

When will the zebra mussel reach Florence? A model for the spread of *Dreissena polymorpha* in the Arno water system (Italy)

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ABSTRACT

The zebra mussel (*Dreissena polymorpha*) is a freshwater bivalve that has caused dramatic ecological and economic impacts worldwide in past decades. Its success as ecosystem invader is mainly due to the species ability of spreading along rivers, together with the extremely high population densities that can be reached by local populations. Here we propose a spatially explicit model aimed at describing the population dynamics of mussel colonies in rivers represented as oriented graphs. We specifically apply the model to the Bilancino-Sieve-Arno water system (Tuscany, Italy), where *D. polymorpha* has been recently sighted. The model accounts for local-scale demographic processes and along-stream transport mechanisms. Because of the different temporal scales involved, we couple continuous- and discrete-time dynamics. Our model produces spatiotemporal scenarios of invasion that present several distinctive features of the zebra mussel invasion patterns observed in nature, including the spatial patchiness and the temporal irregularity of local populations, and the so-called domino effect. The application of our model to the Arno case study shows that *D. polymorpha* could severely threaten the city of Florence within a few years. Control measures aimed at limiting the impact of the species can significantly alter the ecological and environmental parameters. We find that such variations may profoundly impact spatiotemporal invasion patterns, possibly with counter-intuitive effects. For instance, reduced larval input from Lake Bilancino can in some cases produce higher mussel densities in downstream colonies. Therefore, the control of *D. polymorpha* must be planned with care in order to prevent unwelcome outcomes. Copyright © 2009 John Wiley & Sons, Ltd.

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INTRODUCTION

The zebra mussel (*Dreissena polymorpha*, Pallas) is a freshwater bivalve native to Eurasia and nowadays distributed all over Europe and North America. Because of its high fecundity and ability to settle on almost any solid substratum, *D. polymorpha* usually outcompetes resident mussel species (Ricciardi *et al.*, 1996), causes reductions of phytoplankton (Bastviken *et al.*, 1998) and zooplankton abundances (Garton and Haag, 1993), modifies the nutrient cycle (Arnott and Vanni, 1996), causes severe damages to waterworks (Jenner and Janssen-Mommen, 1993) and produces negative effects on tourism (Charles and Dukes, 2007). Such impacts are mainly due to the extremely high population densities (up to 700 000 mussels m⁻², Griffiths *et al.*, 1991) that can be reached by zebra mussel colonies, which can also display irregular demographic dynamics (Ramcharan *et al.*, 1992b; Stańczykowska and Lewandowski, 1993). Zebra mussel invasions are therefore seen as dangerous events not only because of the dramatic ecological implications at

the ecosystem level (MacIsaac, 1996), but also because the species represents a major economic threat. In fact, *D. polymorpha* has been recently estimated to cost at least \$1 billion per year in damages and associated control measures in the United States only (Pimentel *et al.*, 2005).

Recent records of zebra mussel invasions show that the progression of the species along rivers can be remarkably fast. In fact, while the invasion and establishment of *D. polymorpha* in large regions of Europe occurred at reasonable speeds centuries ago (Karatayev *et al.*, 1997), the relatively recent spread in North America has been impressive. Introduced in the Great Lakes region (Michigan), where it was first sighted in 1988 (McMahon, 1999), *D. polymorpha* reached Louisiana along the Mississippi River in 1993. Nowadays, the species is present in much of Central and Eastern USA (Minchin *et al.*, 2002). The rapidity of spread has deeply limited the applicability of actions aimed at preventing the establishment of the species and made the introduction of potential control measures a scramble. Similar speeds have also been recorded in all the recent cases of Dreissenidae invasions, both in the USA (Colorado River, Stokstad, 2007) and in Europe (Ebro River, Spain, Araujo and Álvarez, 2001).

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The success of the zebra mussel as ecosystem invader can be attributed to its adaptability to a wide range of environmental conditions, as well as to the fact that its larvae (also called veligers) can be transported by the water flow. Long-distance dispersal events of both natural and anthropic origin (e.g. veligers may be carried by waterfowls or shipped in boat ballast water) may also play an important role in the spread of the species at the basin scale (Carlton, 1993; Johnson and Carlton, 1996; Buchan and Padilla, 1999).

For all the above-mentioned reasons, the recent sighting of zebra mussel specimens in Lake Bilancino (Tuscany, Italy), an artificial water body with a surface area of about 5 km² connected to the Arno River through the Sieve River, caused considerable concern about the possible arrival of *D. polymorpha* in the Florence area (Lori and Cionfanelli, 2006). Understanding zebra mussel invasions is a complex task, which requires the analysis of processes involving multiple spatial and temporal scales (Johnson and Padilla, 1996). In this work we propose a model for the spread of *D. polymorpha* on a simple river described as an oriented graph and specifically apply it to the Bilancino-Sieve-Arno water system. The model couples long-term demographic dynamics at the local scale with short-term along-stream dispersal processes. From a technical viewpoint, we thus derive a spatially structured model that links discrete- and continuous-time dynamics (hybrid model, see Pachepsky *et al.* 2008 for ecological applications).

Studies on the spatial spread of *D. polymorpha* have already been proposed in the literature, but they have typically focused on evaluating the habitat suitability for the bivalve (Ramcharan *et al.*, 1992b; Mellina and Rasmussen, 1994; Allen and Ramcharan, 2001). Very few works have investigated the population dynamics of the zebra mussel in general, and little has been done to our best knowledge to modelling its natural diffusion along rivers, except for specific stages of the species life cycle (Stoeckel *et al.*, 1997) or small spatial scales (Morales *et al.*, 2006). On the other hand, there is a well-established tradition in the analysis of reaction–diffusion fronts along rivers intended as ecological corridors (e.g. Méndez *et al.*, 2004; Pachepsky *et al.*, 2005; Campos *et al.*, 2006; Bertuzzo *et al.*, 2007). However, all these studies were not tailored on specific target species, thus somehow lacking of an accurate description of possibly important demographic processes. Here we relax the hypothesis of continuous-time logistic population growth often used in the literature (e.g. Campos *et al.*, 2006; Bertuzzo *et al.*, 2007) and introduce a detailed mathematical formalization of the species life cycle, which includes a temporal separation of time scales and complex demographic dynamics at the local scale.

The paper is organized as follows. In the next section we provide an in-depth description of our model; then, we apply the model to the Arno case study and describe the outcomes of several model simulations obtained according to different ecological scenarios; finally, we discuss

how the sensitivity analysis of the model outcomes can give some hints to designing control measures aimed at contrasting the impacts due to *D. polymorpha* in the water system under study.

THE MODEL

The life cycle of *D. polymorpha* presents some characteristics (most notably, the existence of a larval stage) that make it unique among freshwater bivalves (Sprung, 1993). The life of zebra mussel individuals can be roughly subdivided into three main periods: the larval, juvenile and adult stages (Garton and Haag, 1993). The juvenile stage begins after settlement and ends when mussels become sexually mature and reproduce, typically during their first or second year of age (in North America and Europe, respectively), generating a huge number of propagules (Mackie and Schloesser, 1996). Adult mussels are sessile (i.e. they are permanently anchored to a solid substratum) and can live for several years (from 2 to 8 years depending upon place and environmental conditions, (Karateyev *et al.*, 2006)). On the contrary, larvae are planktonic. The larval stage is rather short, lasting from a few days to a few weeks (Sprung, 1993) during which veligers can be transported by the water flow. Since the variability associated with the duration of the veliger stage is high, a sensitivity analysis would be of great interest and importance.

As a result, a model for the spread of *D. polymorpha* along rivers must couple demographic processes with hydrological phenomena. It also specifically requires the study of processes that take place at both the local scale (such as adult establishment and reproduction) and along stream (such as larval transport), as well as of phenomena occurring on long versus short time scales (e.g. inter-annual adult survival vs veliger survival to transport and predation). Remarkably, very few works (MacIsaac *et al.*, 1991; Strayer and Malcom, 2006; Casagrandi *et al.*, 2007) have been devoted even to the study of the local dynamics of *D. polymorpha* populations, which however represents a key factor for understanding the spread of the species, together with a formal description of larval transport. Here, we start from the local demographic model proposed by Casagrandi *et al.* (2007), that is a nonlinear discrete-time model with density dependence and age structure, and extend it to introduce along-stream larval transport.

Local-scale dynamics

We model the demography of each local population in the river according to the Casagrandi *et al.*'s (2007) model. Let $n_k(x, t)$ (no. of mussels m⁻²) be the density of mussels (either juveniles, $k = 1$, or reproductive adults, $2 \leq k \leq 4$) in age class k . Then, the inter-annual dynamics linking the abundance of mussels anchored at location x in year t to that of year $t + 1$ is described by the following system of difference

equations:

$$\begin{aligned} n_1(x, t + 1) &= \sigma_v v_s(x, t) \\ n_2(x, t + 1) &= \sigma_1 n_1(x, t) \\ n_3(x, t + 1) &= \sigma_2 n_2(x, t) \\ n_4(x, t + 1) &= \sigma_3 n_3(x, t) + \sigma_4 n_4(x, t) \end{aligned} \quad (1)$$

in which $v_s(x, t)$ (no. of veligers m^{-2}) is the density of settling veligers, σ_v the probability of survival from veliger to juvenile and the σ_k s (with $1 \leq k \leq 3$) the yearly individual survivorships from stage k to stage $k + 1$. Note that n_4 represents the density of adults that are at least four-years-old, therefore σ_4 is the probability of yearly survival within the 4th age class. The total density of settled mussels is defined as

$$N(x, t) = \sum_{k=1}^4 n_k(x, t)$$

As for the larval life stage, the initial abundance of larvae released during reproduction can be computed as

$$v_0(x, t) = \frac{1}{2} \sum_{k=1}^4 f_k n_k(x, t)$$

where the f_k s (with $1 \leq k \leq 4$) are the batch fecundities (no. of released eggs per adult female) of the k th age class and the factor $1/2$ translates the fact that the sex ratio of *D. polymorpha* populations is typically balanced (Stańczykowska, 1997).

Along-stream dynamics

The local abundance of settling veligers $v_s(x, t)$ is the result of within-year processes, namely larval dispersal and mortality. In particular, the mortality of veligers can depend on predation by feeding adult mussels (density-dependent cannibalism) as well as on other natural causes not related to the presence and abundance of the population itself (MacIsaac *et al.*, 1991; see also Strayer and Malcom 2006; Casagrandi *et al.*, 2007). As for dispersal, we assume that larvae are mainly transported by water flow. However, the presence of vectors other than hydrological transport can be accounted for in the modelling framework.

From a formal viewpoint, all these within-year processes can be described by means of a partial differential equation (PDE) containing advective and diffusive terms (larval transport), along with reactive processes (larval mortality). Let $v(x, t, \tau)$ be the abundance of τ -day-old veligers that are in the water column at spatial location x during the reproductive event that characterizes year t . The abundance $v_s(x, t) = v(x, t, \tau_s)$ of settling larvae at the end of the τ_s -day-long dispersal period can thus be computed by solving the following PDE:

$$\begin{aligned} \frac{\partial v(x, t, \tau)}{\partial \tau} &= -\nabla \cdot [u(x, t, \tau)v(x, t, \tau)] \\ &+ \nabla \cdot \{\delta(x, t, \tau) [\nabla \cdot v(x, t, \tau)]\} \\ &- [\mu + \gamma N(x, t)] v(x, t, \tau) + i(x, t, \tau) \end{aligned} \quad (2)$$

where ∇ is the spatial derivative operator, $u(x, t, \tau)$ (km day^{-1}) and $\delta(x, t, \tau)$ ($\text{km}^2 \text{ day}^{-1}$) represent the mean velocity and the diffusion coefficient of the water flow, respectively, γ ($\text{day}^{-1} \text{ mussels}^{-1} \text{ km}^2$) and μ [day^{-1}] correspond to the mortality rates due to either cannibalism or other causes, and $i(x, t, \tau)$ (veligers $\text{m}^{-2} \text{ day}^{-1}$) is an external flux of veligers (possibly accounting for vectors of spread other than the river flow). Equation (2) must be solved over the time span $[0, \tau_s]$ with the initial condition $v(x, t, 0) = v_0(x, t)$ and suitable boundary conditions.

As a consequence of the peculiarity of the life cycle of *D. polymorpha*, the resulting spatially explicit model (1–2) includes both discrete- and continuous-time processes. Hybrid models of this kind are quite uncommon in ecology and generally referred to as semi-discrete in the relevant literature (see Pachepsky *et al.*, 2008). Notice that if transport processes were not taken into account ($u = 0$ and $\delta = 0$) and there were no larval input ($i = 0$), model (1–2) would exactly reduce to the local discrete-time demographic model proposed by Casagrandi *et al.*, (2007). In fact, under these assumptions, the solution of Equation (2) can be explicitly computed as

$$v_s(x, t) = v_0(x, t) e^{-[\mu + \gamma N(x, t)] \tau_s}$$

which corresponds to the Ricker's (1954) density-dependent form used in Casagrandi *et al.*, (2007) to describe veliger mortality. Such model displays a rich variety of complex and realistic demographic dynamics depending upon parameter values. Interestingly, the local model predicts that non-stationary dynamics (either periodic or chaotic) are the most common, as usually recorded in the field (see the relevant discussion in Casagrandi *et al.*, 2007). We also remark that the duration τ_s of the veliger stage is a crucial parameter in the determination of *D. polymorpha* demographic dynamics, since it contributes to defining the finite growth rate of the population.

Spatial discretization

Rivers can be usefully represented as oriented graphs (Rodríguez-Iturbe and Rinaldo, 1997). On the one hand, in fact, the large spatial scale over which rivers do usually stretch pushes the use of a spatially discrete approach over a spatially continuous one for computational reasons. On the other hand, freshwater species are not expected to colonize the ecosystem in a spatially homogeneous way. In fact, they are more likely to inhabit those locations in the river in which environmental conditions are more suitable for their survival. As an example, zebra mussel larvae need a solid substratum and relatively slow water currents to settle (i.e. less than $1.5\text{--}2.5 \text{ m s}^{-1}$, MacIsaac, 1996). Therefore, a spatially discrete approach is fostered also from an ecological perspective.

In order to apply the model (1–2) to a stream described as an oriented graph, all variables have thus to be suitably discretized over space. From a technical perspective, this task is straightforward for the discrete-time component of the model, since it simply requires the introduction of a

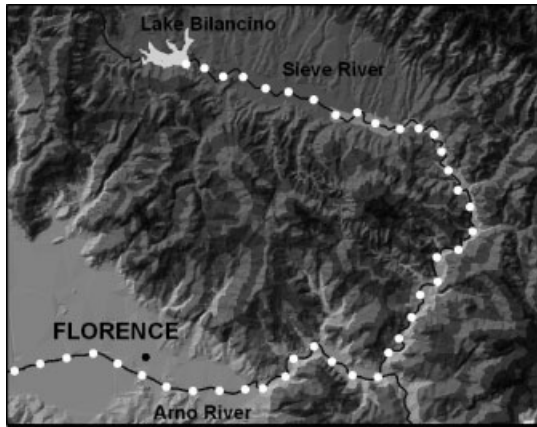


Figure 1. Study area. GIS data have been extracted from the SIRA database (see text). White dots represent the nodes of the graph used to discretize the river in numerical simulations.

replica of Equations (1) for each node j in the graph. On the contrary, the spatial discretization of the continuous-time processes described by Equation (2) needs more advanced numerical techniques, since larval transport must be evaluated along the entire river stream. For the case system under study, we describe the Bilancino-Sieve-Arno water system as a one-dimensional piecewise lattice of nodes consisting of the Sieve River and the branch of the Arno River downstream of the Pontassieve confluence, with Lake Bilancino acting as a larval source term on the first node of the graph (Figure 1). Although our assumption can in general represent an oversimplification, because hydrological networks do typically display fractal topologies (Rodríguez-Iturbe and Rinaldo, 1997), it is usually acceptable for small basins and has already been used to model the Arno River (Marsilli-Libelli and Giusti, 2008).

If the river reach is described as a one-dimensional lattice of nodes, Equation (2) can be discretized and numerically solved by means of standard numerical methods. Specifically, we use the so-called method of lines (Chapter 1 in Wouwer *et al.*, 2001), which consists in two steps. First, spatial derivatives are approximated by means of suitable discretization techniques (e.g. finite differences), thus deriving a system of K ordinary differential equations (ODEs), each of which describes the temporal evolution of the solution of the PDE in a given node j of the computational domain ($j = 1, 2, \dots, K$). Second, the resulting system has to be integrated with standard algorithms for (stiff) ODEs. As for the spatial discretization, we simply apply a first-order upwind method and a centred stencil to resolve the advective and the diffusive components of movement, respectively. In this way, each node in the oriented graph is connected to its two nearest neighbours. The resulting system of ODEs reads as follows:

$$\frac{dv(j, t, \tau)}{d\tau} = 1/h [u(j - 1/2, t, \tau)v(j - 1, t, \tau) - u(j - 1/2, t, \tau)v(j, t, \tau)] + 1/h^2 \{ \delta(j - 1/2, t, \tau)$$

$$\times [v(j - 1, t, \tau) - v(j, t, \tau)] + \delta(j + 1/2, t, \tau) \times [v(j + 1, t, \tau) - v(j, t, \tau)] \} - [\mu + \gamma N(j, t)] v(j, t, \tau) + i(j, t, \tau) \quad (3)$$

where $j = 1, 2, \dots, K$ is the node index and h [km] is the (constant) distance between two neighbouring nodes. Fractional values of the node index represent (linear) interpolation of the values assumed by stream velocity u and diffusion coefficient δ between two adjacent nodes. In case of variable coefficients, in fact, interpolation is needed to preserve the consistency of the numerical scheme (further details in Strikwerda, 1989). System (3) is to be integrated over the timespan $(0, \tau_s)$ with initial condition $v(j, t, 0) = v_0(j, t) = 1/2 \sum_{k=1}^4 f_k n_k(j, t)$ and suitable boundary conditions.

The Bilancino-Sieve-Arno water system

To analyse the spread of *D. polymorpha* in the Bilancino-Sieve-Arno water system, the model (1–2) should be parameterized according to field data collected in the area under study. Unfortunately, demographic data concerning zebra mussel populations in the Bilancino-Sieve-Arno water system are not yet available at present, because the sighting of the species in the area is very recent (see Introduction). However, the absence of data is somehow fortunate in this case, because it implies that the Bilancino-Sieve-Arno water system has not yet been invaded. Therefore, we have to rely on demographic parameters drawn from the literature. In particular, larval (σ_v) and adult survival probabilities ($\sigma_k, 1 \leq k \leq 4$), fecundities ($f_k, 1 \leq k \leq 4$) and the cannibalism rate (γ) are set as in Casagrandi *et al.*, (2007), while the natural mortality rate (μ) has been estimated from Schneider *et al.*, (2003) and Stoeckel *et al.*, (2004a). As for the duration of the larval period (τ_s), the average datum is accompanied by relatively large standard deviation (Sprung, 1993). However, by varying the value attributed to τ_s , the local-scale dynamics can change from a qualitative perspective. Therefore, from now on we develop our analysis under two possible scenarios, respectively characterized either by a low value of τ_s (which induces low veliger mortality, thus resulting in chaotic local dynamics) or by a higher value of τ_s (which produces higher larval mortality and, in turn, periodic local dynamics).

The advantage of our approach is that we can parameterize the model (1–2) at a finer spatial scale compared to spatially implicit modelling. In particular, the survival parameters of *D. polymorpha* do crucially depend upon environmental factors such as water temperature (Baker *et al.*, 1993; McMahan, 1996; Griebeler and Seitz, 2007), calcium concentration (Mellina and Rasmussen, 1994; Hinks and Mackie, 1997; Allen and Ramcharan, 2001; Whittier *et al.*, 2008) and pH (Hinks and Mackie, 1997; Bowman and Bailey, 1998). These parameters have already been used to build non-dynamical, multivariate models aimed at assessing the potential spread of the zebra mussel (Strayer, 1990; Neary and Leach, 1992; Ramcharan *et al.*, 1992a,b).

Data available in the SIRA Geographic Information System (Sistema Informativo Regionale Ambientale, <http://sira.arpat.toscana.it/sira/>) managed by ARPAT (Agenzia Regionale Protezione Ambientale Toscana) show that in the Bilancino-Sieve-Arno system both water temperature and calcium concentration are well within the optimal ranges for the survival of *D. polymorpha*. In contrast, the high pH values registered in the Sieve River can affect adult survival. Therefore, the survival parameters σ_k ($1 \leq k \leq 4$) in the nodes along the Sieve River have to be decreased by 50%, in line with the findings by Hinks and Mackie (1997).

The hydrological parameters u and δ (see again Equation 2) and the lattice structure can be derived from the SIRA database as well. The analysis of the available data shows that two different mean current velocities and diffusion coefficients characterize the Sieve (u_S and δ_S) and the Arno (u_A and δ_A) Rivers, respectively. At the confluence, Equation (3) must be suitably modified in order to guarantee mass conservation. Spatial resolution h is chosen to ensure the stability of the numerical scheme as well as to enhance computational efficiency. According to the physics of our problem, we apply absorbing boundary conditions at the terminal nodes of the graph.

RESULTS

We use the model (1–2) to explore different scenarios characterized by different local mussel demographic dynamics and different assumptions on larval input from Lake Bilancino. We start by describing the outcomes of model simulations in the case of a single release of larvae from Lake Bilancino concentrated in time. Then, we consider the more realistic case in which a resident mussel population is present in the upstream artificial reservoir, so that larvae can be continuously released downstream. We also perform a sensitivity analysis of the model outcomes with respect to some important ecological parameters and discuss the implications for the city of Florence.

Accidental larval release from Lake Bilancino

We first explore what would happen if there was an accidental introduction of veligers from Lake Bilancino in the downstream water system in the absence of pre-existing colonies. From a technical standpoint, this is equivalent to assuming that larval input i at the first node of the graph is impulsive in time. The resulting spatiotemporal pattern of mussel density in case of chaotic (periodic) demographic dynamics is displayed in Figure 2A (Figure 2C), while the local pattern of mussel abundance in Florence (which obviously represents our focal city) is reported in Figure 2B (Figure 2D). Left panels of Figure 2 show that zebra mussels tend to clusterize into patches with high population densities. This peculiar phenomenon predicted by the model has already been recorded in other riverine *D. polymorpha* populations (Stoeckel *et al.*, 1997). We remark that the higher densities found under chaotic

regime are due to the fact that survival parameters are larger in the chaotic than in the periodic scenario.

Figure 2 also shows that temporal patterns of local population densities are expected to be rather irregular, with recurrent demographic explosions, as found in most field records (see Introduction). This result holds in case of both chaotic and periodic local demographic dynamics (Figure 2A and C). The city of Florence is not exceptional in terms of irregular fluctuations of local mussel densities. In particular, we notice that in the case of periodic local dynamics the density of mussels in Florence undergoes an irregular transient pattern of demographic fluctuations, eventually vanishing in the long run (Figure 2D). Under chaotic local demography, irregular fluctuations do not vanish in the long run, yet mean population densities become remarkably lower than in the first decades of the invasion (Figure 2C).

An accidental shedding of larvae from Lake Bilancino is thus sufficient to trigger the invasion of both the Sieve and the Arno Rivers. However, after a transient demographic explosion, in the absence of further external inputs of larvae, the density of local mussel colonies eventually vanishes (with periodic local dynamics) or settles on rather low values (under chaotic regime). The rapidity of this clearing process depends on the geographic position of the colony in the water system, being remarkably lower in the downstream reach. This is indeed what the model predicts for the city of Florence, where zebra mussels are expected to persist for decades at high densities. In fact, the establishment of local populations of adult zebra mussels in riverine systems does crucially depend on the settlement of larvae produced upstream. Due to dispersal and predation, just a very small fraction of veligers is recruited as settling juveniles in the node where they were produced (self-recruitment), while most settling veligers come from upstream colonies. As a consequence, the persistence of downstream colonies positively correlates to the distance from the starting point of the invasion. This complex spatiotemporal pattern of population densities, which has been named domino effect in the relevant literature (Stoeckel *et al.*, 2004b), is thus due to the interplay between local population dynamics and along-stream transport processes.

Continuous larval release

We consider now the scenario in which a resident mussel colony persists in Lake Bilancino and each year releases veligers into the river system during the reproductive season. We assume that lacustrine and riverine colonies are characterized by the same local dynamics. Therefore, we use a consistent pattern of veliger release from Lake Bilancino according to the chaotic/periodic demography in each node of the graph used to describe the river. The two model simulations displayed in Figure 3 show that under such hypotheses the Sieve and the Arno Rivers remain permanently infested (possibly with high population densities) in both demographic scenarios. Left

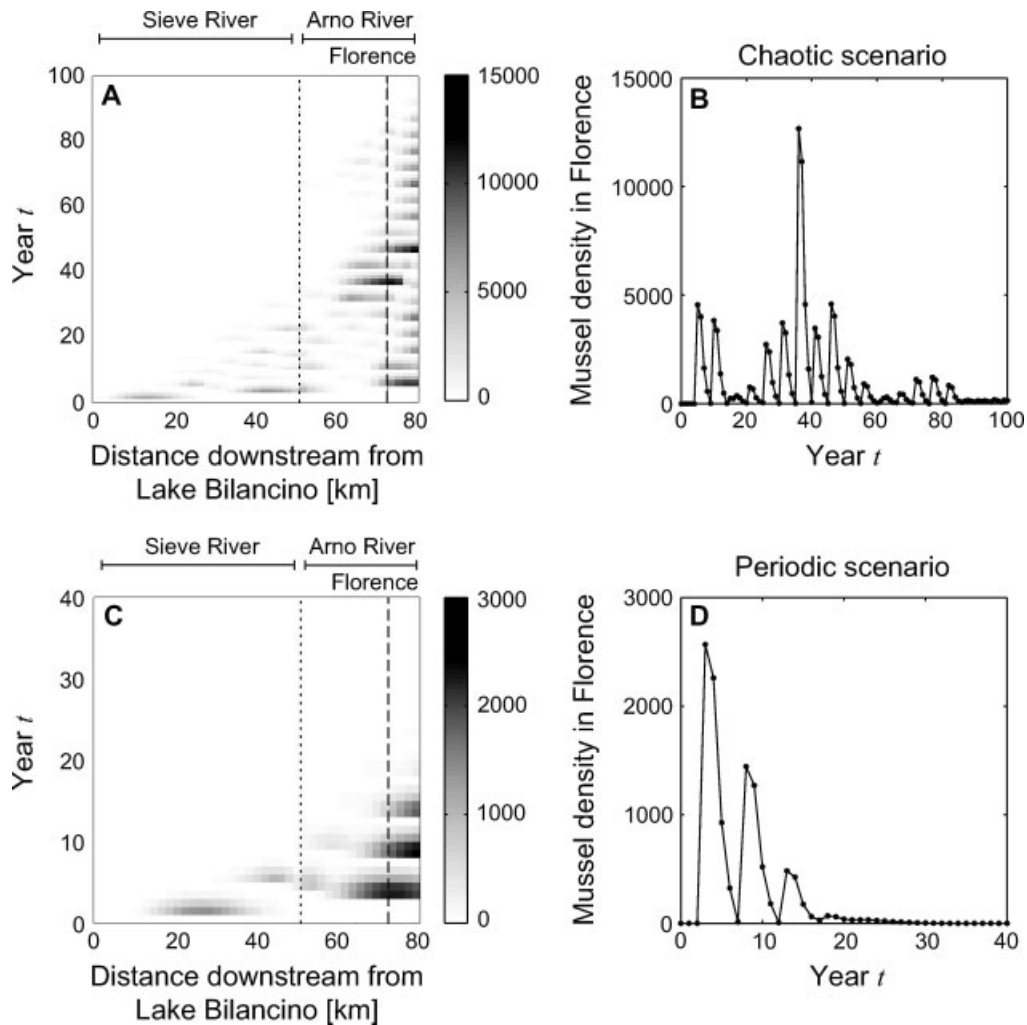


Figure 2. Simulation of model (1–2) with accidental larval release from Lake Bilancino in case of chaotic (top panels) or periodic (bottom panels) demographic dynamics. Panels A and C display the spatiotemporal patterns of mussel density (mussels m^{-2}). Different grey shadings correspond to different population densities. The dotted and the dashed lines mark the position of the nodes identifying the confluence between the Sieve and the Arno Rivers at Pontassieve and the city of Florence, respectively. Panels B and D display the local density of adult mussel in Florence as a function of time. Biological parameters: $\sigma_v = 0.02$, $\sigma_1 = 0.88$, $\sigma_2 = 0.41$, $\sigma_3 = 0.35$, $\sigma_4 = 0.04$, $f_1 = 0$, $f_2 = 0.240 \cdot 10^6$, $f_3 = 0.465 \cdot 10^6$, $f_4 = 0.795 \cdot 10^6$, $\tau_s = 7$ (day) (panels A and B, chaotic dynamics) or $\tau_s = 14$ (panels C and D, periodic dynamics), $\mu = 0.15$ (day^{-1}), $\gamma = 0.01$ (day^{-1} mussels $^{-1}$ km^2). Survival parameters σ_{kS} ($1 \leq k \leq 4$) have been decreased by 50% along the Sieve River to account for survival reduction due to suboptimal pH level (see text). Hydrological parameters: $u_S = 60.5$ (km day^{-1}), $u_A = 40.6$ (km day^{-1}), $\delta_S = 1.56$ (km^2 day^{-1}), $\delta_A = 2.16$ (km^2 day^{-1}), $h = 2$ (km). Larval input: $i(j, t, \tau) = 0 \quad \forall j, t, \tau$, except for $i(1, 1, 0) = 10^7$ (veligers m^{-2}). Absorbing boundary conditions have been applied to the extremes of the graph.

panels of Figure 3 also evidence that the most critical areas are located downstream of Lake Bilancino and of the Sieve-Arno confluence at Pontassieve, in particular in the Florence area (panels A and C). Specifically, the city of Florence is characterized by recurrent demographic explosions with remarkable mean and peak population densities (panels B and D). Annual inputs of veligers in the upstream area of the river (specifically in correspondence to Lake Bilancino) can thus actually promote the long-term persistence of *D. polymorpha* in the river at high population densities, as envisaged by Stoeckel *et al.* (2004b). This also suggests that Lake Bilancino plays a crucial role in determining spatiotemporal invasion patterns.

In order to have a better perception of the scenarios portrayed by our model for the Arno River system, we can usefully display some of the spatiotemporal outcomes

described in Figure 3 in a geographical layout. Figure 4 presents three snapshots of the invasion pattern obtained in the case of chaotic local demography. In particular, panel A shows the colonization of the Sieve River 4 years after the beginning of the invasion from Lake Bilancino ($t = 4$), while panel B represents the first population outbreak in the city of Florence ($t = 6$) and panel C emphasizes the largest demographic explosion that is expected in the Florence area at $t = 11$. According to our simulations, the density of mussels at that time could peak up to about 24 000 mussels per square meters. Such impressive density would of course produce severe impacts in the area.

Apart from the transient invasion wave, it is particularly interesting to analyse the long-term colonization of the Arno water system. More precisely, we evaluate the temporal variation of the total mussel density $N(x, t)$

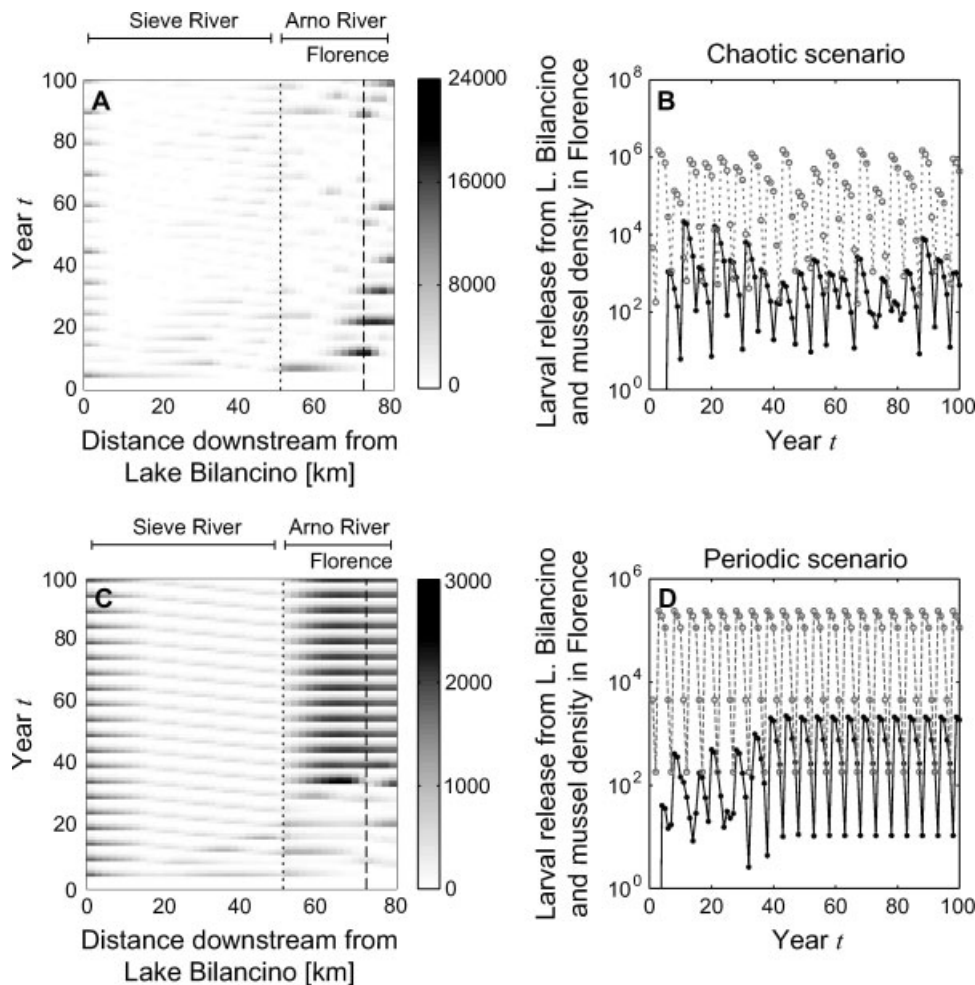


Figure 3. Simulation of model (1–2) with sustained larval release from Lake Bilancino. Panels A and C as in Figure 2. Panels B and D display in grey the daily amount of veligers released from Lake Bilancino during the dispersal season (veligers $\text{m}^{-2} \text{day}^{-1}$) and in black the local density of adult mussel in Florence (mussels m^{-2}) as functions of time. Biological and hydrological parameters as in Figure 2. Larval input: $i(j, t, \tau) = 0 \quad \forall j, t, \tau$ except for $j = 1$ in which $i(1, t, \tau)$ ($1 \leq t \leq 100$, $0 \leq \tau \leq \tau_s$) corresponds to the daily veliger input from Lake Bilancino displayed in right panels.

in each location x of the river over a 100-year timespan. The time-averaged values are plotted in Figure 5 for both the chaotic (panel A) and the periodic demographic scenario (panel B). As already noticed above, zebra mussel colonies can reach extremely high population densities downstream of Lake Bilancino and especially in the Florence area. Moreover, we observe that the locations characterized by higher mean population densities are also those where more variable demographic regimes (i.e. regimes with large demographic fluctuations—of either chaotic or cyclical nature—around the mean value of population density) are recorded. Interestingly enough, in the periodic scenario (Figure 5B) there is a remarkable increase of the time-averaged population abundances at the confluence between the Sieve and the Arno Rivers. This is due to the different hydrological regimes of the two rivers: the Arno River has in fact a slower current velocity than the Sieve River, but a higher diffusion coefficient.

Sensitivity analysis

With the twofold aim of (i) testing the robustness of our results and (ii) analysing how the scenarios considered so

far would be altered by modifying the values attributed to some key ecological parameters, we now perform a sensitivity analysis of the model. In particular, we assume a sustained larval release from Lake Bilancino, so that the long-term persistence of zebra mussel colonies in the river is allowed under both chaotic and periodic local dynamics. Then, we run several simulations of the model by changing only one of the following quantities: (a) larval release from Lake Bilancino $i(1, \cdot, \cdot)$, (b) adult mussel survivals σ_k (with $1 \leq k \leq 4$), (c) mussel fertilities f_k ($1 \leq k \leq 4$), (d) larval mortality μ . As for (b), (c) and (d), we consider both local variations (i.e. limited to the single node of Florence) and basin-scale variations (extended to all nodes, with two different values of intensity). Also, we limit our analyses to variations that are *a priori* expected to produce positive effects on the ecosystem, that is a reduction of mussel density from the baseline patterns shown in Figure 5. The results of our sensitivity analysis are shown in panels A–H of Figure 6.

A 50% reduction of yearly larval release $i(1, \cdot, \cdot)$ from Lake Bilancino is in principle expected to produce remarkable effects on the dynamics of downstream zebra

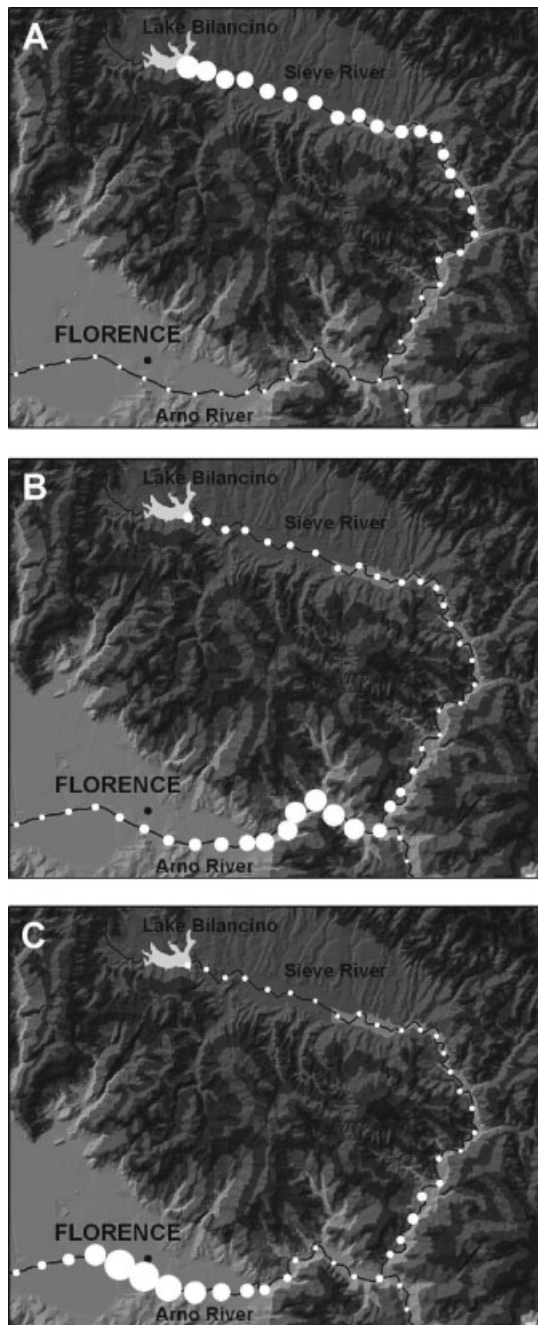


Figure 4. Representative snapshots of the distribution of *D. polymorpha* in the Bilancino-Sieve-Arno water system in case of sustained larval release from Lake Bilancino and chaotic local demography. Panels A, B and C display the densities of local colonies 4, 6 and 11 years after the beginning of the invasion, respectively. The diameter of white circles is proportional to the size of local colonies of adult zebra mussels. Parameter values and simulation details as in top panels of Figure 3.

mussel colonies, or at least a sensible reduction of adult density. This expectation is always satisfied in the close proximity of Lake Bilancino and almost everywhere along the Arno River, but only if the local-scale dynamics is periodic (Figure 6B). In fact, under local chaotic dynamics the time-averaged mussel density appears to be higher with reduced larval inputs than in the reference case in all the nodes that are more than 10 km away from Lake Bilancino (Figure 6A). This seemingly paradoxical result shows that larval supply from the upstream lake

can actually play a nontrivial role in the Sieve-Arno along-stream population dynamics. Crucial to solve the puzzle is the fact that, although veliger input from the external reservoir is essential for the persistence of local downstream colonies, it also crucially contributes to defining density-dependent demographic processes.

Reducing adult mussel survivals ($\sigma_k s$) may or may not produce noticeable ecological effects depending upon the spatial scale at which such reduction is operated, its intensity and the local-scale demographic regime prior to parametric reduction (Figure 6C and D). The interplay of these three components is not trivial at all. For example, halving the survival parameters in the Florence node only (solid line) is very beneficial to the whole Florence area if the local-scale dynamics is chaotic (panel C), while mussel reduction is limited to the Florence municipality in case of periodic dynamics (Figure 6D). Basin-scale reductions of adult mussel survival (dotted and dashed lines) may also be effective in limiting zebra mussel densities in the Florence area. Specifically, it turns out that in the periodic scenario a small reduction (5%, dotted line) of adult survivals is much more effective than a large (50%, solid line) local variation in Florence, while the chaotic case implies the opposite outcome. Larger basin-scale reductions (50%, dashed lines) result in a very remarkable lowering of population densities in the river as a whole (most notably, also in the area downstream of Lake Bilancino).

Panels E and F of Figure 6 point out that reductions of mussel fertilities ($f_k s$) produce much less noticeable effects than decrements of adult mussel survival, with only large basin-scale reductions allowed to result in remarkable effects.

Local or basin-scale increases of larval mortality μ produce quite different results according to the demographic scenario under investigation. In particular, if the local-scale dynamics is chaotic a 50% increase (dashed line) of larval mortality in Florence only can produce positive effects in the whole Florence area (Figure 6G). Even better performances are obtained with small basin-scale variations of larval mortality. On the contrary, these two parametric variations produce little effects (either positive or negative) under periodic demographic regime (Figure 6H). Also, increasing levels of veliger mortality in each node of the graph seem to be rather ineffective in the chaotic case, but highly effective in the periodic case.

The take-home message from this sensitivity analysis is that variations of the ecological parameters may profoundly impact on spatiotemporal invasion patterns. As a result, it is quite difficult to have a clear portrait of the punctual effects caused by each of the possible changes. Therefore, a thorough understanding of both demographic and dispersal dynamics of the zebra mussel is needed in order to achieve accurate predictions.

DISCUSSION AND CONCLUSIONS

In this work we have proposed a model to analyse the spread of the invasive mussel *D. polymorpha* along

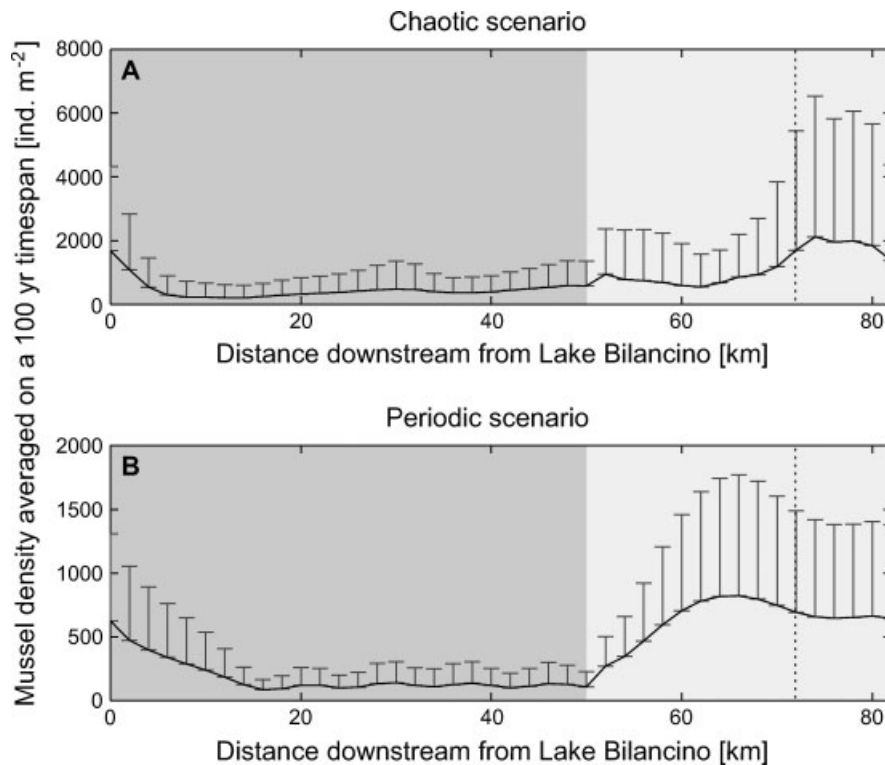


Figure 5. Time-averaged population density over a 100-year interval (black lines) and its standard deviation (grey bars) as a function of distance from Lake Bilancino under chaotic (A) or periodic (B) local population dynamics. Different grey shadings mark the Sieve (dark grey) and the Arno (light grey) Rivers. The dotted vertical line corresponds to the city of Florence. Parameter values and simulation details are as in Figure 3.

ivers. We have specifically used the model to study the spatiotemporal dynamics of zebra mussel populations in the Arno River (Italy), since the recent sighting of the species in Lake Bilancino (Figure 1) has caused considerable concern for a possible demographic outbreak at the regional scale. The proposed model is spatially explicit and time-hybrid. Some simplifying assumptions were necessarily introduced. First, we have considered a one-dimensional topology for the river, which has then be described as a one-dimensional oriented graph. Second, the mechanisms of larval dispersal have been simplified, since we have only considered passive transport by water flow and a strictly deterministic duration of the veliger stage (exactly τ_s days). Despite such limitations, however, we have been able to use the model to produce invasion patterns that display interesting analogies with phenomena often observed in other river systems, including the patchy distribution of zebra mussel colonies, the wild temporal fluctuations of local populations and the so-called domino effect. Our analysis has shown that a resident population in Lake Bilancino is essential to long-term persistence of zebra mussel colonies in the river. The model has also highlighted the critical situation of the city of Florence, where remarkable population outbreaks and significant endemic abundances are expected. Moreover, the sensitivity analysis performed has shown that varying parameter values might or might not have effective consequences in limiting the impacts of *D. polymorpha*, depending on (i) the demographic regime at the local-scale, (ii) the spatial scale at which parameters are varied, and (iii) which particular parameter is modified. All of the

above conditions have obvious, yet profound implications for the potential control strategies that can be adopted to prevent zebra mussel dominance on the ecosystem.

The practical conclusions that can be drawn from our study must be anticipated by the *caveat* that controlling zebra mussel populations in natural water bodies is a very complex problem. Timeliness is of paramount importance, since eradicating the species once it has become established appears to be virtually impossible (Aldridge *et al.*, 2004). Moreover, most of the chemical and mechanical treatments proposed and usually applied in artificial water systems (like power plants or waterworks) infested by *D. polymorpha* cannot be used in rivers. The reduction of mussel fertility through the manipulation of the species reproductive cycle (Ram *et al.*, 1992), the reduction of mussel survival, obtained by either introduced predators (Thorp *et al.*, 1998) or mechanical devices (Jenner and Janssen-Mommen, 1993), the sharp reduction of veliger survival through the use of devices that block larval dispersal (Schneider *et al.*, 2003), and the control of larval supply from upstream sources (Schneider *et al.*, 2004b) have all been proposed as potential measures to limit the spread of *D. polymorpha* in open water systems. However, controlling the zebra mussel in natural ecosystems represents an open issue to date.

Independently of the treatments actually implemented, the outcomes of the sensitivity analysis reported in Figure 6 provide clues to the effectiveness of potential control actions aimed at containing the impacts of the species in the Bilancino-Sieve-Arno water system and, in particular, in the Florence area. Specifically, reducing

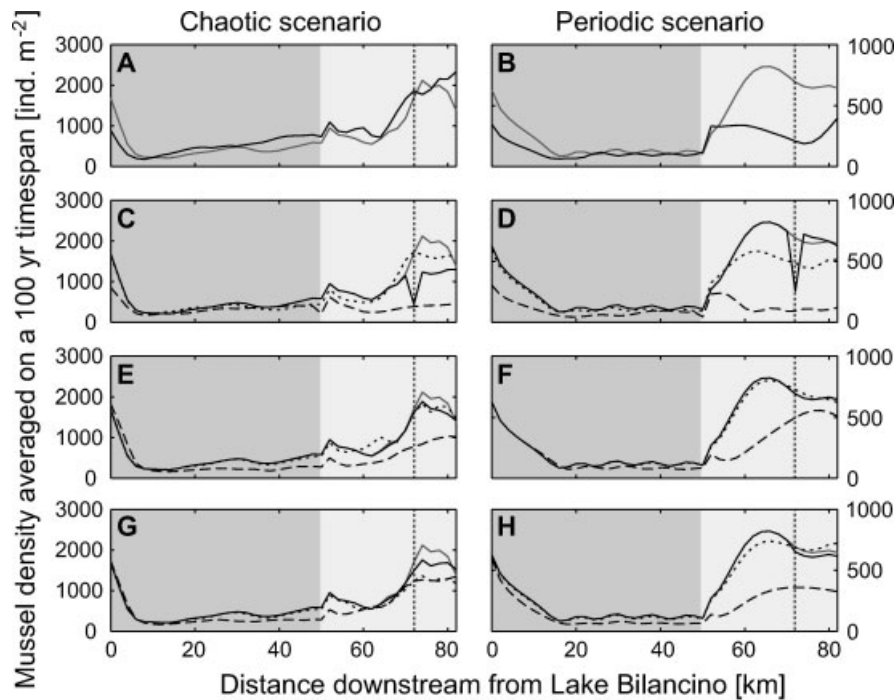


Figure 6. Sensitivity analysis of the model outcomes. The eight panels display the time-averaged population densities computed over a 100-year timespan with several different parameters settings and contrast them to the reference cases of Figure 5 (reported here as grey lines). Left (right) panels are obtained in the chaotic (periodic) demographic scenario. (A and B) 50% reduction of daily larval release from Lake Bilancino; (C and D) reduction of adult mussel survival; (E and F) reduction of mussel fertility; (G and H) increase of larval mortality. In panels C–H the solid lines represent a 50% parameter variation in Florence only, while the dotted (dashed) lines are for a 5% (50%) variation at the basin-scale. Different grey shadings mark the Sieve (dark grey) and the Arno (light grey) Rivers. The dotted vertical lines correspond to the city of Florence. Other parameters and simulation details are as in Figure 3.

larval supply from Lake Bilancino is expected to produce very positive results in the case of periodic demographic dynamics, but little or no positive effects under chaotic regimes. Also, reducing adult survival seems to be more promising than acting on fertility. In the first case, in fact, local actions (under chaotic demographics) or low intensity basin-scale interventions (under periodic demography) are expected to produce remarkable positive effects in the Florence area. In the second case, sensible reductions of mussel densities in the Florence area can occur only with large basin-scale fertility cuts, which would be obviously very difficult to implement, and perhaps expensive as well. Moreover, increasing larval mortality represents an effective way of reducing mussel densities only in the case of basin-scale actions (and if veliger mortality is sensibly increased, at least under periodic demography). In general, local actions in Florence seem to produce positive effects in the whole Florence area only under chaotic regimes, while local control actions seem to be poorly effective under periodic dynamics.

For all these reasons, our analysis suggests that each of the envisaged control measure must be planned with extreme care and requires a thorough understanding of demographic and dispersal dynamics. A modelling approach like ours, supported by extensive *in situ* studies, could actually help environmental managers and decision-makers in facing the urgent problem of the spread of *D. polymorpha* in the Bilancino-Sieve-Arno

water system, which could then be used as a prototype for more complex river networks.

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