Modelling the invasion risk of diapausing organisms transported in ballast sediments

Marjorie J. Wonham, Sarah A. Bailey, Hugh J. MacIsaac, and Mark A. Lewis

Abstract: Biological invasions via ship ballast are a major driver of biodiversity change in aquatic systems. In the Laurentian Great Lakes basin, unique shipping operations pose a particular invasion risk. The majority (>90%) of incoming vessels are not fully loaded with ballast water but carry ballast sediments and residual water. Ballast sediments contain viable diapause organisms that could hatch and be released during routine ballast operations. To assess invasion risk and control of this pathway, we constructed and parameterized a dynamic hatching model for three representative groups of freshwater organisms that undergo diapause: rotifers, cladocerans, and copepods. Numerical model simulations show that ballast sediment is a plausible invasion pathway for all three groups. The model also illustrates that postuptake ballast treatment to remove or kill potential invaders should be applied as late as possible prior to deballasting to minimize the number of live organisms released. Simulations show that the ability of taxa to reproduce parthenogenetically inside a ballast tank greatly influences quantitative predictions of both risk and control.

Résumé : Les invasions biologiques par l'intermédiaire des eaux de ballastage des navires sont des causes majeures de changements de biodiversité dans les systèmes aquatiques. Dans le bassin hydrographique des Grands Lacs laurentiens, des opérations de transport maritime particulières posent une risque spécial d'invasion. La majorité (>90 %) des navires qui y pénètrent ne portent pas une pleine charge d'eau de ballastage, mais contiennent des sédiments et de l'eau résiduelle dans leurs ballasts. Les sédiments dans les ballasts contiennent des organismes viables en diapause qui peuvent éclore et être libérés durant les opérations de ballastage de routine. Afin d'évaluer le risque d'invasion et le contrôle de cette voie d'introduction, nous avons construit un modèle dynamique de l'éclosion pour trois groupes d'organismes d'eau douce qui subissent la diapause, les rotifères, les cladocères et les copépodes, et nous en avons précisé les paramètres. Des simulations du modèle numérique montrent que les sédiments des ballasts sont une voie plausible d'invasion pour l'ensemble des trois groupes. Le modèle démontre aussi que le traitement des eaux de ballastage après le remplissage afin d'éliminer ou de tuer les organismes envahisseurs possibles devrait se faire le plus tard possible avant la vidange des ballasts, afin de réduire au minimum le nombre d'organismes vivants libérés. Les simulations montrent que la capacité des taxons de se reproduire par parthénogenèse dans les ballasts influence fortement les prédictions numériques à la fois du risque et du contrôle.

[Traduit par la Rédaction]

Introduction

Biological invasions are one of the major agents of global biodiversity change in aquatic systems (e.g., Sala et al. 2000; MacIsaac et al. 2001). In the Laurentian Great Lakes basin, current invasion rates exceed background by several orders of magnitude, and published records document at least 170 established nonindigenous species (Ricciardi 2001; Hebert and Cristescu 2002; Holeck et al. 2004). Because anthropogenic invasion pathways remain active, new species are predicted to invade the Great Lakes successfully in the future (Table 1) (Vanderploeg et al. 2002; Grigorovich et al. 2003; Rixon et al. 2005).

Ballast water is widely recognized as the major introduction pathway in many aquatic systems (Carlton 1998; MacIsaac et al. 2002; Grigorovich et al. 2003). In the Great Lakes, however, ship surveys indicate that fewer than 10% of commercial vessels entering the lakes are registered in

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Table 1. Nonindigenous species with diapause stages established (E) in the Laurentian Great Lakes, nonindigenous species predicted (P) to invade from the Ponto-Caspian region, and viable diapausing taxa collected (C) in ballast sediments arriving in the Great Lakes (Ricciardi 2001; Bailey et al. 2003; Grigorovich et al. 2003) and the origin for established and predicted invaders.

Group	Species	E	P	C	Origin
Rotifers	*Asplanchna girodi*			×	
	Brachionus angularis			×	
	Brachionus budapestinensis			×	
	Brachionus calyciflorus			×	
	Brachionus diversicornis			×	
	Filina sp.			×	
	Ploesoma sp.			×	
Cladocerans	*Bythotrephes longimanus*	×			Eurasia
	Bosmina coregoni	×			Eurasia
	Bosmina maritima	×			Eurasia
	Cercopagis pengoi	×			Black Sea
	Daphnia lumholtzi	×			Africa, Asia
	Bosmina obtusirostris		×		Ponto-Caspian
	Podovadne trigona ovum		×		Ponto-Caspian
	Cornigerius maeoticus maeoticus		×		Ponto-Caspian
	Daphnia cristata		×		Ponto-Caspian
	Bosmina liederi			×	
	Bosmina sp.			×	
	Ceriodaphnia pulchella			×	
	Daphnia ambigua			×	
	Daphnia longiremis			×	
	Daphnia magna			×	
	Daphnia sp.			×	
	Diaphanosoma brachyurum			×	
	Diaphanosoma sp.			×	
	Moina affinis			×	
	Moina micrura			×	
Copepods					
Calanoids	*Eurytemora affinis*	×			Cosmopolitan
	Skistodiaptomus pallidus	×			North America
	Calanipedia aquaedulcis		×		Ponto-Caspian
	Heterocope appendiculata		×		Ponto-Caspian
	Heterocope caspia		×		Ponto-Caspian
	Unidentified calanoids			×	
Harpacticoids	*Heteropsyllus* cf. *nunni*	×			Ponto-Caspian
	Nitocra hibernica	×			Ponto-Caspian
	Nitocra incerta	×			Ponto-Caspian
	Onychocamptus mohammed	×			Ponto-Caspian
	Schizopera borutzkyi	×			Ponto-Caspian
	Ectinosoma abrau		×		Ponto-Caspian
	Paraleptastacus spinicaudata triseta		×		Ponto-Caspian
Cyclopoids	*Cyclops strenuus*	×			Eurasia
	Megacyclops viridis	×			Europe
	Cyclops kolensis		×		Ponto-Caspian

ballast (Colautti et al. 2003). The remaining >90% are registered as NOBOB (no ballast on board), but nonetheless carry, on average, some 10–15 metric tons (t) of sediment and 40–50 t of residual, unpumpable ballast water (Bailey et al. 2003; Colautti et al. 2003). Both the sediment and residual water may contain live organisms and viable resting stages (e.g., Bailey et al. 2003, 2005*a*; Colautti et al. 2003). By loading and discharging ballast water within the Great Lakes, NOBOB vessels provide the opportunity for nonindigenous species to be released from these ballast residuals (MacIsaac et al. 2002; Colautti et al. 2003; Bailey et al. 2005*b*). The relative risk of invasion via ballast water, ballast sediment, and residual ballast water remains unknown. Here, we focus on characterizing the invasion risk posed by the diapausing freshwater organisms in ballast sediment, up to the point of release into the new environment.

Sediment accumulates in ballast tanks during the years between dry dock cleanings and contains a variable density and diversity of live organisms as well as the viable diapause stages of diatoms, dinoflagellates, ciliates, flagellates, and invertebrates (e.g., Smith et al. 1999; Bailey et al. 2003, 2005*a*). Diapausing eggs and other resting stages provide a temporal refuge from adverse environmental conditions, particularly between temperate growing seasons. They may also predispose species to successful transport and possible invasion via human activities.

In general, diapausing eggs undergo an obligate resting, or refractory, period of weeks to months before becoming receptive to hatching cues. They can then hatch out in response to a variety of factors including light, temperature, salinity, and oxygen (e.g., Hairston et al. 1995; Cáceres 1997; Gray et al. 2005). If the ballast tanks of NOBOB vessels remained sealed through the Great Lakes, diapausing organisms would pose no invasion risk. However, the addition of water while operating on the Great Lakes can alter conditions in the tanks and stimulate hatching (Bailey et al. 2005*b*), allowing organisms to be released.

To assess the invasion risk associated with diapausing stages of freshwater organisms in ballast sediments, we construct a dynamic model of hatching within ballast tanks of NOBOB vessels entering the Great Lakes. Our goal is to explore the simplest-case scenarios of single-species population growth and control for ballast sediment organisms. We parameterize our model for several common diapausing species found in ballast sediments or introduced into the Great Lakes. We then identify the optimal timing of ballast treatment to minimize the release of live organisms.

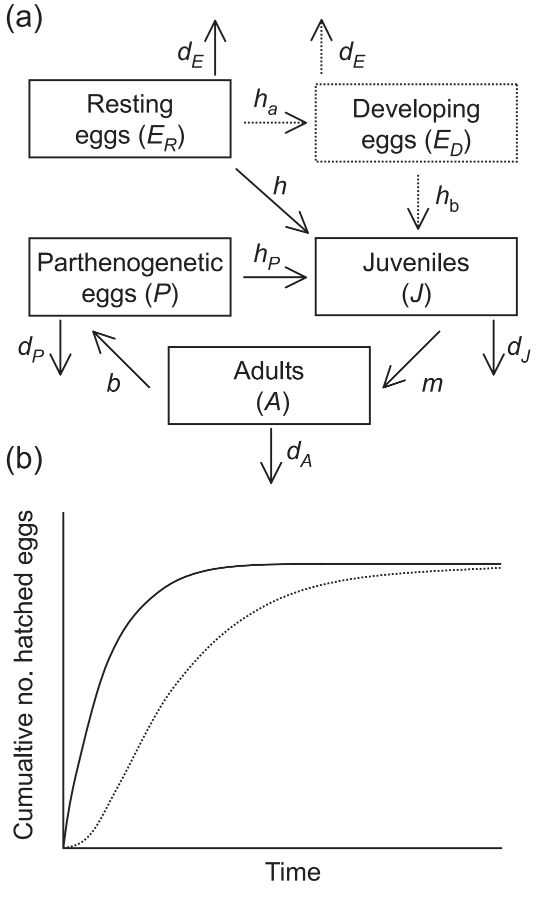
Model development

Invasion pathway

Most NOBOB ships in the Great Lakes discharge cargo and load ballast water at all but the last port of call, where the majority then load cargo and discharge the accumulated water. Most (84%) first ports of call are on Lakes Ontario and Erie, and most (74%) ballast discharges occur in Lake Superior (for vessels entering the Great Lakes from 1994 to 2000; Colautti et al. 2003). The average ship transit time from water intake in western Lake Ontario to discharge in Lake Superior is 7–14 days, including stops at other ports (Bailey et al. 2003). Laboratory and ballast tank studies show that resting stages of freshwater taxa may hatch in as few as 2 days following freshwater immersion, which would allow eggs to hatch in Great Lakes ballast well before final discharge (Bailey et al. 2003, 2005*b*).

Physical conditions in ballast tanks are variable, and although heavy mortality is typically observed, the occasional presence of gravid females, loose eggs, and early larval stages suggests that successful reproduction may occur in a variety of taxa (e.g., Smith et al. 1999; Gollasch et al. 2000; Wonham et al. 2001). We therefore consider two hypothetical ballast tank scenarios: (*i*) conditions that allow sediment organisms to hatch and develop from diapausing eggs but not to reproduce and (*ii*) conditions that allow hatching, development, and reproduction.

Fig. 1. (*a*) Simplified life cycle of parthenogenetic organisms hatching from diapausing eggs in ballast sediments, including stages and rate parameters. In model 1 (solid boxes and lines), diapausing eggs hatch to larval or juvenile stages following an appropriate environmental cue and then mature to adults. Adult females typically produce parthenogenetic eggs; sexual diapausing eggs may be produced later, but as this is unlikely to occur within the relatively short time frame of ballast transport in the Great Lakes, it is not included in the model. For copepods, we assume that sexual egg production can be approximated in the confines of a ballast tank by parthenogenesis. In model 2, a developing egg compartment is added (broken boxes and lines). (*b*) Both convex (solid line) and sigmoid (broken line) cumulative hatching profiles are observed in the laboratory for different species and can be generated by models 1 and 2, respectively.



The majority of diapausing eggs in incoming ballast sediments to the Great Lakes are rotifers and cladocerans (Table 1) (Bailey et al. 2003, 2005*a*). Copepod eggs are found less frequently in sediments, but live individuals are nearly ubiquitous in ballast water samples (e.g., Smith et al. 1999; Gollasch et al. 2000; Wonham et al. 2001). Within these three groups, we summarized records of nonindigenous species established in or predicted to invade the Great Lakes and viable taxa collected as diapausing eggs from ballast sediments entering the lakes (Table 1). Rotifer species were commonly collected from ballast sediments (seven taxa), but no established rotifer invaders were reported from this region. Cladoceran species were also commonly collected (11 taxa), although typically at low abundance, and were commonly reported or predicted to invade (nine species). Copepods were also commonly reported and predicted to invade (15 species); although diapausing eggs have been collected frequently from ballast sediments,

Table 2. Diapausing egg hatching parameters estimated from the literature for species hatching from ballast sediments.

Species	$t_{\min}$	$\tilde{i}$	h	n	Reference(s)
Asplanchna girodi	1	1.30	1.460	86	*a*
Brachionus budapestinensis	1	1.80	0.809	61	*a*
Brachionus calyciflorus	0	2.07	0.658	56	*a*
Bosmina liederi	2	2.16	0.623	51	*a*
Bythotrephes longimanus	24	46.66	0.022	29	*b*
Daphnia longiremis	2	5.56	0.198	25	*a*
Eurytemora affinis	0.75	1.42	1.216	30	*c*

Note: $t_{\min}$, first observed hatching day minus one, following the cue; $\tilde{t}$, mean number of days to hatching following $t_{\min}$; h, maximum-likelihood estimated of daily per capita hatching rate; n, total number of hatched eggs. References: (*a*) Bailey et al. (2003) and S. Bailey, unpublished data; (*b*) Yurista (1992); and (*c*) Ban and Minoda (1992).

Table 3. Literature data for species collected from ballast sediments (or for related species if data unavailable).

Species	Juvenile duration (days)	Adult life span (days)	Parthenogenetic eggs (days)	Fecundity (no. of eggs)	Reference(s)
Asplanchna girodi	—	4.8–8.7	—	15.6–21.7·female^{-1}	*a*
Brachionus calyciflorus	0.8–1.0	1–9	0.7–1.2	3.6–34.1·female^{-1}	*b*
Bosmina longisrostris	1–8	10–30	2.1–5.4	3·female^{-1}·day^{-1}	*c*
Bythotrephes longimanus	14–23	6.4–13.0	11–14	—	*d*
Daphnia spp.	2–17	8–70	2–4	0.1–4.4·female^{-1}·day^{-1}	*e*
Eurytemora affinis	11.4–37	5–73	1.0–2.2*	2.1–34.2·female^{-1}·day^{-1}	*f*

Note: Daily per capita rate parameters were taken as follows: juvenile maturation rate, m, as 1 over the juvenile duration; adult mortality rate, d_A, as 1 over the adult life span; and parthenogenetic hatching rate, h_P, as 1 over the egg development time. Parthenogenetic fecundity is given as eggs per female per day or total number of eggs per female, as indicated; daily parthenogenetic fecundity ($1/b$) was estimated where necessary by dividing total fecundity by mean adult life span. Parameter values used in the simulations are given in the figure captions. References: (*a*) Sarma et al. (2003); (*b*) Pourriot et al. (1982), Herzig (1983), Rothhaupt (1990), Fernández-Casalderrey et al. (1993), Hettiarachchi et al. (1995), Mnatsakanova and Polishchuk (1996), Wang and Li (1997), and Xi and Huang (2001); (*c*) Kwik and Carter (1975), Lynch (1980), Hanazato and Yasuno (1985), Urabe (1991), and McCauley et al. (1996); (*d*) Sprules et al. (1990), Yurista (1992), Lehman and Branstrator (1995), Yurista and Schulz (1995), and Lehman et al. (1997); (*e*) Lynch (1980), Gurney et al. (1990), McCauley et al. (1990*a*, 1990*b*), Teschner (1995), Arbaciauskas and Gasiûnaitë (1996), and McCauley et al. (1996); and (*f*) Heinle and Flemer (1975), Allan and Daniels (1982), Gaedke (1990), Ban (1992), Hirche (1992), Nagaraj (1992), Koski et al. (1999), Lee and Petersen (2002), Reinikainen et al. (2002), and Hairston et al. (1995).

*For the copepod *E. affinis*, we use sexual egg development time.

species identifications are few (Table 1). We chose representative species from each group to model their relative invasion risk from diapausing eggs in ballast sediments.

Model structure

We represent the general rotifer, cladoceran, and copepod life cycle as a simplified cycle of four stages, which can be modelled with a system of four ordinary differential equations (Fig. 1*a*; eq. 1). We consider an initial population of viable diapausing eggs (E_R) that hatch in response to an environmental cue into a larval or juvenile stage (J), mature to adults (A), and produce parthenogenetic eggs (P) (Fig. 1*a*):

$$(1a)\qquad \underbrace{\frac{\mathrm{d}E_R}{\mathrm{d}t}}_{\text{resting eggs}} = -\underbrace{\frac{hE_R}{2}}_{\text{hatching}} - \underbrace{d_E E_R}_{\text{mortality}}, \qquad h = \begin{cases} 0, & t < t_{\min} \\ h, & t \geq t_{\min} \end{cases}$$

$$(1b)\qquad \underbrace{\frac{\mathrm{d}J}{\mathrm{d}t}}_{\text{juveniles}} = \underbrace{\frac{hE_R}{2}}_{\substack{\text{hatching from}\\ \text{resting eggs}}} + \underbrace{h_P P}_{\substack{\text{hatching from}\\ \text{parthenogenetic}\\ \text{eggs}}} - \underbrace{mJ}_{\substack{\text{maturation}\\ \text{of juveniles}}} - \underbrace{d_J J}_{\text{mortality}}$$

$$(1c)\qquad \underbrace{\frac{\mathrm{d}A}{\mathrm{d}t}}_{\text{adults}} = \underbrace{mJ}_{\substack{\text{maturation}\\ \text{of juveniles}}} - \underbrace{d_A A}_{\text{mortality}}$$

$$(1d)\qquad \underbrace{\frac{\mathrm{d}P}{\mathrm{d}t}}_{\substack{\text{parthenogenetic}\\ \text{eggs}}} = \underbrace{bA}_{\substack{\text{production by}\\ \text{adult females}}} - \underbrace{h_P P}_{\text{hatching}} - \underbrace{d_P P}_{\text{mortality}}$$

Parameters are further defined in Tables 2 and 3. For copepods, which do not reproduce parthenogenetically, we make the simplifying assumption here that egg fertilization in the confines of a ballast tank is not limited by sperm availability, so sexual reproduction can be approximated by parthenogenesis.

We treat the hatching of diapausing eggs as a series of independent, one-step events that can be modelled as a Poisson process, which generates an exponential distribution of egg hatching times. This distribution is modelled with the constant hatching rate parameter h (eqs. 1*a* and 1*b*). The resulting convex profile of cumulative eggs hatched over time is consistent with observed laboratory data for certain species (e.g., Bailey et al. 2003) and can be visualized by setting all other parameters to zero and solving for the total number of hatched organisms, $J(t) = E_R(0)(1 - e^{-ht})$ (Fig. 1*b*).

Other species show a sigmoid cumulative hatching profile (Ban and Minoda 1992; Yurista 1992, 1997). To better account for this shape, we developed a second model that considers egg development as a two-stage process (Fig. 1; Appendix A). Since this more complex model was not supported significantly better by the data (Appendix A), we use the simpler model throughout.

The life cycle model assumes that the species' life stages are adequately represented by these equations, that sexual diapausing egg production is insignificant in the short time frame of interest, and that all parameter values remain constant over time (cf. Arbaciauskas and Gasiûnaitë 1996). We note that by using experimental laboratory data to estimate parameter values, we may be overestimating survival and development rates (Bailey et al. 2005*a*). Nonetheless, our results remain qualitatively similar over a range of parameter values. We use this simple deterministic model to simulate a 14-day ballast water voyage through the Great Lakes in which the environmental hatching cue occurs on the first day.

Parameter estimation

We used laboratory and literature data to obtain parameter estimates for representative species from Table 1 (Tables 2 and 3; Fig. 2). For diapausing eggs, we estimated the mean time to hatching based on literature and laboratory data. From each study, we assumed that only those eggs hatching within the study period were viable (i.e., that no more would have hatched had the experiment been longer). For studies that reported multiple laboratory trials, we preferentially chose those conducted at 0‰ salinity, 10–20 °C, and 24 h dark regimes. We pooled data from multiple replicates and studies to obtain a single hatching rate estimate for each species using maximum likelihood. There were insufficient data available to estimate parameter distributions. For each species, the initial delay before hatching, $t_{\min}$, was taken as the day prior to the first reported hatching. The hatching time, t_i, for each egg i (up to n, the total number that hatched in the laboratory trial) was calculated as the observed hatching day less $t_{\min}$. The mean observed hatching time is denoted $\bar{t} = \sum_{i=1}^{n} t_i/n$.

Since hatching is a continuous process through time, we represent it with an ordinary differential equation model (eq. 1). However, the laboratory data used to estimate hatching rates are typically recorded at discrete daily time points, where each observation represents the number of eggs hatched in the previous day. To estimate hatching rates, we determined the continuous probability density function (pdf) for hatching times, integrated this to obtain the probability of an egg hatching in a given 1-day period, and calculated the likelihood function for the hatching rate. The time to hatching, T, has pdf he^{-ht}. The probability of an egg hatching during a 1-day period from $j - 1$ to j is thus

$$(2)\qquad \Pr\{j-1 < T < j\} = \int_{j-1}^{j} he^{-ht}\mathrm{d}t = e^{-hj}(e^{h}-1)$$

Given observed hatching times t_i, the negative log-likelihood function for the hatching rate h is

$$(3)\qquad -l(h\,|\,t_1,\ldots,t_n) = -\ln\left[\prod_{i=1}^{n} e^{-ht_i}(e^{h}-1)\right] = -n\ln(e^{h}-1) + hn\bar{t}$$

By minimizing this function, we obtained hatching rate estimates (Table 2; Fig. 2; Appendix A).

The remaining life cycle parameter estimates were obtained from the literature (Table 3). When data were not available for a particular species, values from closely related species were used as follows: *Asplanchna girodi* juvenile and parthenogenetic egg durations were based on those of *Brachionus calyciflorus*; all *Brachionus* spp. life cycle parameters were based on those of *Brachionus calyciflorus*; *Bosmina liederi* life cycle parameters were based on those of *Bosmina longisrostris*; and *Daphnia longiremis* life cycle parameters were based on those of *Daphnia galeata* and *Daphnia pulex* (Tables 2 and 3).

Estimates of mortality rates at egg and juvenile stages were generally not available, so for most simulations, d_E, d_P, and d_J were set to zero. The effects of additional mortality were explored for *Eurytemora affinis* by adding juvenile mortality, $d_J = 0.2\cdot\text{day}^{-1}$, and reducing egg viability to 70% (as per sources in Table 3; Heinle and Flemer 1975).

Model analysis

We first simulated ballast tank conditions in which individuals could hatch and develop but not reproduce. For the six species shown, the brief period from the hatching cue to the first juveniles corresponded to $t_{\min}$ (Fig. 3). Rotifer abundance increased and then declined by the end of the 14-day simulation as the supply of diapausing eggs was depleted (Figs. 3*a*–3*c*). The two cladocerans *Bosmina liederi* and *D. longiremis*, which hatched and developed more slowly, showed a similar but slower trend (Figs. 3*d* and 3*e*). For the copepod *E. affinis*, which hatched relatively quickly but had a longer development period to reproductive maturity, only the juveniles began to decline within the 14-day simulation (Fig. 3*f*).

When we allowed parthenogenetic reproduction to occur, all six species produced new generations within the model time frame (Fig. 4). Again, the rotifer populations increased the fastest, followed by the cladocerans and the copepod (Figs. 4*a*–4*f*). Adding juvenile and parthenogenetic egg mortality for *E. affinis* reduced the final hatched populations fivefold in both scenarios (Figs. 3*g* and 4*g*). The cladoceran *Bythotrephes longimanus*, which had the longest $t_{\min}$ and the slowest hatching rate of the species considered, would be unable to hatch from diapausing eggs within 14 days using these parameter values (Tables 2 and 3). Even when hatching and development rates were reduced by an order of magnitude, all of the taxa illustrated in Figs. 3 and 4 were capable of hatching within the model time frame (results not shown).

A variety of physical and chemical ballast water treatments have been proposed to reduce invasion risk (e.g., Kuzirian et al. 2001; Tamburri et al. 2002; Waite et al. 2003). We asked how the timing of treatment influenced its effectiveness in minimizing the final abundance of live organisms. For simplicity, we assume that treatment kills a

Fig. 2. Observed (points) and predicted (solid lines, model 1; broken lines, model 2) number of diapause eggs hatching on each day following $t_{\min}$ for (*a*) *Asplanchna girodi*, (*b*) *Brachionus budapenstensis*, (*c*) *Brachionus calyciflorus*, (*d*) *Bosmina liederi*, (*e*) *Bythotrephes longimanus*, (*f*) *Daphnia longiremis*, and (*g*) *Eurytemora affinis*. The original authors collected data daily for Figs. 2*a*–2*d* and 2*f*; we assumed the same for Fig. 2*e*. Model 1 fit the data significantly better than model 2 (Appendix A) and is used for all simulations.

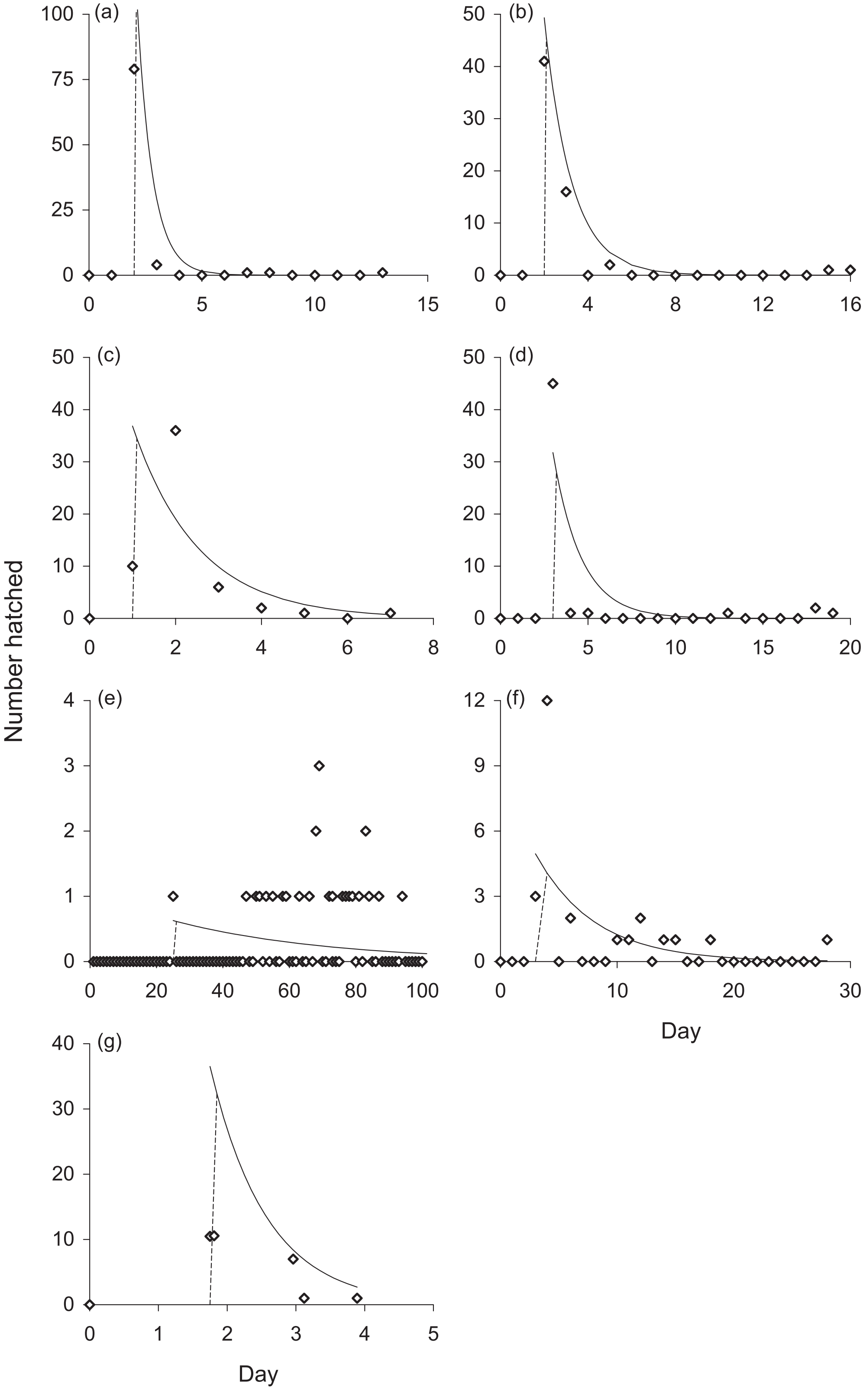
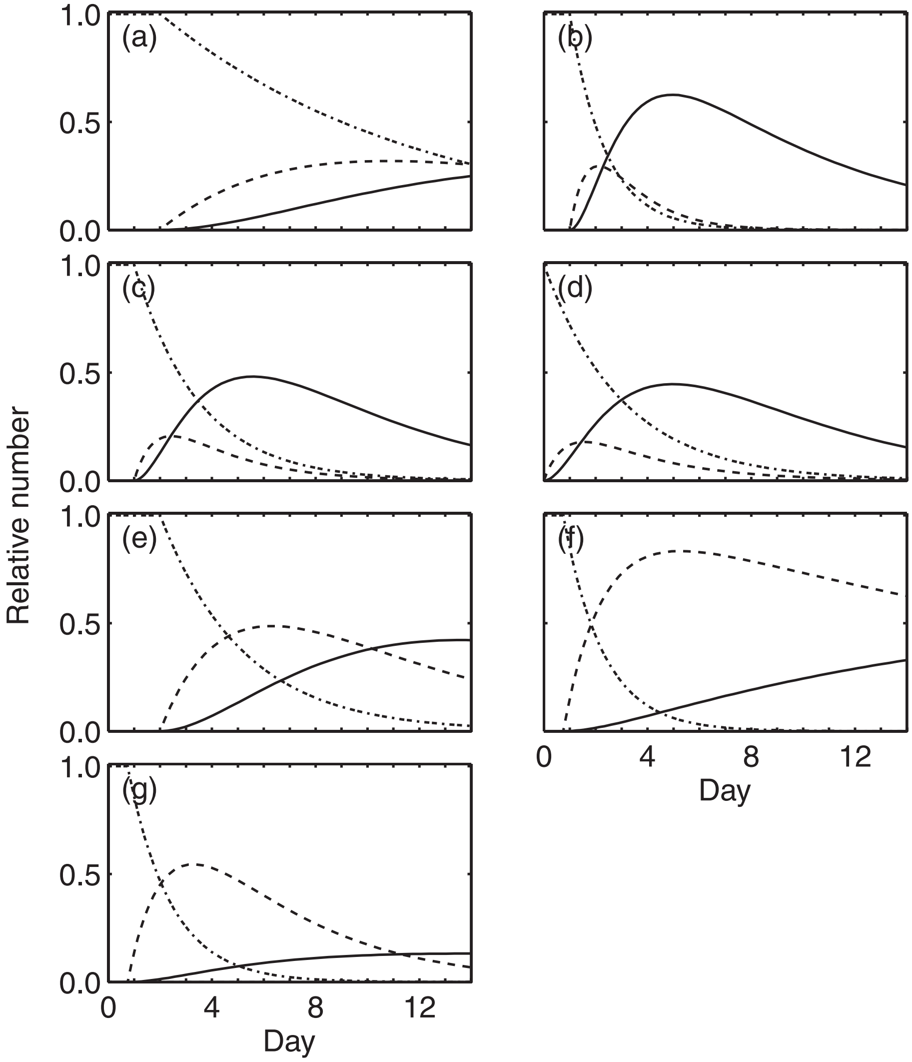


Fig. 3. Simulated population dynamics of six representative species hatching from ballast sediments under tank conditions in which they were allowed to hatch and develop but not reproduce. The numbers of viable diapausing eggs (dotted line), juveniles (dashed line), and adults (solid line) are scaled to the initial number of viable diapausing eggs on the *y* axis. Days following hatching cue on the *x* axis. Daily per capita rates and other parameters are as follows (minimum time to hatching from diapause egg, $t_{\min}$; diapause hatching rate, *h*; juvenile maturation rate, *m*; adult mortality rate, d_A): (*a*) *Asplanchna girodi* (1, 1.460, 1.11, 0.15); (*b*) *Brachionus budapestinensis* (0, 0.658, 1.1, 0.20); (*c*) *Brachionus calyciflorus* (1, 0.809, 1.1, 0.20); (*d*) *Bosmina liederi* (2, 0.623, 0.28, 0.05); (*e*) *Daphnia longiremis* (2, 0.198, 0.13, 0.10); (*f*) *Eurytemora affinis* (0.75, 1.216, 0.04, 0.02); and (*g*) *Eurytemora affinis* with added juvenile mortality, d_J (0.75, 1.216, 0.04, 0.02, d_J = 0.2). In all cases, mortality rates of diapausing eggs are zero, and in all cases except (*g*), the juvenile mortality rate is zero.



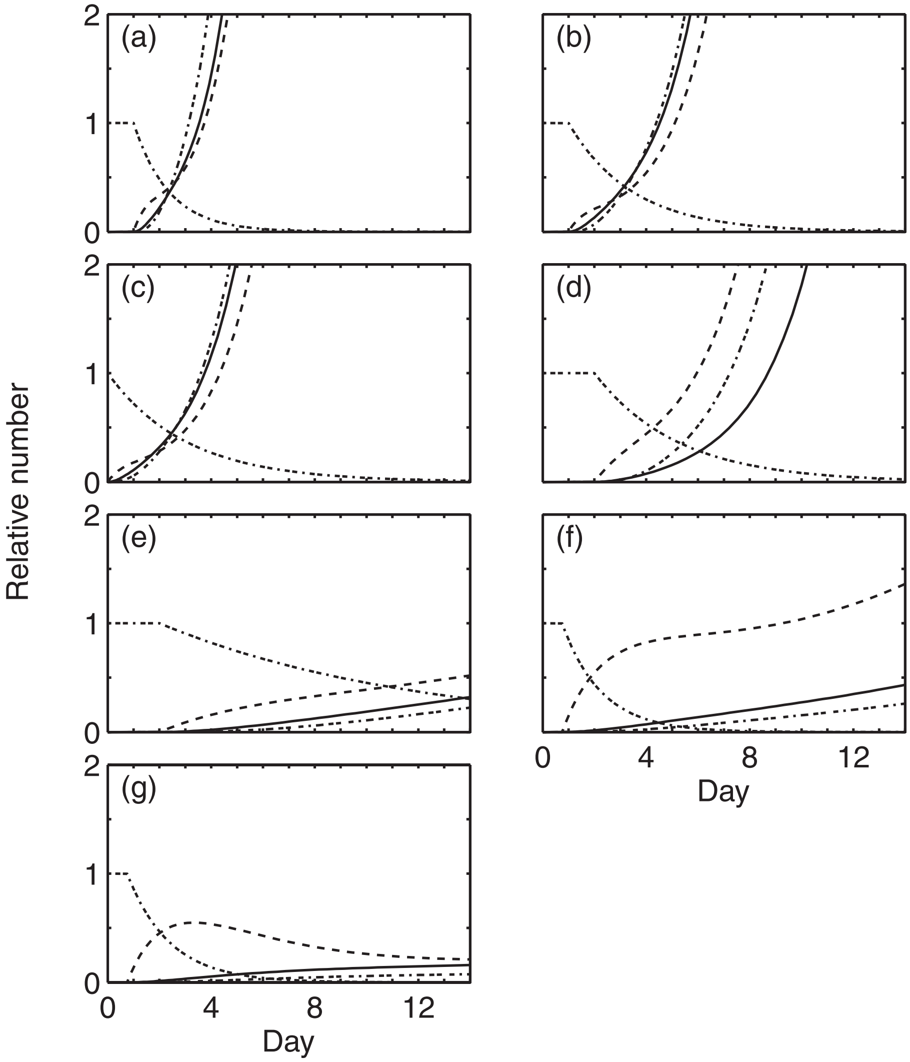
fixed proportion of juveniles, adults, and parthenogenetic eggs but does not affect resting or developing diapausing eggs. We also assume that the treatment is effective only on the day of application and that hatching and development rates are the same before and after treatment.

Clearly, any treatment during ballast uptake will reduce the initial ballast population and therefore the subsequent propagule pressure. Once ballast is in the tank, however, treatment of a population later rather than earlier will always result in a lower abundance of live organisms. This is due to the cooperative (positive feedback) nature of this system in which eggs become juveniles, which in turn become adults, which produce more juveniles (Smith and Waltman 1995). Example results for two species illustrate how successful reproduction can influence the relative abundance of different taxa following treatment (Fig. 5). For the same initial population size, and in the absence of reproduction, final abundance was higher for the cladoceran *D. longiremis* than for the rotifer *Brachionus calyciflorus* (Fig. 5*a*). This is because the cladoceran hatches more slowly, so the pool of diapause eggs available to repopulate the tank following treatment persists longer. With reproduction, however, the abundance of the faster-developing *Brachionus calyciflorus* was higher than that of *D. longiremis* (Fig. 5*b*).

Discussion

Preventing future invasions requires understanding and interrupting the invasion process. The success of an invasion

Fig. 4. Simulated population dynamics of six representative species under tank conditions in which parthenogenetic reproduction occurs. The numbers of viable diapausing eggs (dotted line), parthenogenetic eggs (dot-dashed line), juveniles (dashed line), and adults (solid line) are scaled to the initial number of viable diapausing eggs on the *y* axis. Days following hatching cue on the *x* axis. Daily per capita rates and other parameters are as follows (minimum time to hatching from diapause eggs, $t_{\min}$; diapause hatching rate, *h*; juvenile maturation rate, *m*; adult mortality rate, d_A; parthenogentic egg production rate, *b*; parthenogenetic egg hatching rate, h_P): (*a*) *Asplanchna girodi* (1, 1.460, 1.11, 0.15, 2.8, 1.0); (*b*) *Brachionus budapestinensis* (0, 0.658, 1.1, 0.20, 1.8, 1.0); (*c*) *Brachionus calyciflorus* (1, 0.809, 1.1, 0.20, 1.8, 1.0); (*d*) *Bosmina liederi* (2, 0.623, 0.28, 0.05, 3.0, 0.27); (*e*) *Daphnia longiremis* (2, 0.198, 0.13, 0.10, 0.33, 0.33); (*f*) *Eurytemora affinis* (0.75, 1.216, 0.04, 0.02, 0.44, 0.62); (*g*) *Eurytemora affinis* with added juvenile mortality, d_J (0.75, 1.216, 0.04, 0.02, 0.31, 0.62, d_J = 0.2). In all cases, mortality rates of diapausing eggs are zero, and in all cases except (*g*), the juvenile mortality rate is zero.



depends on the invader's propagule pressure, environmental match, and biotic interactions (e.g., Williamson 1996; Ruiz et al. 2000; Rouget and Richardson 2003). With respect to propagule pressure, theory predicts that the chances of successful invasion will increase with the number of individuals released and the frequency of release (e.g., Allee et al. 1949; Grevstad 1999; Rouget and Richardson 2003). The larger and more frequent the releases, the more likely it is that the invader will overcome problems that plague small populations, such as Allee effects, genetic bottlenecks, demographic stochasticity, and environmental stochasticity. Reducing propagule pressure should therefore reduce invasion risk (e.g., Locke et al. 1993; Drake and Lodge 2004; International Maritime Organization 2004).

The propagule pressure of potential invaders of a region depends on the nature of the invasion pathways. To reduce propagule pressure and invasion risk from ship ballast in the Great Lakes, voluntary and mandatory ballast water exchange guidelines were implemented in 1989 and 1993, respectively (Locke et al. 1993). However, the expected subsequent reduction of successful invasions has not yet been seen (Ricciardi 2001; Holeck et al. 2004). We propose several nonmutually exclusive hypotheses to explain this apparent discrepancy: (1) exchange reduces invasion risk from ballast water but (*i*) other important pathways are operating, (*ii*) ballast volume or propagule quality has increased, (*iii*) the Great Lakes have become easier to invade, or (*iv*) there will be a delay before its effects are seen because previously introduced species are still increasing to the threshold abundance for detection; or (2) exchange does not effectively reduce invasion risk. Here, we explored the first hypothesis, namely that NOBOB vessels entering the Great Lakes may be an additional and important invasion pathway to this region (Bailey et al. 2003; Colautti et al. 2003).

From 1999 to 2000, some 400–600 vessels, both in ballast and NOBOB, entered the Great Lakes each year (Colautti et al. 2003). The invasion risk posed by these two vessel classes depends on their relative frequency and the abundance of viable organisms released. Ships in ballast represent less than 10% of incoming vessels but carry an average of 3–8.5 × 10^3 t of (exchanged) ballast water containing on the order of 10^9 bacteria·L^{-1}, 10^6 autotrophic picoplankters·L^{-1}, and 10^3 zooplankters·L^{-1} (Locke et al. 1991, 1993; MacIsaac et al. 2002). In contrast, NOBOBs make up over 90% of vessels. These ships carry an average of 10–15 t of sediment containing an average of 1.3 × 10^6 animals·t^{-1} and 7.2 × 10^5 diapausing eggs·t^{-1}, with an additional average of 47 t of residual water containing 1.1 × 10^4 animals·t^{-1} (Bailey et al. 2003, 2005*a*; Colautti et al. 2003). The invasion risk associated with each vessel type depends, ultimately, on the number of viable individuals of each species that are released. Here, we have focused on characterizing the invasion risk associated with the sediment reservoir of diapausing ballast organisms.

Ballast sediment invasion risk

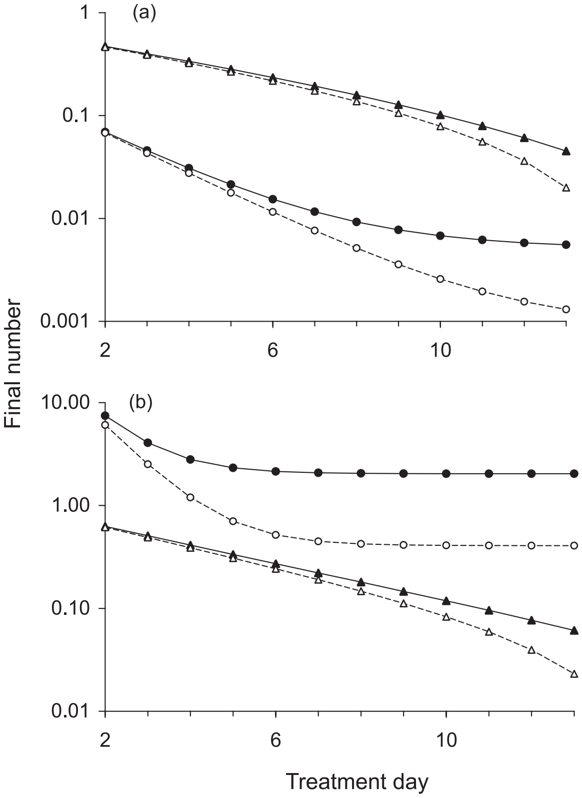
Our model clearly illustrates the potential for a range of freshwater taxa to hatch from diapause within the time frame necessary to be released in routine deballasting operations. Based on propagule pressure, our model predicts that species of all three taxonomic groups considered could readily hatch and be available for introduction from diapause populations.

Rotifers, whose diapausing eggs are abundant in ballast sediments (Bailey et al. 2003) and which grow and reproduce rapidly, would be the most likely invaders from this pathway. Although nonindigenous rotifer species have been reported from the Great Lakes and elsewhere (e.g., Josefsson and Andersson 2001; Gray et al. 2005), there has not yet been confirmation of any established populations in the Great Lakes. Since rotifers are a diverse and taxonomically challenging group, and since they may also be widely distributed by other pathways including wind (e.g., Jenkins and Underwood 1998), we suggest that past invasions may have occurred and that future genetic analysis could reveal the presence of introduced species from this group.

Cladocerans are widely collected from ballast sediments, albeit at low density, and nonindigenous cladocerans are both established in the Great Lakes and predicted to invade in the future. Their population dynamics indicate that diapausing eggs in NOBOB sediments are a possible invasion pathway. A notable exception is *Bythotrephes longimanus*, a successful invader in the lakes (e.g., Vanderploeg et al. 2002) whose lengthy development period suggests that hatched diapausing eggs from ballast sediment may have been an unlikely source.

Many nonindigenous copepods established in or predicted to invade the Great Lakes can undergo diapause, and the population dynamics of *E. affinis* indicate that ballast sediment is a possible invasion pathway. However, since copepod eggs are rare in sediments but their planktonic stages are ubiquitous in ballast water (e.g., Locke et al. 1993; Smith et al. 1999; Wonham et al. 2001), ballast water may be a more likely pathway for this group.

Fig. 5. Effects of simulated ballast water treatment on number of surviving organisms in a tank assuming (*a*) no reproduction and (*b*) parthenogenetic reproduction for the rotifer *Brachionus calyciflorus* (circles) and the cladoceran *Daphnia longiremis* (triangles). The final total number of live juveniles and adults combined is scaled to the initial number of viable diapausing eggs following a one-time 95% (solid symbols and solid line) or 99% (open symbols and broken line) mortality on each of days 2–13 of a 14-day ballast voyage. Daily per capita rates and other parameters are as follows (minimum time to hatching from diapause eggs, t_{min}; diapause hatching rate, *h*; juvenile maturation rate, *m*; adult mortality rate, d_A; parthenogenetic egg production rate, *b*; parthenogenetic egg hatching rate, h_P): (*a*) *Brachionus calyciflorus* (1, 0.809, 1.1, 0.20) and *D. longiremis* (2, 0.198, 0.13, 0.10); (*b*) *Brachionus calyciflorus* (1, 0.809, 1.1, 0.20, 1.8, 1.0) and *D. longiremis* (2, 0.198, 0.13, 0.10, 0.33, 0.33).



Reducing invasion risk

Complete invasion risk reduction for ballast sediments would require zero ballast discharge, but careful ballast management could nonetheless significantly reduce invasion risk. The simplest approach to risk reduction from NOBOB vessels would be to discharge water when the abundance of hatched organisms is minimal (e.g., Drake and Lodge 2004; International Maritime Organization 2004). Under the scenarios modelled here, the minimum (zero) abundance of all diapause species occurs only during the egg development period between the environmental cue (i.e., water uptake at first port of call) and the onset of hatching. For the invertebrate species considered here, the window is typically up to 1–3 days; for algae and microbes, it would be substantially less.

When environmental conditions in the tank do not permit parthenogenetic reproduction, a second minimal abundance of faster-developing species such as rotifers could occur towards the end of the 2-week period. In general, however, this decline should not be anticipated for the entire hatching assemblage, since the abundance of slower-growing and more starvation-resistant species such as cladocerans and copepods would remain high even after 2 weeks. Thus, the predicted optimal deballasting time for minimizing the discharge of nonreproducing diapause organisms is only during the brief time window before the eggs begin hatching. (We note, however, that if diapausing eggs are resuspended in the water during ballasting, they pose an additional invasion risk not treated here.) Considering the operational schedules of vessels operating on the Great Lakes, it would be infeasible to implement this strategy because the ballast water would, in most cases, be needed to stabilize the vessel for a longer period of time.

The physical nature of the invasion pathway can influence propagule pressure over orders of magnitude by allowing parthenogenetic reproduction (Bailey et al. 2005*b*; present study). Since we cannot assume that hatched organisms will fail to reproduce, it appears that any deballasting strategy would be most effective when combined with ballast water treatments (e.g., Kuzirian et al. 2001; Tamburri et al. 2002; Waite et al. 2003). Regardless of population dynamics, postuptake treatment should be applied as late as possible prior to deballasting (allowing time for sufficient mortality and chemical neutralization if necessary) to minimize the number of surviving organisms.

The single-species population dynamics simulated here are clearly simplifications of the multispecies interactions that would be observed in a community of organisms hatching from ballast sediments. Nonetheless, this simple modelling approach provides insights into the nature of this invasion pathway and its effective management for invasion risk reduction.

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Appendix A

The cumulative hatching curves reported for some diapause species appear convex (Bailey et al. 2003), but others appear sigmoid (Ban and Minoda 1992; Yurista 1992, 1997) (Fig. 1*b*). We therefore developed model 1, a single-step hatching process (eq. 1) that can generate only a concave cumulative hatching curve, and model 2, a two-step process (eq. A1) that can also generate a sigmoid hatching curve (Fig. 1):

$$(\mathrm{A}1a)\quad \underbrace{\frac{\mathrm{d}E_{\mathrm{R}}}{\mathrm{d}t}}_{\text{resting eggs}} = -\underbrace{\frac{h_a E_{\mathrm{R}}}{2}}_{\text{initiating development}} - \underbrace{d_{\mathrm{E}} E_{\mathrm{R}}}_{\text{mortality}},$$

$$h_a = \begin{cases} 0, & t < t_{\min} \\ h_a, & t \ge t_{\min} \end{cases}$$

$$(\mathrm{A}1b)\quad \underbrace{\frac{\mathrm{d}E_{\mathrm{D}}}{\mathrm{d}t}}_{\text{developing eggs}} = \underbrace{\frac{h_a E_{\mathrm{R}}}{2}}_{\text{initiating development by resting eggs}} - \underbrace{h_b E_{\mathrm{D}}}_{\text{hatching}} - \underbrace{d_{\mathrm{E}} E_{\mathrm{D}}}_{\text{mortality}}$$

$$(\mathrm{A}1c)\quad \underbrace{\frac{\mathrm{d}J}{\mathrm{d}t}}_{\text{juveniles}} = \underbrace{h_b E_{\mathrm{D}}}_{\text{hatching from developed resting eggs}} + \underbrace{h_{\mathrm{P}} P}_{\text{hatching from parthenogenetic eggs}} - \underbrace{mJ}_{\text{maturation of juveniles}} - \underbrace{d_{\mathrm{J}} J}_{\text{mortality}}$$

The equations for adults and parthenogenetic eggs in model 2 are the same as those in model 1 (eqs. 1*c*–1*d*). Model 1 is the simplest representation of the observed transition from diapausing egg to hatched juvenile, whereas model 2 inserts a compartment for the developing embryo between the resting and hatched stages (Fig. 1*a*). Model 1 is nested within model 2 in that as $h_b \to \infty$, model 2 → model 1. In other words, as the second step of the hatching process becomes infinitely fast, model 2 reverts to model 1 (Fig. 1*b*).

Biologically, model 2 may be interpreted as, first, responding to the hatching cue by initiating development at rate h_a and, second, hatching from the egg at rate h_b. Mathematically, this formulation allows the sigmoid hatching profile that is consistent with observed laboratory data for certain species (e.g., Ban and Minoda 1992; Yurista 1992, 1997) and can be obtained by setting parameters d_{E}, m, and d_{J} to zero and solving for

$$(\mathrm{A}2)\quad J(t) = E_{\mathrm{R}}(0)\,\frac{h_a(\mathrm{e}^{-h_b t} - 1) - h_b(\mathrm{e}^{-h_a t} - 1)}{h_b - h_a}$$

For model 2, the time from diapausing egg E_{R} to developing egg E_{D} has pdf $h_a\mathrm{e}^{-t_a h_a}$ and mean $\bar{t}_a$. The time from E_{D} to hatched juvenile J has pdf $h_b\mathrm{e}^{-t_b h_b}$ and mean $\bar{t}_b$. The total waiting time from E_{R} to J has pdf

$$(\mathrm{A}3)\quad f(t) = \int_0^t h_a h_b \mathrm{e}^{-t_a h_a} \mathrm{e}^{-(t-t_a)h_b}\,\mathrm{d}t_a = \frac{h_a h_b(\mathrm{e}^{-t h_a} - \mathrm{e}^{-t h_b})}{h_b - h_a}, \qquad h_b > h_a$$

with mean $\bar{t} = \bar{t}_a + \bar{t}_b$. The probability of an egg hatching in the time period $j - 1$ to j is

$$\begin{aligned}(\mathrm{A}4)\quad \Pr\{j-1 < T < j\} &= \frac{h_b}{h_b - h_a}\int_{j-1}^{j} \mathrm{e}^{-t h_a}\,\mathrm{d}t - \frac{h_a}{h_b - h_a}\int_{j-1}^{j} \mathrm{e}^{-t h_b}\,\mathrm{d}t \\ &= \frac{h_b}{h_b - h_a}\,\mathrm{e}^{-h_a i}(\mathrm{e}^{h_a} - 1) - \frac{h_a}{h_b - h_a}\,\mathrm{e}^{-h_b i}(\mathrm{e}^{h_b} - 1)\end{aligned}$$

The corresponding negative log-likelihood function for the two hatching rates is

$$(\mathrm{A}5)\quad -l(h_a, h_b \mid t_1, \ldots, t_n) = n\ln(h_b - h_a) - \sum_{i=1}^{n} \ln[h_b\mathrm{e}^{-t_i h_a}(\mathrm{e}^{h_a} - 1) - h_a\mathrm{e}^{-t_i h_b}(\mathrm{e}^{h_b} - 1)]$$

For all species, the maximum-likelihood estimate of h_a and h_b in model 2 was obtained as $h_b^{-1} \to 0$ and $h_a \to h$. In other words, model 1 fit the data better than model 2 in all cases (Fig. 2).

Appendix references[2]

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