Minimizing invasion risk by reducing propagule pressure: a model for ballast-water exchange

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Biological invasions are a major and increasing agent of global biodiversity change. Theory and practice indicate that invasion risk can be diminished by reducing propagule pressure, or the quantity, quality, and frequency of introduced individuals. For aquatic invasions, the primary global invasion pathway is ballast-water transport, and the primary risk reduction strategy is currently open-ocean exchange. Exchange was developed with shipping between freshwater ports in mind, but the majority of shipping connects brackish and marine ports. A worldwide convention, adopted in 2004 by the International Maritime Organization, now mandates ballast-water exchange (or equivalent management) for its 164 member states. Will exchange be as effective in reducing invasion risk for euryhaline species (those capable of tolerating a wide range of salinity levels) in saltwater ports? Here we develop a simple mathematical framework for optimizing ballast-water exchange in terms of exchange level, timing, and species salinity tolerance. Our model shows that when species survival is worse in the post-exchange than in the pre-exchange water, exchange is always effective. However, when survival is equal or better following exchange, a critical level and timing are required for effective exchange. We illustrate the model's applications with a variety of introduced marine and estuarine organisms.

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Biological invasions, a major and increasing agent of global biodiversity change, are often the result of inadvertent releases from trade and travel pathways (Levine *et al.* 2003; Ruiz and Carlton 2003; Drake and Lodge 2004). Empirical and theoretical evidence indicate that invasion risk can be decreased by reducing propagule pressure, specifically, the quantity, quality, and frequency of introduced individuals (Grevstad 1999; Rouget and Richardson 2003; Drake and Lodge 2004; Verling *et al.* 2005). In marine and estuarine systems, the dominant invasion pathway worldwide is the ballast water of commercial ships (Carlton and Geller 1993; Carlton 1998; Ruiz and Carlton 2003; Drake and Lodge 2004; Holeck *et al.* 2004). Current estimates suggest that a global fleet of approximately 35 000 commercial vessels transports an annual volume of about 3.5 x 10^9 metric tons of ballast water, containing some 7000–10 000 species – mostly marine – at any one time (Carlton 1999; Endresen *et al.* 2004; Figure 1)

This invasion pathway is currently managed primarily by open-ocean ballast-water exchange (IMO 2004; Minton *et al.* 2005). Under this practice, a ship's ballast tanks are loaded as usual at the start of a voyage, emptied and refilled in mid-ocean, and subsequently emptied in or near the destination port (Figure 2). Exchange is based on three assumptions: (1) that most initial organisms are flushed out; (2) that remaining organisms survive poorly, if at all, in the newly ballasted ocean water; and (3) that oceanic organisms released in the destination port pose a minimal invasion risk. We focus here on the interaction between the first and second assumptions in determining exchange effectiveness.

Ballast-water exchange was originally developed in the context of ships sailing from fresh- through saltwater back to freshwater, so that any freshwater organisms remaining after exchange would be expected to die in the newly loaded oceanic water. Exchange has since been recommended or required by a number of coastal ports and nations, and a recently adopted International Maritime Organization convention now requires vessels arriving in all 164 member states to conduct open-ocean exchange or equivalent management (IMO 2004; Minton *et al.* 2005). However, it is not clear if exchange would be as effective for saltwater organisms, where post-exchange survival in oceanic water could be equal to or greater than that in the initial water.

Here we develop a simple theoretical framework for evaluating and maximizing the effectiveness of ballast-water exchange. Using this framework, we show when exchange is predicted to reduce propagule pressure, and when it can, counterintuitively, increase propagule pressure relative to a nonexchanged tank. We then apply the model to evaluate exchange effectiveness for a series of

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Figure 1. *Vessel deballasting in coastal waters.*

introduced marine and estuarine species. Although this framework is developed with reference to exchange, it could readily be applied to other ballast treatment methods (eg Waite *et al.* 2003; Minton *et al.* 2005) during or at either end of a voyage.

Ballast-exchange model

Model structure

Our goal is to model organism survival in ballast-water tanks with and without exchange. Based on empirical results (Gollasch *et al.* 2000; Wonham *et al.* 2001; Drake *et al.* 2002; Taylor *et al.* 2002; Murphy *et al.* 2004), we model the abundance of a single species in a single ship as declining exponentially both before and after exchange. We use the following equation modified from equation 7 of MacIsaac *et al.* (2002):

$$(1)\quad \underbrace{n(T)}_{\text{final abundance}} = \underbrace{n(0)}_{\text{initial abundance}} \underbrace{e^{-\mu_1 t_B}}_{\text{survival before exchange}} \underbrace{r}_{\text{retention during exchange}} \underbrace{e^{-\mu_2 (T-t_B)}}_{\text{survival after exchange}} = n(0)e^{(-Mt_B-\mu_2 T)}r$$

Here, $n(T)$ is the final organism abundance at the end of a ballast voyage of length T days and $n(0)$ is the initial abundance. Exchange occurs on day $t_B < T$, and r is the proportion of organisms retained during exchange, giving exchange efficiency as $1 - r$. The difference in per capita daily mortality rates in initial (μ_1) and exchanged (μ_2) water is $M = \mu_1 - \mu_2$. Since we are considering organism abundance within the ship only, we leave off the original ballast discharge parameter r_1. In the absence of exchange, equation (1) simplifies to:

$$(2)\quad \underbrace{n(T)}_{\text{final abundance}} = \underbrace{n(0)}_{\text{initial abundance}} \underbrace{e^{-\mu_1 T}}_{\text{survival over voyage}}$$

as in MacIsaac *et al.* (2002) equation 8.

For simplicity, we consider the abundance of a single ballasted species, and do not consider any new organisms produced during the voyage, loaded during open-ocean ballast exchange, or hatched from ballast sediments (eg Gollasch *et al.* 2000; Wonham *et al.* 2001; Taylor *et al.* 2002; Murphy *et al.* 2004; Wonham *et al.* in press). Species mortality rates μ_1 and μ_2 are not associated with freshwater and saltwater per se, as in MacIsaac *et al.* (2002), but simply with pre-exchange and post-exchange ballast water. We assume that both mortality rates are constant, which is consistent with empirical data for many but not all taxa (Gollasch *et al.* 2000; Wonham *et al.* 2001; Drake *et al.* 2002; Taylor *et al.* 2002).

Model analysis

We define exchange as effective if it reduces the final organism abundance $n(T)$ relative to that in a non-exchanged tank. To obtain the conditions for effective exchange, we set equation (1) < equation (2), and find that exchange is effective if, and only if:

$$(3)\quad r < e^{M(t_B - T)}.$$

When the mortality rate is greater after than before exchange, $M < 0$ and inequality (3) always holds. For $M \geq 0$, inequality (3) means that effective exchange occurs only below a threshold value of exchange retention $r < r^* = e^{M(t_B-T)}$. Assuming $r < 1$, this expression can be rearranged to give the threshold exchange day $t_B > t^*_B = \ln(r)/M + T$, or the threshold difference in mortality rates, $M < M^* = \ln(r)/(t_B - T)$ required for effective exchange. In the last expression, a higher value of M^* generated by more efficient or later exchange (ie as $r \to 0$ or $t_B \to T$) indicates that exchange will be effective over a wider range of $M \geq 0$. As M^* decreases with lower or earlier exchange (ie as $r \to 1$ or $t_B \to 0$), exchange will be effective only for species with lower values of M.

This model illustrates that for species with $M < 0$, exchange is always effective (Figure 3a). We would generally expect this to be the case for freshwater organisms exposed to seawater during open-ocean exchange. For estuarine and marine organisms, we might still expect $M < 0$ if the ocean water were less hospitable than the initial water in terms of salinity or other factors. On the other hand, if the ocean water were equally or more hospitable, we could find $M \geq 0$. In this case, exchange effectiveness would depend on the exchange retention and timing (Figure 3a).

For a given M value, exchange operations can be optimized to minimize the final organism abundance $n(T)$. This is illustrated for a fixed value of $r = 0.1$, with examples of earlier ($t_B = 3$) and later ($t_B = 7$) exchange (Figure 3b). When $M < 0$, earlier exchange leads to the lowest value of $n(T)$. When $0 < M < M^*$, later exchange leads to the lowest $n(T)$. In the region $M > M^*$, $n(T)$ is minimized by not exchanging ballast water (Figure 3b).

The above calculations would ensure effective exchange when that is defined simply as a reduction in $n(T)$ relative to a non-exchanged tank. In a more realistic approach, we consider a target reduction in organism abundance to be x% of a nonexchanged tank. We then obtain, for $M \geq 0$, the more general threshold expressions for effective exchange, $r < r^* = xe^{M(t_B - T)}$, $t_B > t^*_B = \ln(r/x)/M + T$, and $M < M^* = \ln(r/x)/(t_B - T)$. In other words, the lower the value of x, the lower r must be, the later t_B must be, or the lower M must be for effective exchange. To illustrate the model's application to particular species, we use the special case shown in inequality (3) where $x = 1$.

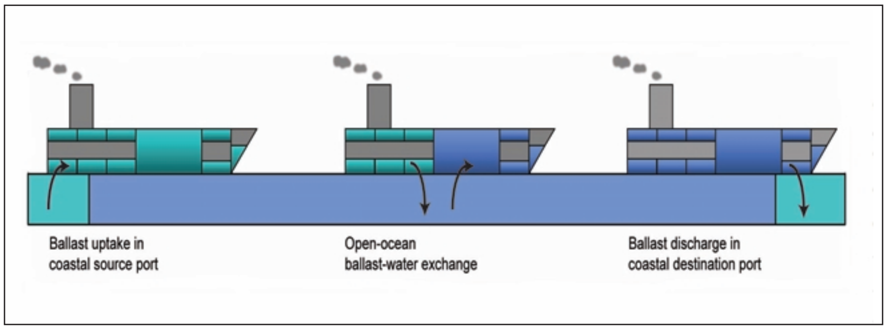

Figure 2. *Illustration of the ballast-water exchange process.*

Application to estuarine and marine species

To illustrate the application of this model, we assumed as a first approximation that the only difference between the initial and oceanic ballast water was salinity. We conducted a literature search to obtain published data on proportional survival p over a given number of days d at lower and higher salinity levels i for known introduced estuarine and marine species. We then estimated each species' daily mortality rate μ_i as $e^{-\mu_i d} = p$ (following MacIsaac *et al.* 2002). We assumed that the lower salinity mortality rate applied in the pre-exchange coastal water, and the higher salinity rate in the post-exchange oceanic water. From these mortality rates, we determined the threshold retention r^* and timing t^*_B of exchange. When multiple data were available in the original sources, we preferentially selected those for planktonic larval and juvenile stages at temperatures 10–20 °C, with salinities as close as possible to the lower range 20–29‰ and the higher range 30–35‰. Although the laboratory studies we used were not designed explicitly to test ballast exchange, they provide preliminary data for examining the biological constraints on effective exchange.

Of the resulting mortality rate estimates, almost all were in the range $0 \leq \mu_i < 0.3$, which is generally consistent with the empirically observed range for invertebrate zooplankton in ballast tanks (eg 0.02–0.22; Wonham *et al.* 2001; Table 1). In approximately half the cases, $M \leq 0$. In these cases, any exchange level $r < 1$ is predicted to reduce $n(T)$ relative to a non-exchanged tank (Table 1). Of these cases, when $M = 0$, exchange timing does not affect $n(T)$; when $M < 0$, exchange on any day is effective and the earlier the exchange, the greater its effectiveness.

For the remaining half of the cases, $M > 0$. Here, exchange is effective only for certain values of r and t_B. For example, if we fix $t_B = 5$ and $T = 10$, the threshold retention value r^* ranges from 0.12–0.99, corresponding to a minimum exchange efficiency of $1 - r^* = 0.01$–0.88 (Table 1). If $r < r^*$, exchange would lead to a higher $n(T)$

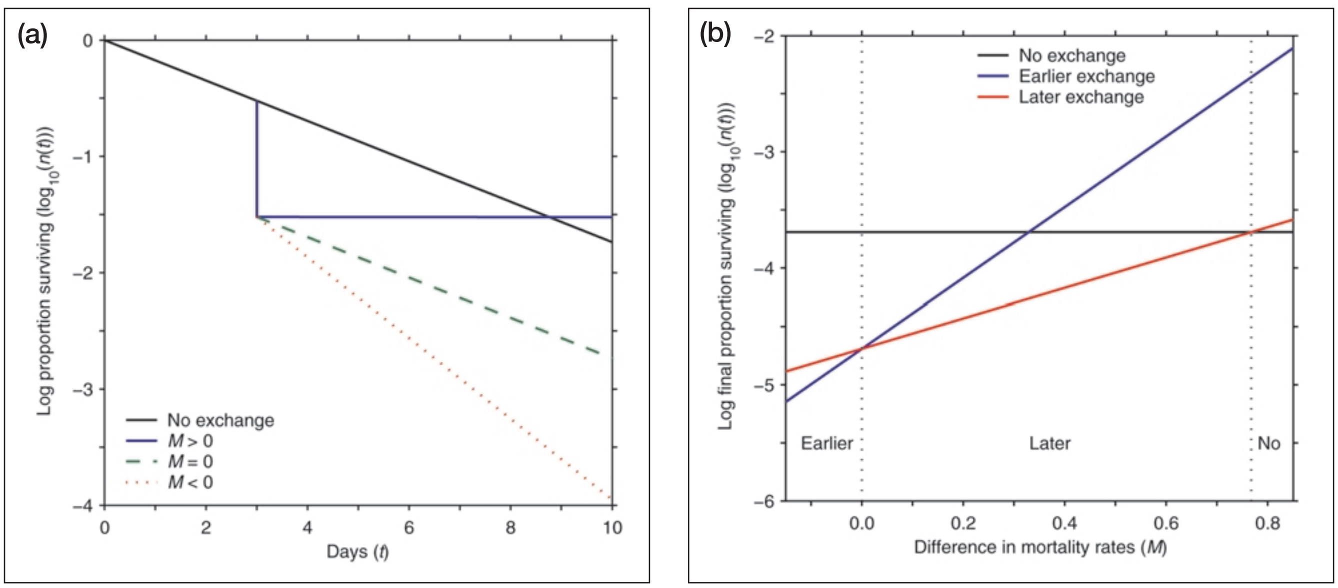

Figure 3. *Ballast-exchange model predictions. In (a), the proportion of organisms surviving in a ballast tank depends on the difference in mortality rates* $M = \mu_1 - \mu_2$, *(parameter values* $\mu_1 = 0.4$; $\mu_2 = 0.001$ *[blue solid], 0.04 [green dashed], 0.8 [red dotted];* $r = 0.1$; $t_B = 3$; $T = 10$*). In (b), vertical dotted lines separate regions of* M *for which no, later, and earlier exchange minimize* n(T) *(parameter values* $\mu_1 = 0.85$, $\mu_2 = [0, 1]$; $r = 0.1$; $t_B = 3$ *[earlier], and 7 [later];* $T = 10$*).*

Table 1. Critical retention and timing of ballast exchange required to ensure effectiveness

Species [a]	*Stage*	μ_1	μ_2	M	r*	t^*_B
Japanese oyster[1]	early larvae	0.000	0.000	0.000	1.00	-
	late larvae	0.000	0.063	-0.063	1.00	+
Eastern oyster[2]	embryos	0.015	0.200	-0.185	1.00	+
Atlantic pearl oyster[3]	larvae	0.602	0.178	0.424	0.12	2.3
Mediterranean mussel[4]	larvae	0.090	0.088	0.002	0.99	3.9
Japanese littleneck clam[5]	larvae	0.000	0.000	0.000	1.00	-
Veined rapa whelk[6]	early larvae	0.093	0.255	-0.162	1.00	+
	late larvae	0.005	0.020	-0.015	1.00	+
Signal crayfish[7]	juveniles	0.004	0.111	-0.108	1.00	+
Eurasian green crab[8]	zoea 1	0.182	0.032	0.150	0.47	2.4
	zoea 2	0.099	0.068	0.031	0.86	2.6
	zoea 3	0.090	0.046	0.045	0.80	2.5
	zoea 4	0.095	0.037	0.058	0.75	2.5
Chinese mitten crab[9]	zoea 1	0.025	0.054	-0.030	1.00	+
	zoea 2	0.008	0.013	-0.005	1.00	+
	zoea 3	0.000	0.000	0.000	1.00	-
	zoea 4	0.015	0.000	0.015	0.93	2.8
	zoea 5	0.009	0.005	0.004	0.98	3.5
	megalopa	0.018	0.038	-0.020	1.00	+
Gammarid amphipod[10]	adults	0.098	0.768	-0.669	1.00	+
Calanoid copepod[11]	juveniles	0.048	0.005	0.044	0.80	2.5
Northern Pacific seastar[12]	larvae	0.227	0.231	-0.004	1.00	+

For selected introduced invertebrates, daily per capita mortality rates μ_1 at lower and μ_2 at higher salinity determine $M = \mu_1 - \mu_2$, for which sample calculations show r^* and t^*_B. Under t^*_B, – indicates that exchange timing does not influence effectiveness; + indicates that exchange on any day is effective, and that effectiveness increases as t_B decreases.

[a] Species names, lower and higher salinities (‰), and sources: 1. *Crassostrea gigas* (24, 32; Yaroslavtseva *et al.* 1991); 2. *Crassostrea virginica* (23, 33; Davis 1958); 3. *Pinctada imbricata* (30, 35; O'Connor and Lawler 2004); 4. *Mytilus galloprovincialis* (20, 30; Matson 2003); 5. *Ruditapes philippinarum* (26, 33; Namaguchi 1998); 6. *Rapana venosa* (25, 32; Mann and Harding 2003); 7. *Pacifastacus leniusculus* (21, 35; Holdich *et al.* 1997); 8. *Carcinus maenas* (20, 32; Anger *et al.* 1998); 9. *Eriocheir sinensis* (25, 32; Anger 1991); 10. *Dikerogammarus villosus* (15, 25; Bruijs *et al.* 2001); 11. *Eurytemora affinis* (10, 27; Lee and Peterson 2002); 12. *Asterias amurensis* (28, 35; Sutton and Bruce 1996).

than in a nonexchanged tank. For comparison, empirical estimates of exchange efficiency range from < 0.5 to > 0.99 (eg Taylor *et al.* 2002), which corresponds to r-values from under 0.01 to over 0.5.

Alternatively, if we fix $r = 0.1$ and $T = 10$, we obtain the threshold value t^*_B, which ranges from 2.4–3.9. For M > 0, exchange would be effective only if conducted on day $t_B > t^*_B$; prior to t^*_B, it would be counterproductive (Table 1). These critical exchange rates would be more readily achieved on some voyages than others. For example, the average voyage distances of vessels arriving in US ports are 1100 km and 8275 km (Drake and Lodge 2004), which at an average sailing speed of 15 knots corresponds to voyage lengths of approximately 1.6 and 12.4 days. These estimates are consistent with observed intracoastal and interoceanic voyage lengths reported for selected US ports (Smith *et al.* 1999; Verling *et al.* 2005). Thus, values of t_B greater than 2 to 4 days would be more feasible for longer transoceanic than for shorter intracoastal voyages.

More generally, we can visualize the range of effective combinations of ballast exchange retention and timing by plotting contour values of r^* as a function of t_B and M (Figure 4a). For a species with a given M value, multiple combinations of r and t_B can be determined to ensure effective exchange. For example, exchange would be effective for the pearl oyster (*Pinctada imbricata*; M = 0.42) with a combination of $r < 0.9$ and $t_B > 4.5$, or $r < 0.7$ and $t_B > 7$ (Figure 2a). For the Eurasian green crab (*Carcinus maenas*), which has a lower M value (first zoeal stage M = 0.15), effective exchange on the same days would require more efficient exchange with a lower r value (Figure 4a).

Some species have different M values at different life stages (Table 1), in which case the same exchange strategy may not be optimal for all stages (Figure 4b). In the Chinese mitten crab (*Eriocheir sinensis*), for example, the first and second zoeal stages have M < 0 so earlier exchange would minimize $n(T)$. In the third stage, where M = 0, exchange timing would not affect $n(T)$. In the fourth and fifth stages, M > 0, so later exchange would minimize $n(T)$ (Figure 4b).

Summary

Population and genetic theory predict that the chances of successful biological invasion increase with the number, frequency, and quality of individuals released. Ballast-water exchange represents a global-scale implementation

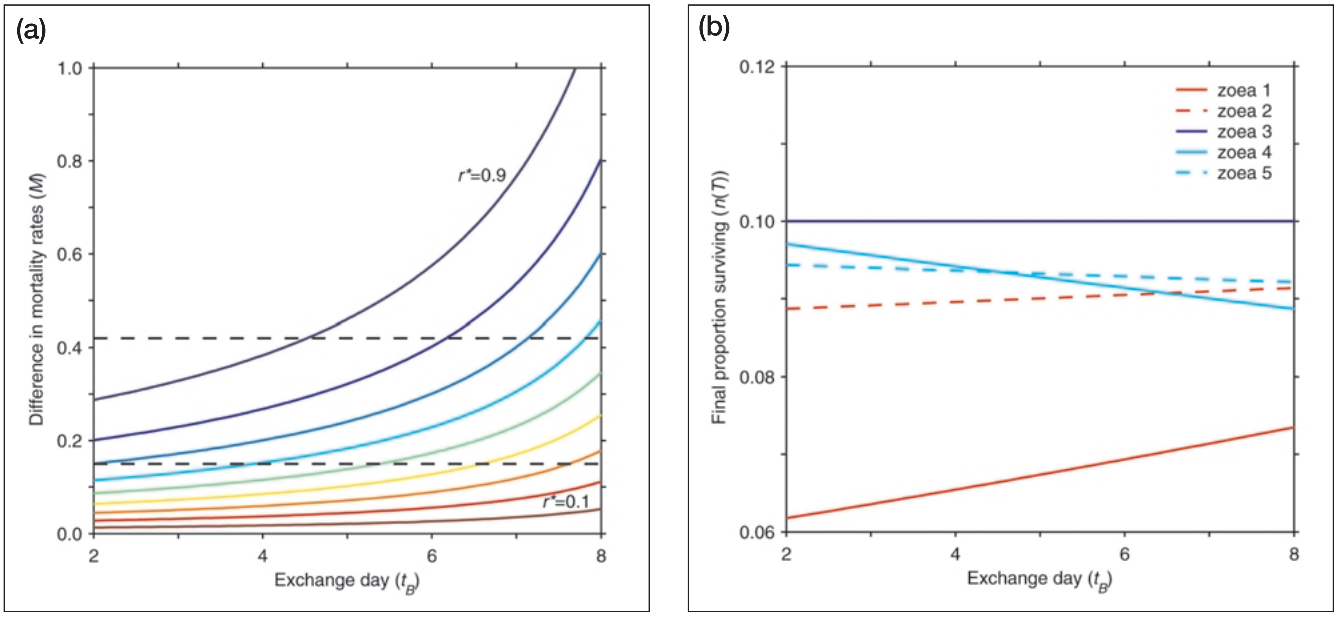

Figure 4. *Using the ballast-exchange model to optimize exchange strategy. In (a), contours of the critical value* r^* *from 0.1 to 0.9 are plotted as a function of* M *and* t_B. *For a given species' M value, shown as lower horizontal dashed line for Eurasian green crab* (Carcinus maenas) *and upper for Atlantic pearl oyster* (Pinctada imbricata), *different effective combinations of* r *and* t_B *can be selected to ensure effective exchange. In (b), five larval stages of the Chinese mitten crab* (Eriocheir sinensis) *have different* M *values and therefore different optimal exchange strategies (shown for* r = 0.1 *and* T = 10).

of this theory designed to reduce propagule pressure and invasion risk in aquatic and marine systems. Although exchange is increasingly being adopted by port states worldwide (IMO 2004) it has been tested empirically in only a few instances (eg Taylor *et al*. 2002).

Here, we have provided a simple model to investigate when and how much exchange reduces propagule pressure, and how this reduction can be optimized. Depending on the species, maximum invasion risk reduction may be achieved by early exchange, late exchange, or no exchange at all. Although there exists a parameter space in which exchange is counterproductive, leading to increased propagule pressure relative to a nonexchanged tank, we find that exchange is generally predicted to be effective for the introduced estuarine and marine species we examined. In many cases, though, there is a minimum exchange level or timing required for effectiveness. Of course, these calculated critical values would apply only to a vessel far enough from the coast to conduct open-ocean exchange, since exchanging too close to the departure or arrival port would defeat the purpose (Taylor *et al*. 2002; IMO 2004).

To introduce this modeling framework, we made several simplifying assumptions that could be investigated with further extensions to the model. Our model incorporates the first two underlying assumptions of ballast exchange, organism flushing during and mortality following exchange, but the third assumption of minimal survival of oceanic organisms in coastal waters remains to be assessed. Although we developed this model for a single species or life stage, a ballast assemblage typically consists of multiple species and life stages, with a resulting wide range of optimal exchange strategies that need to be considered together. Additional aspects of the ballast community, including organisms hatching and reproducing during the voyage, could also be incorporated (eg Wonham *et al*. in press). We assumed that exchange affected only ballast-water salinity, although it may also affect oxygen, pollutant, and nutrient levels, as well as species composition, all of which could influence mortality rates. We also assumed that mortality rates

Panel 1. Model parameters

Symbol	*Meaning*
$n(0)$	initial organism abundance in ballast tank
$n(T)$	final organism abundance in ballast tank
μ_1	daily per capita mortality rate before exchange, $0 \le \mu_1 \le 1$
μ_2	daily per capita mortality rate after exchange, $0 \le \mu_2 \le 1$
T	voyage duration in days
M	difference in mortality rates, $\mu_1 - \mu_2$
M^*	critical difference: only when $M < M^*$ will exchange reduce $n(T)$ relative to a nonexchanged tank
t_B	day of ballast exchange, $t_B < T$
t^*_B	critical exchange day: only when $t_B > t^*_B$ will exchange reduce $n(T)$ relative to a nonexchanged tank
r	proportion of organisms remaining following exchange, $0 \le r \le 1$
r^*	critical proportion: only when $r < r^*$ will exchange reduce $n(T)$ relative to a nonexchanged tank
$1 - r$	exchange efficiency

before and after exchange were constant, although empirical evidence shows that they can vary (Gollasch *et al.* 2000; Wonham *et al.* 2001; Drake *et al.* 2002; Taylor *et al.* 2002). A more complex model could incorporate a range of mortality functions dependent on multiple environmental variables. Finally, the observed variation in the ballast assemblage and environment indicates the importance of considering alternate management strategies to complement ballast-water exchange in reducing invasion risk (eg Carlton 1998; Taylor *et al.* 2002; Minton *et al.* 2005). Modifications of our model could be readily used for similar analyses of other emerging ballast-treatment methods.

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