Am. Midl. Nat. 154:459–470

Theory and Preliminary Analysis of Species Invasions from Ballast Water: Controlling Discharge Volume and Location

JOHN M. DRAKE[1] AND DAVID M. LODGE
Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana 46556

AND

MARK LEWIS
Department of Mathematical and Statistical Sciences, and Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2G1, Canada

ABSTRACT.—Introductions of non-indigenous species in ballast water are one of the greatest threats to freshwater and marine ecosystems worldwide. New approaches to reducing the release of organisms from ballast water are under consideration nationally and internationally. Unfortunately, the development of scientifically defensible policy for controlling introductions from ballast water has been retarded by the lack of relevant ecological theory and a shortage of information about the identity and numbers of organisms in ballast. Here, we present a novel quantitative approach to estimating the risk of species establishment by combining a model for population spread with known allometric correlations between body size and population growth rate for broad taxonomic categories. Our approach is applicable to sexually reproducing, planktonic taxonomic groups including ctenophores, cnidaria, arthropods, annelids, mollusks and (as an approximation) echinoderms and fishes. As expected, the allowable volume of ballast discharge depends strongly on the acceptable level of risk (which is a societal decision), the taxonomic group of concern and the characteristics of the receiving environment. For example, for a risk tolerance equivalent to establishment of one in one hundred introduced species, independent releases of untreated ballast water should not exceed around 50,000 metric tons. Because of differences in horizontal mixing in different environments, releases in harbors are more risky than releases in open water. These results provide quantitative guidelines that could immediately lower the risk of species invasion while other more permanent technological solutions are developed.

INTRODUCTION

The transportation and release of untreated ballast water is the leading cause of introductions of non-indigenous aquatic species into navigable coastal waters and large inland lakes and seas worldwide (National Research Council, 1996). Introductions of such non-native species as zebra mussels (*Dreissena polymorpha*) and comb jellies (*Mnemiopsis ledyi*) have caused large irreversible changes to food webs, ecosystem cycles and other environmental processes. In order to combat this biological pollution, technologies are being developed and tested to treat ballast water (Raymakers, 2001; Tamburri *et al.*, 2002) while local, national and international legislative bodies are considering the establishment of sanitation standards for ballast water discharge (Marine Environmental Protection Committee, 2002). However, if such efforts are not based on scientific data, the potential effectiveness of proposed standards cannot be predicted and the risk of future invasions will continue to be sub-optimally managed. Here we suggest a new conceptual approach to

---

[1] Corresponding author current affiliation: National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara, California 93101; e-mail: drake@nceas.ucsb.edu

evaluating the risk of ballasting practices which could complement any other approach, including approaches based on reduction of propagules in ballast or regulating total maximum daily loads (NRC, 2001). Short-term recommendations that emerge from this approach would probably not require substantial new technologies and could, therefore, be implemented to reduce the risk of ballast-mediated introductions until technological solutions are developed and installed. The approach could also inform any design standards for longer-term solutions such as shipboard filtration or other technologies.

Alternative approaches to regulating ballast water discharge are currently under consideration, both in the United States 109th Congress (S.770, HR.1591) and internationally (Marine Environmental Protection Committee, 2002). An absolute quantitative standard would set a limit on the number or density of propagules that could be released [International Convention for the Control and Management of Ships' Ballast Water and Sediments Regulation D-2, Ballast Water Exchange Standard; S.770 §3(f)]. Such a limits-based standard could be used either as a benchmark for the effectiveness of treatment technologies or for legislating actual ballast water discharges. Litigation and enforcement scenarios for such a standard might be comparable to effluent standards for water quality and atmospheric discharge. In contrast, another proposed approach would quantify ballast water treatment effectiveness as a percentage reduction from initial concentration of organisms. We believe that the latter, relative approach, which has been adopted by the International Maritime Organization's International Convention for the Control and Management of Ships' Ballast Water and Sediments (Regulation D-1) and embodied in the pending U. S. National Aquatic Invasive Species Act [109th Congress, S.770 §3(e), HR.1591 §101(b)], is not sufficiently based on scientific knowledge of invasions. If initial numbers of organisms in ballast are high, even large percentage reductions could allow the release of enough organisms to pose an unacceptably high risk of population establishment.

Current research in invasion biology indicates that the probability of establishment increases with the number of biological propagules released (Green, 1997; Grevstad, 1999; Kolar and Lodge, 2001; Lockwood *et al.*, 2005). However, since ships differ greatly in the volumes of water and the densities of organisms in the water that they release (National Research Council, 1996; National Ballast Information Clearinghouse, http://invasions.si.edu/ballast.htm), we believe that reducing organism densities by a specified percentage has little meaning with respect to the probability of establishment because the density of organisms remaining after reduction would depend on initial densities. Moreover, as a relative standard, treatment efficiency creates a disincentive for ship operators to implement practices that reduce the number of propagules in ballast tanks (*e.g.*, drawing ballast in deep water, interchange with water of different salinity and regular cleaning and maintenance of ballast tanks) by rendering specified removal efficiencies more difficult to attain. For example, reducing densities of organisms from 1000 m^{-3} to 50 m^{-3} is probably less costly than a reduction from 20 m^{-3} to 1 m^{-3} although both represent a reduction of 95%. The conceptual framework we present here suggests that a third approach could contribute to overall strategies of risk reduction: diluting the release of non-indigenous species by limiting the volume or location of ballast water discharges.

Our analyses are guided by the rationale that any ballast water standard should meet the following three criteria. First, the approach should be based on current knowledge in invasion biology, which indicates that spatial spread and nonlinearities in population dynamics create thresholds in the probability of establishment, at least for sexually reproducing species (Lewis and Kareiva, 1993). This is important for managing invasion risk because control efforts that do not lower populations below threshold levels for persistence will be highly ineffective. On the other hand, the marginal benefits obtained by increasing efforts beyond these thresholds are negligible, although setting target standards at some level below these thresholds may be desirable for mitigating uncertainty. Second, methods should account for differences among species. The number of individuals required to establish a viable population will generally be inversely proportional to body size (*see* later development of this idea), *i.e.*, one expects that fewer fish than copepods are required to establish a viable population. Interspecific differences in mobility, mate-finding and other behaviors will cause noise around this pattern. However, the general relationship implies that technologies that more efficiently remove large organisms, such as filtration technologies, should not necessarily be disregarded because they fail to reduce the number of microorganisms to levels appropriate for macroscopic species. Third, any approach must be applicable to a range of species. This is essential in order for standards to be practically implemented and politically feasible. Any framework must be general enough to assess the probability of establishment for a range of life histories and mating systems, but specific enough to provide reasonably accurate and biologically meaningful standards.

We developed a method based on reaction-diffusion models and allometric scaling rules that meets these criteria and provides reasonable order-of-magnitude estimates of safe release volumes of ballast water at specified levels of risk. While better parameter estimates could improve future applications of this approach, current data are sufficiently robust to derive short-term—perhaps stopgap—guidelines for discouraging the discharge of a volume of ballast water greater than those that cause a given acceptable risk.

Reaction-diffusion equations have long been used to model population spread (Skellam, 1951; Kierstead and Slobodkin, 1953; Patlak, 1953). These equations combine a dynamical model of population growth (the "reaction dynamics") with spatial spread through the concept of diffusivity, a regular rate at which organisms are redistributed in space. For species that exhibit Allee effects—diminished per capita population growth rates at low densities–reaction-diffusion models predict that a minimum area must be initially occupied for establishment to occur (Lewis and Kareiva, 1993). This effect is exhibited by all sexually reproducing species due to mate limitation in sparse populations, including many species of concern in ballast water such as most cnidarians, ctenophores, amphipods, copepods, ostracods, barnacles, decapods, other arthropods, leeches, polychaetes, mollusks, echinoderms and fishes. Mate limitation will not affect asexual microorganisms, including phytoplankton, cladocera (during most parts of their life cycles) and oligochaetes, though Allee effects in these species could possibly result from other mechanisms. Our approach overcomes the specificity of reaction-diffusion models (and of population growth models in general) by fixing one parameter, the severity of the Allee effect, at a moderate but reasonable value (*see* Methods) and by applying a known allometric relation between intrinsic rate of increase and individual body mass to estimate population growth rates (Blueweiss *et al.*, 1978; Peters, 1983). Because this method regresses intrinsic rate of increase on a wide range of body sizes, and does not explicitly address the aspects of life history that are unique to individual species, it cannot provide precise predictions of establishment probability for particular species. Rather, species' idiosyncrasies are reflected in the distribution of growth rates for all species considered together in order to focus on the predictability of invasion rates over all species. Moreover, because uncertainty is explicitly incorporated in the calculation of invasion risk, this method should be robust for the large number of releases of many species that occurs in ballast water discharge. As explained in subsequent sections, our method propagates uncertainty in three parameters: the severity of the Allee effect; differences in population growth rate among species; and diffusivity.

METHODS

Our analysis proceeds in four steps. First, we describe the appropriate reaction-diffusion equations for modeling biological invasions of sexually reproducing species. Second, we describe how uncertainty is handled within each step of the subsequent modeling. Third, we employ an allometric relationship between body size and intrinsic rate of population increase (r) to project the minimum population size, in terms of area occupied, that ensures establishment. Finally, based on diffusivities estimated from previous studies we project invasion risk as a function of body size, which we relate to broad taxonomic groupings.

REACTION-DIFFUSION EQUATIONS

After the initial release of ballast water, the growth of introduced populations will depend on the outcome of a race between population growth through reproduction and propagule dispersal from the release point. For sexually reproducing species, individuals that are transported sufficiently far from the core population will fail to reproduce because they cannot find a mate. Thus, some populations will diffuse faster than they reproduce so that they decrease until extinct; populations that reproduce faster than they diffuse will increase in density and establish viable "beachhead" populations. Because our approach applies to organisms released at densities above the Allee threshold, and ultimately models a race between two rates (population growth and diffusion), the density of organisms is factored out. In the end, we calculate our results in terms of volume of water released.

We start, however, with a typical reaction-diffusion model of the form

$$\frac{\partial u}{\partial t} = D\nabla^2 u + f(u) \tag{1}$$

where ∇ denotes the spatial gradient, t is time, u is the local population density scaled by the carrying capacity (often described as "relative density"), D is diffusivity and $f(u)$ describes local population growth (Lewis and Kareiva, 1993). We modeled the growth of populations subject to an Allee effect with the Nagumo function

$$f(u) = ru(1-u)(u-a) \tag{2}$$

where populations exhibit negative growth rates below a critical threshold a and positive growth rates above a, $0 < a < 0.5$ (Lewis and Kareiva, 1993). (For this reason a is known as the *critical density*.) For simplicity and generality we make the assumption that the introduced population occupies a radially symmetric area around the release point from which organisms diffuse in all directions. Under the assumption of a mild Allee effect, necessary and sufficient conditions for the establishment of the population are

$$R_{\min} = \frac{1}{1/2 - a}\sqrt{\frac{D}{2r}} \tag{3}$$

where $R_{\min}$ is the radius of the initially occupied area (Lewis and Kareiva, 1993). In the derivation of eq. (3) it is assumed that the original release density u_0 is considerably above the Allee threshold a. If we could release ballast water with organisms at densities below a there would be relatively little threat of invasion. However, the parameter a typically is very small and highly uncertain, rendering such an approach impractical. Our analysis, therefore, is restricted to the alternative case where the release density is considerably above a, but the area of release is limited to a certain radius.

Of course, ballast water releases are three-dimensional, occupying a volume rather than an area. However, under most circumstances (*see* Discussion), horizontal diffusivity is orders

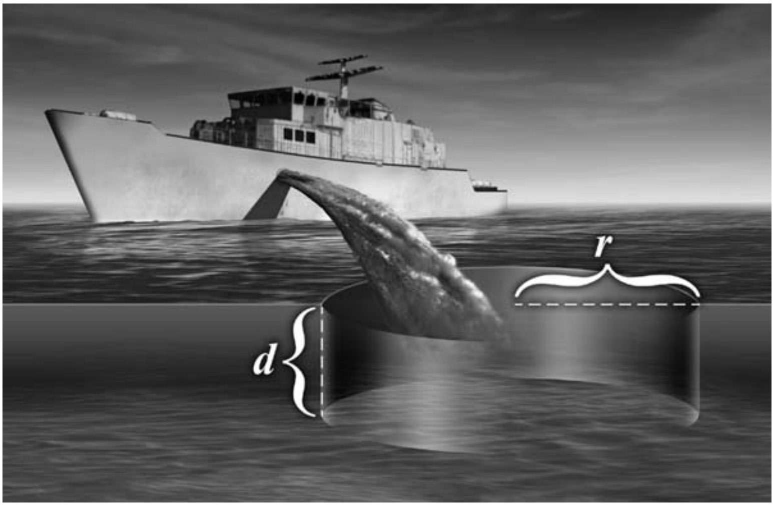

FIG. 1.—Schematic model of ballast water release. The modeling framework here assumes a depth (d) of 10 m for a volume with radius r. This allows an essentially two-dimensional approach to estimating the maximum volume of water that may be released to maintain the risk of population establishment at or below a level that would be specified by policy

of magnitude larger than vertical diffusivity; therefore, the hydrological processes responsible for ecological diffusion occur primarily in the horizontal plane (Imboden and Wüest, 1995). Thus, for the current application it is most appropriate to consider spread in only two dimensions. To transform the three-dimensional problem (the release of a volume of ballast water) into a two-dimensional problem we assume that the volume of ballast water released takes the shape of a cylinder, the minimum radius of which is given by eq. (3). Then, the volume of ballast water that can be safely released is determined by $R_{\min}$ and the length d (depth) of the cylinder through the standard relation $V = \pi r^2 d$, $r = R_{\min}$ (Fig. 1). For the remainder of this analysis we assume $d = 10$ m and report our results in volumetric terms, designating $V_{\max}$ as the theoretical maximum volume of water that can be released at a specified level of risk. Provided that our choice of d is reasonable, the exact value is not hugely important since $V_{\max}$ scales linearly with d.

REPRESENTING UNCERTAINTY

In managing the risk of biological invasion our task is to estimate the qualitative dynamics – whether a population will establish or not – for an acceptable risk threshold ρ, with the interpretation that society will tolerate an establishment rate of $(\rho)100\%$; *i.e.,* if we accept $\rho = 0.01$ then, on average, we expect that one out of 100 introduced species will invade. We distinguish ρ from the α of ordinary statistical inference to emphasize the difference between risk (ρ), which is a combination of natural variation and epistemic uncertainty, and statistical uncertainty (α), and to clarify in places where usage might be ambiguous. That is, in this paper, we adopt the convention $\alpha = 0.05$ for the significance of the hypothesis test that intrinsic rate of increase scales with organism body size (*see* below), whereas we suppose that society will generally be concerned with lower thresholds of invasion risk, *e.g.,* $\rho = 0.01$ (*see* below).

ALLOMETRIC RELATIONS BETWEEN BODY MASS AND RATE OF INCREASE

We exploit the variation in growth rate among species in our assessment of invasion risk as follows. First we specify ρ, which is defined in the previous section as a tolerance threshold and which we suppose is set by policy. Over 21 orders of magnitude, population growth rate is highly predictable from body size for a wide range of taxonomic groups ($P < 0.0001$, $R^2 = 0.904$; Blueweiss *et al.*, 1978). We repeated the regression of Blueweiss *et al.* (1978) (data were obtained by digitizing Fig. 17 of their paper) to obtain confidence bands on the predicted intrinsic rate of increase. We use the upper (1–2 ρ) prediction interval, *i.e.,* the confidence interval on the observations, from the allometric regression in Blueweiss *et al.* (1978) to probabilistically bound intrinsic rate of increase in the reaction-diffusion model. This means that the probability that an unknown species has a maximum per capita population growth rate higher than our value is precisely ρ. We interpret the allometric result reported by Blueweiss *et al.* (1978) as the maximum per capita population growth rate. This is related to our parameter r in the following way. The maximum per capita population growth rate is given by $r_{\max} = 4r/(1-a)^2$ [eq. (4) in Lewis and Kareiva, 1993]. For small a, $r_{\max} \approx 4r$. Rearranging, our parameter r is given by $r_{\max}/4$, where $r_{\max}$ is given by the upper (1–2 ρ) prediction interval of the regression Blueweiss *et al.* (1978). Equivalently, inserting $r_{\max}$ in place of r in eq. (3), the minimum radius is given by

$$R_{\min} = \frac{2}{1/2 - a}\sqrt{\frac{D}{2r_{\max}}} \tag{4}$$

Now, for given a, D, and d, $V_{\max}$ is calculated as a function of body size.

Critical density (a) governs the severity of the Allee effect. Since Allee effects have rarely been measured in natural populations and are difficult to predict theoretically (Fowler and Baker, 1991; Liermann and Hilborn, 1997) , to compute recommended standards we assumed that $a = 0.01$, *i.e.,* that a population will not exhibit deterministic decline until it reaches a level equivalent to 1% of carrying capacity. Errors in $V_{\max}$ resulting from errors in this parameter will have the same sign, *i.e.,* if a is underestimated, $V_{\max}$ will be underestimated. Over the range of r and for small a, $V_{\max}$ is relatively insensitive to changes in a (Fig. 2). For example, at the lower end of diffusivities (0.02 m^2s^{-1}), for a population exhibiting a maximum per capita population growth rate of 0.83 individuals d^{-1}, a change in the Allee effect threshold from $a = 0.01$ to 0.03 (a change of 300%) corresponds to a change in releasable volume of approximately 8.7%. Thus, we do not consider uncertainty in this parameter further.

ESTIMATING THE DIFFUSION COEFFICIENT

Though difficult to measure, diffusion in large water bodies, horizontal diffusivity in particular, has a long history of theoretical and empirical analysis. A comprehensive review for medium-sized (480–21, 790 ha) Swiss lakes found that D varied between 0.02 m^2s^{-1} and 0.3 m^2s^{-1} in dye release experiments (Peeters *et al.*, 1996), a result that is consistent with an earlier measurement of horizontal diffusivity in Lake Ontario (Murthy, 1976). Because we compute our standards for the minimum (0.02 m^2s^{-1}) and maximum (0.3 m^2s^{-1}) values reported, our estimates bound the range of expected invasion probabilities. Imboden and Wüest (1995) observe that these rates are about five times smaller than measurements of horizontal diffusivity in the oceans. Thus, our estimates should be adjusted upward by 5× for managing risk in marine systems (*i.e.,* acceptable release volumes in the ocean could be larger than in lakes for the same level of risk). Because of the variability among locations and over time it is unreasonable to expect that more precise estimates of D would be

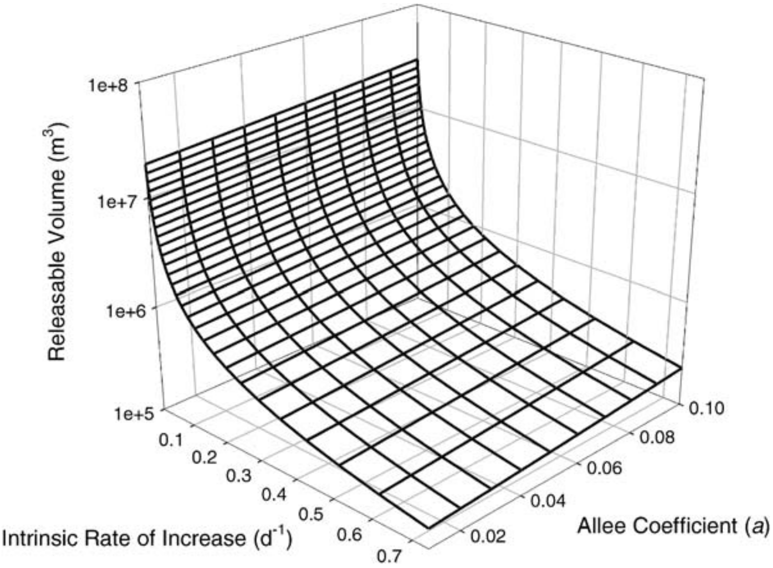

FIG. 2.—Sensitivity of allowable release volume. Allowable discharge volumes are more sensitive to changes in population growth rate (d^{-1}) than critical density (*a*)

meaningful for developing general models of invasion probability. Further, since the precise distribution of D for even one location is unknown, it is not reasonable to incorporate variation in D in our estimates of invasion probability (which might otherwise be accomplished using parametric statistics or Monte Carlo techniques). For these reasons, we consider the uncertainty in D by analysis on the interval [0.02, 0.3]. Hence, our result consists of two bands that bound V_{max} for a given risk tolerance ρ. In using hydrological diffusivity to describe animal movement we assume that organisms are truly planktonic, *i.e.,* that their dispersal is entirely passive. Of course, most organisms, especially fish, have some powers of mobility and aggregation and can, therefore, counteract the influence of Allee effects to some extent. Our approach therefore underestimates the chance of invasion.

RESULTS

For invasion risk tolerances $\rho = 0.01$, 0.001 and 0.0001 we calculated the maximum volume of water that can be released (V_{max}) for species ranging in size from 1.1×10^{-5} g (small copepods) to 2.0×10^{1} g (ctenophores) (Fig. 3). The risk associated with each ρ is bounded by two lines, corresponding to the interval of realistic organism diffusion coefficients from horizontal mixing reported by Peeters *et al.* (1996). The solution in eq. (3) obtained by Lewis and Kareiva (1993) relies on the assumption that population dynamics are relatively fast compared to organism redistribution through diffusion. Because the values used in this paper occupy regions of parameter space near the boundary of where this condition obtains, we conducted extensive numerical simulations to confirm the appropriateness of our reported results. For most of the relevant parameter space this solution is indeed acceptable. However, where diffusivity is great and population growth is slow (upper lines to the right of the vertical dashed line in Fig. 3) the analytic

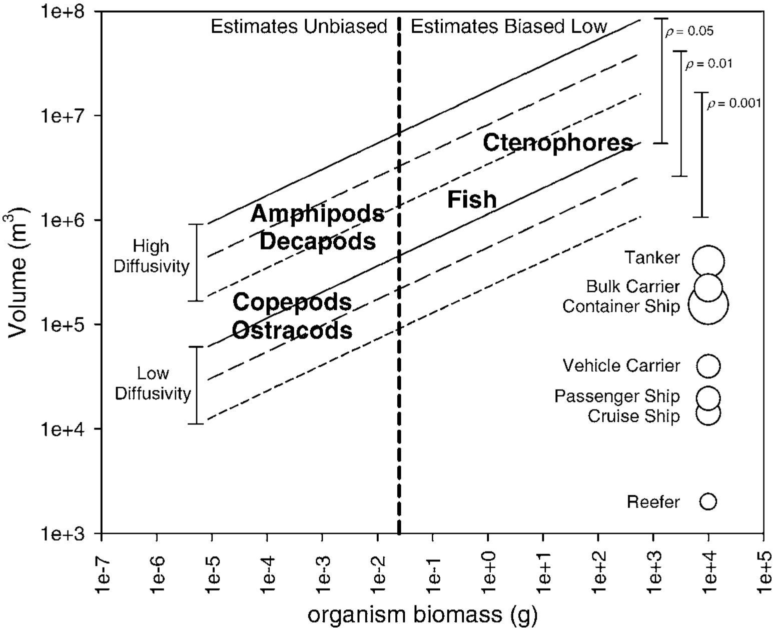

FIG. 3.—Maximum safe release volumes for target taxa. Confidence bands are shown for risk tolerances ρ = 0.01, 0.001 and 0.0001. Band width determined from the interval of measured diffusivities (see text). Organism size (x-axis) is for the lower boundary of adult organism size by taxonomic group. Circles indicate the approximate volume of ballast water carried by different types of ships; circle area indicates relative abundance of ships entering coastal waters of the United States. Estimated releasable volume in the biased region (right side of graph) is underestimated by the method of Lewis and Kareiva (1993; *see* text)

approximation of acceptable volume (*see* Reaction-diffusion equations) is underestimated. This bias does not affect other regions of this graph. These results are most easily applied to specific taxonomic groups by allowing discharge of ballast water volumes no larger than the smallest maximum volume for each group (Table 1).

Determining the acceptable level of risk is a societal (not purely technical) problem, and the difficulty of conceptualizing such probabilities in familiar terms, is often an obstacle to deciding risk thresholds. In addition, quantitative metrics like the probabilities that scientists and social scientists often use to communicate risk often fail to fully capture societal concerns, especially for low probability, high severity hazards such as biological invasions (Sunstein, 2002). Therefore, to make these probabilities more intuitive, we present the chance of invasion by at least one species as a function of the number of different species introductions whose chances of establishment are independent. For simplicity, we narrow our focus to one organism body size, that of the smallest copepods. Because the chance of invasion for one introduction is ρ, the chance of one invasion occurring in N introductions is $1 - (1 - \rho)^N$. Thus, we can illustrate how the chance of one invasion changes as a function of the number of introductions for each hypothetical risk threshold (Fig. 4).

Finally, the results shown in Figure 3 depend strongly on horizontal diffusivity, which varies greatly across aquatic environments (Fig. 5). Clearly, the location of discharges may be

TABLE 1.—Acceptable volumes of ballast water discharge depend on social risk tolerance. For risk thresholds $\rho = 0.01$, $\rho = 0.001$ and $\rho = 0.0001$ chance of establishment per introduction, we calculated the maximum acceptable volume for discharged ballast water for representative groups of potential invasive species

	Acceptable volume (metric tons)		
Taxon	$\rho = 0.01$	$\rho = 0.001$	$\rho = 0.0001$
Copepods	122,000	52,000	24,000
Amphipods	244,000	104,000	49,000
Decapods	291,000	124,000	58,000
Fish	1,393,000	592,000	278,000
Ctenophores	4,724,000	2,007,000	943,000

as important to invasion risk as the volume of ballast water discharged or the density of organisms it contains, so that discharging organisms in enclosed harbors where diffusivity is small is riskier than in open waters or in the open ocean. Thus, for a particular volume of ballast there is a tradeoff between the chance of invasion and the costs and risks to ship safety of discharging in different environments.

DISCUSSION

We combined invasion theory (reaction-diffusion models), the best empirical estimates of diffusivity and allometric scaling of population growth rates to derive a new approach to

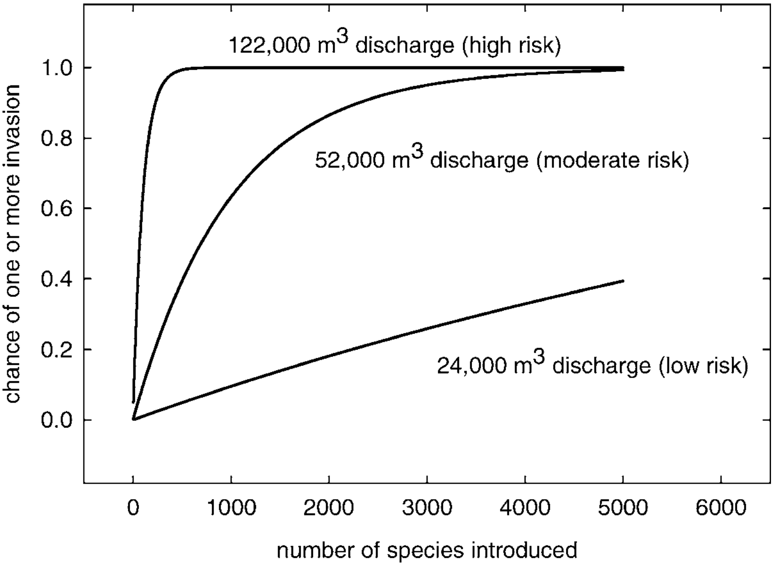

FIG. 4.—Risk of invasion increases with the number of releases. Graph shows cumulative chance of a copepod invasion (as an example) at different levels of discharge. This is representative of the relationship between acceptable invasion risk, discharge volume, and number of introductions in general

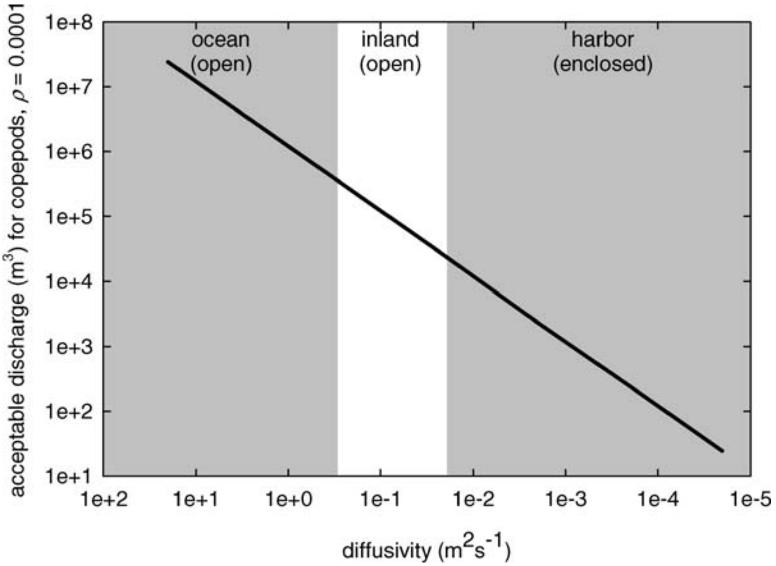

FIG. 5.—Acceptable discharge volume depends on water body. Results for copepods and one risk level illustrate that discharge in waters with low levels of horizontal mixing and low diffusivity (*e.g.,* harbors) is riskier than discharge in water with higher levels of horizontal mixing and high diffusivity (*e.g.,* ocean)

estimate risk of invasion from release of ships' ballast. This approach suggests that even in the absence of detailed information about the identity and numbers of organisms in ballast, reasonable risk management—at least until better technologies are available—could proceed for some species on the basis of volumes and location of water released. To effectively manage ballast water invasions with such an approach, the allowable release volume must be set for the smallest-bodied species. For example, for a risk tolerance of 0.01% chance of invasion per introduction of a species, this is about 24,000 metric tons; this increases to 52,000 and 122,000 metric tons for risk tolerances of 0.1% and 1% chances of invasion, respectively. The acceptable release volumes for all three levels of risk tolerance modeled in this study are lower than the total maximum volume of ballast carried by container, bulk, and tanker ships (Fig. 3); volumes of actual releases of ballast water of many ship types are commonly of the same order of magnitude as acceptable releases (National Ballast Information Clearinghouse).

Although our approach overcomes some challenges and can help inform ongoing discussions about regulatory standards, it also underscores the difficulty of developing scientifically informed, data-driven standards that are generally applicable. Assumptions we have made in order to achieve the required generality include that all species are sexually reproducing; that each release of ballast water is biophysically independent of other releases with respect to invasion risk; that ballast water is released into open systems (*i.e.,* where dispersal of propagules from the population is not impeded by rigid boundaries); and that all species are planktonic (cannot aggregate themselves). Clearly, our approach does not apply to asexually reproducing species (microorganisms, cladocera and oligochaetes), highlighting the importance of ballast water treatment for these taxa. If multiple ships release the same species near the same place around the same time, the risk of invasion may be higher than that calculated under our assumption of independent releases. Because ballast water is often released in confined areas like harbors, not only is the independence assumption likely to be violated, but the assumption of unimpeded dispersal is also likely to be incorrect. In addition to rigid physical boundaries, unimpeded dispersal would also be violated if discharged ballast was of higher density (*e.g.,* higher salinity) and became trapped in holes or local depressions, such as would occur if marine ballast water was discharged in freshwater ecosystems, but not if fresh ballast water was discharged in marine ecosystem. Finally, many species are not planktonic. Some are strongly benthic (*e.g.,* decapods, amphipods, some fishes) while others are strong swimmers and able to locate one another in the pelagic zone (*e.g.,* many fishes). Each of these common violations of our assumptions works in the same direction: our estimates of risk are likely to be too low, but incorporating quantitative corrections for these assumptions awaits further research.

High priorities for future research should be to examine alternative models for population growth that would be relevant to asexually reproducing species (*e.g.,* stochastic versions of the reaction dynamics); to examine how the frequency of ballast water release interacts with volume released to increase invasion risk; to gather more precise empirical estimates of horizontal diffusivity, and the influence of various boundary conditions like those that might apply in harbors; and to estimate quantitatively how aggregation of different species increases estimated risk of invasion.

In conclusion, this approach suggests that for planktonic organisms, the volume and location of ballast water released might be more important for determining establishment success than the number or density of organisms it contains. This is because establishment failure results when organisms are lost to the population through diffusion faster than they are produced. An approach to ballast water management based on releasing smaller volumes at multiple independent locations is different than ideas currently under consideration, and provides unique practical opportunities for supplementing other potentially effective management strategies. Indeed, the current practice in which a large number of ships release water into a single confined harbor probably increases the rate of invasion compared to reasonable alternatives. Perhaps, for some special cases such as ships carrying small volumes of ballast, costly technologies need not be employed for ballast water management, though without experimental confirmation, policy that does not require reducing propagule pressure would be imprudent. We underscore that although ballast water discharge is not the only way in which introductions of non-indigenous species are associated with shipping, it is believed to be the leading one (Fofonoff *et al.*, 2003). We submit that controlling discharge volume and location, or otherwise increasing diffusivity (*e.g.,* by redirecting water flow in harbors; Varden, 2005), may be an economical stopgap solution to species invasions caused by ballast water discharge and indeed may even play a role in larger comprehensive programs for invasive species management.

Acknowledgments.—We thank Dorn Carlson, Dean Wilkinson, Richard Everett and Allegra Cangelosi for useful discussions. This paper was considerably improved by comments from anonymous reviewers. This project was supported by an EPA STAR grant (to DML and G. Dwyer), a Great Lakes Fishery Commission grant (to DML), an EPA STAR Graduate Research Fellowship (to JMD), a scholarship from the Illinois-Indiana Sea Grant (to JMD), a University of Notre Dame Schmitt Graduate Student Research Fellowship (to JMD), an NSERC Collaborative Research Opportunities grant (to MAL) and a Canada Research Chair (to MAL). It is also a contribution from the Integrated Systems for Invasive Species (ISIS) project (DML, P.I.), funded by the National Science Foundation (DEB 02-13698) and the University of Notre Dame.

LITERATURE CITED

BLUEWEISS, L., H. FOX, V. KUDZMA, D. NAKASHIMA, AND R. PETERS, ET AL. 1978. Relationships between body and size and some life history parameters. *Oecologia,* **37**:257–272.

FOFONOFF, P. W., G. M. RUIZ, B. STEVES AND J. T. CARLTON. 2003. In ships or on ships? Mechanisms of transfer and invasion for nonnative species to the coasts of North America, p. 152–182. *In:* R. M. Ruiz and J. T. Carlton (eds.). Invasive species: vectors and management strategies. Island Press, Washington, D.C.

FOWLER, C. W. AND J. D. BAKER. 1991. A review of animal population dynamics at extremely reduced population levels. *Rept. Intl. Whal. Comm.,* **41**:545–554.

GREEN, R. E. 1997. The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. *J. Anim. Ecol.,* **66**:25–35.

GREVSTAD, F. S. 1999. Experimental invasions using biological control introductions: the influence of release size on the chance of population establishment. *Biol. Inv.,* **1**:313–33.

IMBODEN, D. M. AND A. WÜEST. 1995. Mixing mechanisms in lakes, p. 83–138. *In:* A. D. Lerman, D. M. Imboden and J. Gat (eds.). Physics and chemistry of lakes, 2nd ed. Springer-Verlag, Berlin.

KIERSTEAD, H. AND L. B. SLOBODKIN. 1953. The size of water masses containing plankton blooms. *J. Mar. Res.,* **12**:141–147.

KOLAR, C. AND D. M. LODGE. 2001. Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.,* **16**:199–204.

LEWIS, M. A. AND P. KAREIVA. 1993. Allee dynamics and the spread of invading organisms. *Theor. Pop. Biol.,* **43**:141–158.

LIERMANN, M. AND R. HILBORN. 1997. Depensation in fish stocks: a hierarchic Bayesian meta-analysis. *Can. J. Fish. Aquat. Sci.* **54**:1976–1984.

LOCKWOOD, J. L., P. CASSEY AND T. BLACKBURN. 2005. The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol.,* **20**:23–228.

MARINE ENVIRONMENTAL PROTECTION COMMITTEE. 2002. Report of the Marine Environmental Protection Committee 48/21. International Maritime Organization, London.

MURTHY, C. R. 1976. Horizontal diffusion characteristics in Lake Ontario. *J. Phys. Oceanogr.,* **6**:76–84.

NATIONAL RESEARCH COUNCIL. 1996. Stemming the tide. National Academy Press, Washington, D.C. 141 p.

———. 2001. Assessing the TMDL approach to water quality management. National Academy Press, Washington, D.C.

PATLAK, C. S. 1953. Random walk with persistence and external bias. *Bull. Math. Biophys.,* **15**:311–338.

PEETERS, F., A. WÜEST, G. PIEPKE AND D. M. IMBODEN. 1996. Horizontal mixing in lakes. *J. Geophys. Res.,* **101**:18361–18375.

PETERS, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge. 345 p.

RAYMAKERS, S. 2001. 1st International ballast water treatment R&D symposium, IMO London 26–27 March 2001: symposium proceedings. International Maritime Organization, London. 171 p.

SKELLAM, J. G. 1951. Random dispersal in theoretical populations. *Biometrika,* **38**:196–218.

SUNSTEIN, C. R. 2002. Risk and reason: safety, law and the environment. Cambridge University Press, Cambridge. 352 p.

TAMBURRI, M. N., K. WASSON, AND M. MATSUDA. 2002. Ballast water deoxygenation can prevent aquatic introductions while reducing ship corrosion. *Biol. Cons.,* **103**:331–341.

VARDEN, S. G. 2005. Propelling hope for baby beach. *Orange County Register,* 11 March 2005.

SUBMITTED 13 JANUARY 2005 ACCEPTED 13 MAY 2005