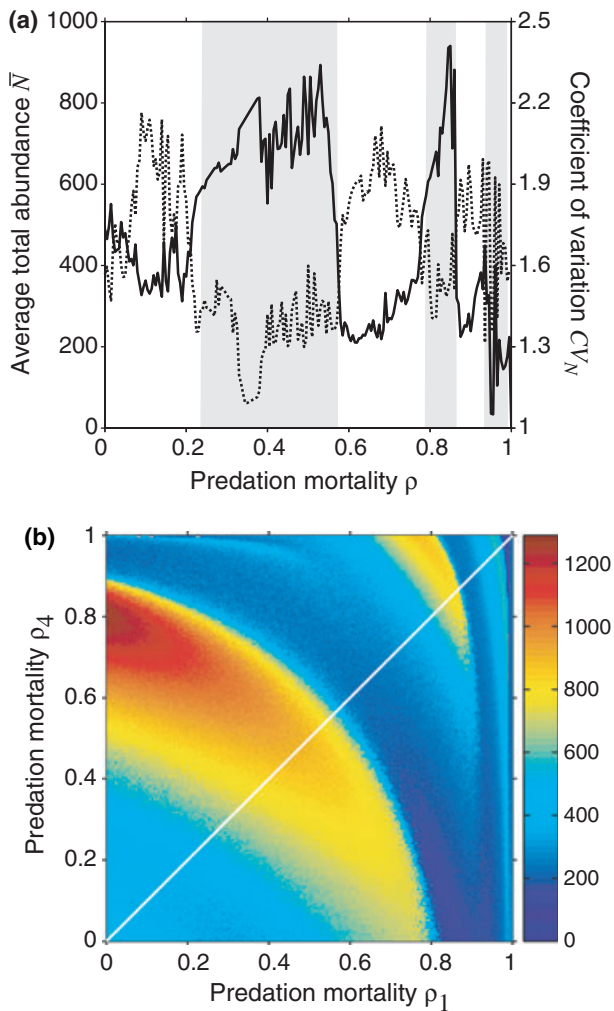


Fig. 5 The effect of predation intensity on zebra mussel population abundance. (a) The mean total abundance (solid line, left axis) and the coefficient of variation (dotted, right axis) as functions of the (constant) intensity of predation ρ are evaluated with the model by averaging the results of 10 simulations (1000 years each) with randomly selected initial conditions. To help the reader in discriminating between irregular and cyclical temporal patterns, we mark with grey vertical strips the parameter intervals where the dynamics is non-chaotic, namely strictly periodic. Here the maximum Lyapunov exponent (MLE) of the model is negative. We evaluated the MLE via standard algorithms (Sprott 2003); (b) the mean total abundance as a function of the survival reductions due to size-selective predation. Results are obtained from the model with environmental stochasticity (noise logvariance $\xi^2 = 0.01$) and predation mortality linearly varying between ρ_1 (mortality in age class 1) and ρ_4 (mortality in age class 4). Ten randomly initialised simulations are averaged for each parameter setting. The two regions separated by the white line – corresponding to the case of non-selective predation – refer to preference for larger (upper triangle) or smaller (lower triangle) mussels, respectively. All unspecified parameters as in Fig. 2a.

adult mortality caused by predation, the nonlinear model is characterised by qualitatively different attractors (remember our Fig. 3), thus exhibiting diversified dynamics, either periodic or chaotic. The periods vary from 5 years (or multiples) for low values of ρ to 3 years (or multiples) for higher ρ . It is important to remark that the average population density does not monotonically decline for increasing values of predation mortality: rather, intermediate values of ρ , giving raise to periodic dynamics, can lead to larger average density. On the other hand, the CV is lower when the dynamics are periodic, meaning that the deviation of population density from its average is less pronounced in regular than in chaotic regimes. It is worth noting that the non-monotonic decline of zebra mussel abundance with increasing levels of predation may represent a serious limitation to control policies based on predatory regulation which have sometimes been invoked in the literature (Tucker *et al.* 1996; Thorp *et al.* 1998).

Even more interesting is the case of age-selective predation. In Fig. 5b we show how the average population density is modified by different predation intensities. As we assume that the ρ_i values are either linearly increasing or decreasing with age, the values of ρ_1 and ρ_4 are sufficient to fully describe size-selective mortality. A point on the 45° line in the parameter space (ρ_1, ρ_4) of Fig. 5b corresponds to the limit case of non-selective predation, while points above (below) such a line correspond to predators preferring larger (smaller) mussels. The distance of a point from the origin of the parameter space (ρ_1, ρ_4) is a measure of the intensity of overall predation mortality. The main result of our analysis is that the variation of mussel density with increasing predation intensities (affecting either smaller or larger individuals) is generally non-monotonic. This counterintuitive feature is observed both with environmental stochasticity (as in Fig. 5b) and without (not shown). It is a generalisation of what we obtained with non-selective predation (solid line of Fig. 5a). More interestingly, if predation is predominantly exerted on larger mussels, the model predicts particularly high values of *D. polymorpha* density.

Although both density and biomass can be used as measures for zebra mussel abundance, they do not convey the same biological information. For instance, Hamilton *et al.* (1994) reported that diving ducks feeding on zebra mussel in Lake Erie had no

measurable impact on mussel population density but reduced mussel biomass by 57% during the period of heaviest feeding. That the temporal regime of biomass can be decoupled from that of density is well known in the literature (see, for instance, Young *et al.* 1996 and Burlakova *et al.* 2006, for a recent discussion) and is caused by the underlying population age structure. A complete analysis of the effects of predators on mussel bed dynamics should be conducted by looking not only at variations in density, but also at those of total biomass.

The total mussel biomass $B(t)$ in our model can be roughly estimated as

$$B(t) = b_1n_1(t) + b_2n_2(t) + b_3n_3(t) + b_4n_4(t)$$

where the parameters $b_1 = 1, b_2 = 10, b_3 = 21, b_4 = 38$ represent the average body masses (fresh weight in mg, shell not included) of *D. polymorpha* individuals in each of the four age classes and have been estimated from data in Annoni *et al.* (1978). Panel (a) of Fig. 6 displays the effect of non-selective predation on the average total biomass

$$\bar{B} = \frac{1}{T} \sum_{t=1}^T B(t)$$

and its CV

$$CV_B = \frac{1}{\bar{B}} \sqrt{\frac{\sum_{t=1}^T [B(t) - \bar{B}]^2}{T}}$$

for the same parameter settings of Fig. 5a. Again, the biomass \bar{B} does not monotonically decrease with intensity of predation and grows when the regime is periodic. Interestingly, though, the range of \bar{B} is much larger than that of \bar{N} . For $\rho \geq 0.55$, i.e. when the mortality induced by predators is higher than 55%, there is a substantial reduction of \bar{B} . The biomass increase corresponding to periodic dynamics is caused by the fact that population density is not evenly distributed within the four age classes. In fact, a peculiar feature of our model is that in many circumstances, even in the absence of predators, one of the age classes predominates over the others each year (see Fig. 6b). The presence of a dominant cohort of individuals in zebra mussel populations is well documented (e.g. see Dorgelo 1993; Strayer & Malcom 2006). It is easy to obtain the time-averaged age structure of the population with the model under different ecological conditions. Panels (c) and (d) show the age structures corresponding to chaotic and

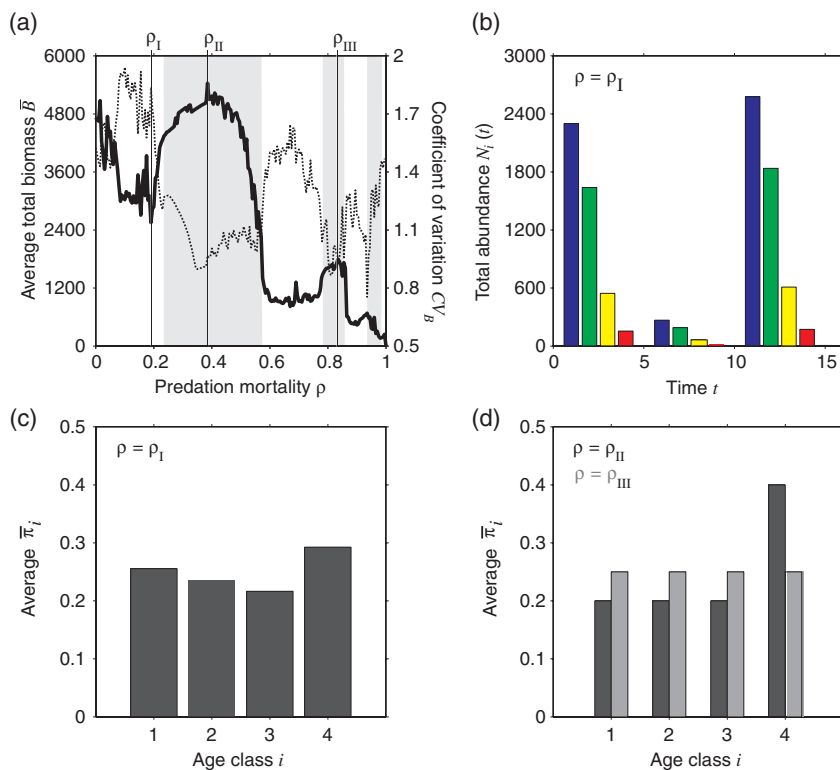


Fig. 6 The effect of constant predation on the zebra mussel population. (a) The average total biomass \bar{B} (solid line, left axis) and the coefficient of variation (dotted, right axis) as functions of the intensity of predation ρ ; (b) the total population density plotted against time to show the presence of a dominant cohort: each year, one single age class is almost completely predominant (approximately 100% of the total population). Blue, green, yellow and red bins indicate the abundance of individuals aging one, two, three and four or more years, respectively. (c) The time-averaged age structure of the population corresponding to $\rho = \rho_I$; (d) the time-averaged age structures of the population corresponding to $\rho = \rho_{II}$ and $\rho = \rho_{III}$. All unspecified parameters as in Fig. 2a.

periodic temporal patterns, respectively. Contrasting the histogram in panel (c) – $\rho = \rho_I = 0.19$, chaotic dynamics – with the dark coloured histogram in panel (d) – $\rho = \rho_{II} = 0.385$, 5-year cycle – reveals that this higher level of predation intensity induces a regime in which mature individuals (4+ years old) are dominant more frequently than with lower predation mortality. The light coloured histogram in panel (d) is obtained for $\rho = \rho_{III}$, where the dynamics are cyclical with a period of 4 years. Although the model predicts comparable population densities for $\rho = \rho_{II}$ and $\rho = \rho_{III}$ (see Fig. 5a), the large difference in underlying age structures (old 4+ mussels are predominant for $\rho = \rho_{II}$) is evidently responsible for the much smaller biomass corresponding to $\rho = \rho_{III}$ (see again Fig. 6a).

It is thus clear that predation can have a strong impact on the age structure of zebra mussel populations. This has been already pointed out in the literature but ascribed to age (size)-dependent predation (Hamilton *et al.* 1994; Thorp *et al.* 1998; Petrie & Knapton 1999). While it is expected that selective predation may alter the age structure of the population, our analysis suggests that even non-selective predators can produce similar results, at least in the long term. Therefore, the analysis of size-frequency distributions alone might not be sufficient to evidence the selectivity of mussel predators.

Discussion

We have proposed a model to understand the possible mechanisms underlying the irregular dynamics of *D. polymorpha* populations at the local scale. The model is extremely simple, being an age-structured dynamical system in discrete time with Ricker-like density dependence. However, the temporal patterns obtained via model simulations under various ecological conditions can be complex and are consistent with empirical evidence. This suggests that the model may be used as a management tool in closed water bodies, such as ponds or lakes. In particular, for those cases where the so-called ‘unstable dynamics’ prevail, we have explored the possibility of predicting the abundance of the next zebra mussel outbreak on the basis of information exclusively concerning the abundance characterizing the last peak. Moreover, we have found that both size- and non-selective predation can significantly alter the dynamics of a zebra mussel population in terms of abundance (density or biomass) and

age structure. Contrary to intuition, increasing levels of predation may actually result in higher abundances of *D. polymorpha*. Thus, mitigation policies based on biological control must be planned with care. Moreover, non-selective predation can result in skewed size–frequency distributions which, therefore, are not necessarily the footprint of the predators’ preference for larger or smaller zebra mussels.

One may wonder whether the results obtained in the present study are robust to changes of model parameters and structure. This is indeed so, as it turns out from a sensitivity analysis of the model. First, by changing survivals and fecundities within the biologically plausible ranges summarised in Table 1, we have obtained outcomes qualitatively similar to those presented above. Secondly, as the choice of considering four age classes may appear somehow limiting, we have studied how the bifurcation structure of the model varies if we consider a different population age structure (i.e. a model with fewer, or more, than four state variables). The regions in parameter space where the model displays cycles or chaos are quite large, even if the number of age classes explicitly taken into account as state variables of the system is not four. Furthermore, as suggested by many *D. polymorpha* time series, the periods of cycles or the return times of peaks in chaotic dynamics turn out to be comparable with the mussels’ lifespan. Thirdly, we have studied the model behaviour under different assumptions concerning the form of the population density dependence at the veliger and postveliger stage. In particular, instead of assuming a Ricker-like exponential form as above, we have repeated the analyses using a generalised Beverton–Holt functional relationship of the form

$$\sigma(N) = \frac{\sigma_0}{[1 + pN(t)]^q}$$

where σ_0 represents the veliger survival, and p and q are two parameters accounting for the intensity of density dependence (Hassell 1975). This is a more flexible description of density dependence (three instead of two parameters). Models incorporating this relation can exhibit periodic or chaotic dynamics if $q > 1$. The bifurcation analysis of the modified model has many similarities with the one discussed above, especially because the ordered fold-flip scenario (see Appendix) to chaos is preserved (there are some more cyclical windows of higher periods, though).

Therefore, despite its simplicity, our model prove to be reliable for understanding the temporal patterns of *D. polymorpha*, predicting its outbreaks and studying the effects of predation. On the other hand, there are two serious limitations to the present approach: (i) our model can be effectively used only if there is a reliable estimate of site-specific model parameters; (ii) the model lacks a spatial dimension. The first limitation could be overcome by suitable statistical methods (Dennis & Taper 1994; Dennis *et al.* 1998) if sufficiently long-time series were available. Unfortunately, this is not usually the case, because local zebra mussel abundances are rarely collected for periods longer than a decade or two. Piccardi (2006) has recently proposed a novel approach based on the symbolic analysis of time series for estimating the parameters of our model. This method seems to be very effective even with very short-time series, as well as other very recent approaches (Corani & Gatto 2007). The second limitation is even more important. To understand the rapid spread of this invasive organism (e.g. in North America) the crucial role of veliger dispersal must be taken into account. However, no spatial mathematical model aimed at explaining the mechanisms generating the observed spatial patterns can even be conceived without a formal description of what happens at the local scale. This justifies the importance of our study. Nevertheless, it is our intention for the future to incorporate the model into a network of water bodies (Rodriguez-Iturbe & Rinaldo 1997; Power & Dietrich 2002) to explore how network topology and zebra mussel population demography at the local scale interact to produce spatio-temporal dynamics.

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Appendix: Bifurcation analysis of the model

Fig. 3 is only a summary of the main dynamical properties of our model. The detailed bifurcation diagram is reported in Fig. A1. Panel (a) is simply a magnification of panel (b) for very small values of veliger survival σ_0 . Along the various curves shown in the panels, the system dynamics undergo structural changes. To better understand how the model behaviour changes for different values of σ_0 and σ_4 , it is convenient to increase both survivals along a straight line starting at the origin of the cartesian planes of Fig. A1 and ending at the opposite corner of the right panel. In this way we can encounter all the bifurcation curves reported in the figure. In what follows, we describe the two main bifurcation sequences involving attractors exhibited by the model. From a graphical viewpoint, they are distinguished in Fig. A1 with the help of colours.

For extremely low values of the parameter σ_0 , on the order of 10^{-5} , the population is doomed to extinction because the reproduction number R_0 , i.e. the number of females generated by one adult female during its entire life, is lower than unity. Under such circumstances, the equilibrium point $\bar{x}_0 = [0, 0, 0, 0]^T$ is the only attractor of the system. As soon as the transcritical bifurcation curve tc is crossed (see the dotted red curve in Fig. A1a), the

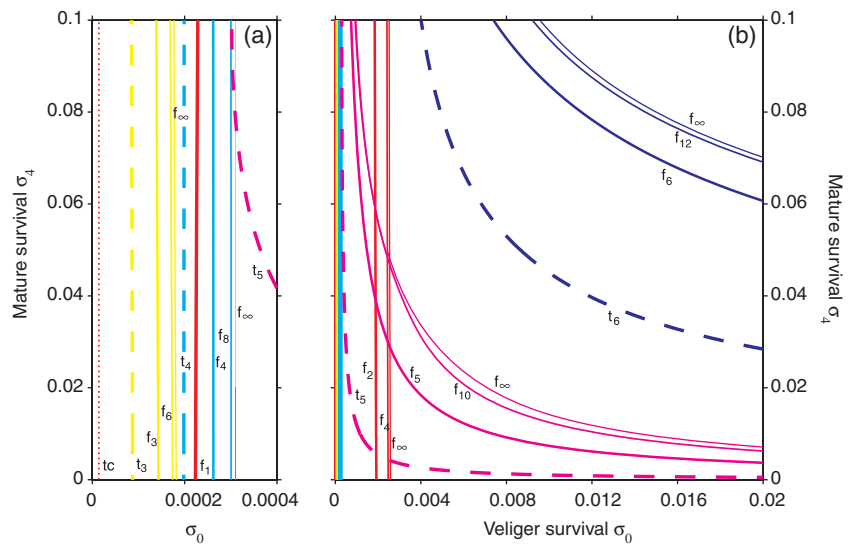


Fig. A1 Local bifurcation structure of the model in the parameter space (σ_0, σ_4). Panel (a) is a magnification of panel (b) for very small values of σ_0 , the veliger survival. Colours are explained in the text. The symbols tc , t and f stay for transcritical, tangent and flip bifurcation, respectively. The subscript to the tangent bifurcation symbols represent the period in years of the shorter cycle involved. The subscripts to the flip bifurcation symbols indicate the period which is doubling. Details on the bifurcation diagram are presented in the text.

zebra mussels can persist at a positive equilibrium \bar{x}_{low} , characterised by positive, yet low, population densities in the four age classes. The curve t_c begins the first of the two bifurcation sequences of the model. The equilibrium \bar{x}_{low} remains stable for further increases of the parameter σ_0 until the flip bifurcation curve f_1 is crossed (see the solid red curve in panel A1a). After having crossed that curve, the equilibrium \bar{x}_{low} becomes unstable and the system is attracted to a cycle with a period of 2 years: each year with 'low' population densities is in fact systematically followed by a year with 'high' densities. The flip bifurcation curve f_1 is simply the first of an infinite sequence of period doubling bifurcations ($f_2, f_4, \dots, f_\infty$) that accumulate one close to the other. In fact, for higher values of σ_0 , the 2-year cycle becomes unstable (along f_2) and the system is attracted to a 4-year cycle, and so on. After the f_∞ flip curve is crossed, i.e. at the end of the so-called Feigenbaum cascade (Feigenbaum 1979), the temporal regime becomes chaotic. For reasons that will be explained in the description of the second bifurcation sequence (see below), the strange attractor originated at f_∞ disappears for larger σ_0 's via a collision with an unstable invariant of the system. Technically, this is not a local bifurcation, which practically means that it is not detectable with software implementing continuation techniques. Therefore, we cannot precisely detect the boundary where the chaotic regime will end.

The second sequence of bifurcation curves that are encountered for increasing σ_0 and σ_4 involves attractors that are far away from the original equilibrium \bar{x}_{low} . The first curve of the yellow series (t_3) is a tangent bifurcation of cycles: on the right of t_3 there exists a couple of 3-year cycles in the state space, only one of them being stable. Note that just to the right of t_3 , the equilibrium \bar{x}_{low} is

still stable. This means that there is bistability and the long-term dynamics of the model is crucially dependent upon initial conditions. A further, significant increase in survivorship σ_0 can cause the 3-year stable cycle to undergo a Feigenbaum cascade (f_3, f_6 , etc.). Therefore, there is another parametric region (to the right of the yellow f_∞ bifurcation curve) where the model behaves chaotically. Moreover, this region is quite small. In fact, after each of the k -th flip bifurcations in the cascade, there exists an attractive cycle of period $2k$ and a repelling cycle of period k . As the sequence is infinite, there is a positive probability that, for a given parameter combination within the region corresponding to chaos, one of the many unstable cycles collides with the strange attractor and destroys it (technically, this phenomenon is termed *crisis*). Most probably, a crisis is exactly what happens along the cyan bifurcation curve t_4 , where an attractive 4-year cycle arises together with its unstable counterpart in coincidence with the disappearance of the chaotic regime. The sequence of bifurcations involving the 3-year cycle we have just described repeats with the very same structure for the 4-year cycle which undergoes a Feigenbaum cascade. An almost identical bifurcation structure repeats for a 5-year cycle (see the magenta series of curves), then for a 6-year cycle (blue series) and beyond (the 7-, 8- and 9-year structures occur for too high values of σ_0 and are not shown). A bifurcation scheme similar to that of our model has been formerly (but not formally) discussed in the literature by Higgins *et al.* (1997) and Gao & Chen (2005).

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