Modeling ships' ballast water as invasion threats to the Great Lakes

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Abstract

The spread of nonindigenous species in aquatic ecosystems provides an opportunity to develop new perspectives on the invasion process. In this paper we review existing invasion models, most of which were developed to describe invasions of terrestrial habitats, and propose an alternative that explores long-distance invasions mediated by discharge of contaminated ballast water by ships in-bound to the Great Lakes. Based on current knowledge of shipping traffic to the Great Lakes, our model predicts that mid-ocean exchange of ballast water lowers propagule delivery by approximately three to four orders of magnitude relative to unexchanged ballast water. Propagule pressure of individual ships that enter the Great Lakes loaded with cargo and which declare 'no ballast on board' (NOBOB) is typically one to two orders of magnitude higher than that of vessels that exchange ballast. Because NOBOB vessels dominate (~90%) inbound traffic into the Great Lakes, these vessels collectively appear to pose the greatest risk of new introductions mediated via ballast water.

Introduction

Dispersal ability is a primary factor affecting species ranges. Classical invasion models assume that the environment is homogeneous and continuous. This is rarely the case for aquatic invasions, at least over large spatial scales. For example, species dispersal between freshwater lakes requires either a water connection or some form of 'jumping' mechanism. For freshwater organisms or their resting stages, ‘jumps’ may occur naturally or through human intervention. For example, aquatic organisms or their resting stages may be dispersed by wind or rain. The effectiveness of these dispersal vectors varies by species, distance from the colonization source, and wind speed or storm intensity. Smaller-bodied organisms and their resting stages are carried by wind and or rain more commonly than are larger ones, although, with major storms, individuals as large as fish and turtles can be transported through the air. However, Jenkins and Underwood (1998) determined that wind dispersed only one rotifer species and rain only four rotifers species, and argued that these vectors were relatively ineffective at dispersing zooplankton. Aquatic taxa are more readily dispersed inside of or attached to other species. For example, many studies have reported dispersal of aquatic taxa in the digestive tract of fish, or in the digestive tract or on the plumage or other external features of waterfowl (e.g., Johnson and Carlton 1996); insects and mammals less commonly disperse species.

The importance of natural dispersal vectors in expanding distributions of many aquatic taxa has been supplanted by that associated with human activities (see Hebert and Cristescu 2002). Virtually all large aquatic ecosystems support nonindigenous (i.e., NIS) species that were deliberately or unintentionally introduced by humans. As examples, the Laurentian Great Lakes and the Caspian, Azov, Black and Baltic Seas in Eurasia, have all been extensively invaded by NIS (Grigorovich et al. 2001; Ricciardi 2001; Leppäkoski et al. 2002;). Recent patterns of introduction indicate that these geographically remote ecosystems are now linked biologically, either directly by canals and rivers or indirectly by long-distance transfer mediated by commercial shipping (e.g., Ricciardi and MacIsaac 2000; Bij de Vaate et al. 2002; MacIsaac et al. 2002). As examples, both the amphipod *Echinogammarus ischnus* and the waterflea *Cercopagis pengoi* spread from their native range in the Black and Caspian Sea region to northern and western Europe, and then to the Great Lakes (see (Cristescu et al. 2001; Bij de Vaate et al. 2002). The Black, Azov and Caspian (i.e., Ponto-Caspian) seas have been the primary donor regions for NIS in the Great Lakes in recent years, even though little commercial vessel traffic links these regions (Colautti et al. 2002).

Many of the recent invasions of the Great Lakes and of the Caspian, Azov, Black and Baltic Seas have resulted from shipping activities, particularly through the release of contaminated ballast water (Ricciardi and MacIsaac 2000; Bij de Vaate et al. 2002). Efforts to reduce invasions to the Great Lakes have focused primarily on ballast water management in consequence. Legislation covering the Great Lakes was implemented in 1993 by the United States of America, and mandates that all ships carrying ballast water originating in foreign, fresh- or brackish water sources conduct ballast water exchange while at least 320 km offshore in water not less than 2000 m depth (United States Coast Guard 1993). This policy was predicated on the concept that virtually all freshwater organisms carried in ballast tanks would be expelled during ballast discharge, while those remaining in residual water would be killed by highly saline water following exchange (Locke et al. 1991, 1993).

A more detailed approach to exotic species management relies on quantitative risk assessment (Hayes 1998). If exotic species, ports of ballast origin, and shipping routes can be identified in advance, then risk assessment methodologies can be employed to estimate the likelihood of transfer of live organisms or viable resting stages to the first scheduled port of deballast, and a management strategy appropriate to perceived risk can be implemented (Hayes 1998). With this approach, regular shipping routes would thus be identified on a continuum from low to high risk. Estimation of risk is more problematic for ships that do not operate on regular, defined routes. This condition appears to apply to many ships. For example, 45% of the overseas vessels that entered the Great Lakes between 1989 and 1997 did so only once (Niimi 2000). Australia is presently developing a multi-tiered program to protect coastal waters from NIS that incorporates risk assessment based both on ships that operate on regular routes as well as those that do not (Hayes 1998). Ricciardi and MacIsaac (2000) implicated ports on the Baltic Sea and lower Rhine River as waypoints in the transfer of Ponto-Caspian invertebrates to the Great Lakes. Despite this apparent pattern, to date, no attempts have been made to develop an explicit risk-based assessment procedure for ships coming to the Great Lakes carrying ballast water from the Baltic Sea or any other region.

It is unlikely that ballast water exchange or risk-based management strategies can fully protect the Great Lakes from additional invasions because compliance with the ballast water legislation is less than complete, because some species may survive in ballast tanks either as live organisms or viable resting stages, and because not all high-risk donor areas or species can be identified in advance (e.g., Locke et al. 1993; Aquatic Sciences 1996). At least one species, *C. pengoi*, has been successfully introduced to Lake Ontario following implementation of the mandatory ballast water exchange program (MacIsaac et al. 1999).

Modeling offers an alternative starting point for prevention of further invasions by identifying the most important stages of the invasion process. Models have been used to assess spread of colonizing species with local dispersal for more than 60 years, although those describing long-distance dispersal have a more recent history but are relevant to invasions of remote, aquatic ecosystems. Most efforts to model invasions have not addressed long-distance dispersal, but rather have focused on 'local' dissemination of individuals in an expanding, invading population (see below). These models have found widespread application in descriptions of spread by terrestrial species, but much less commonly so in aquatic ecosystems. An alternative, 'risk-based' approach involves prediction of the likelihood that species' propagules will reach a previously uncolonized site, whereupon the population may or may not successfully colonize to establish a breeding population. The classical and risk-based modeling approaches are complementary, as population range expansion is possible only for the subset of invasions where species successfully colonize new habitats. In this paper, we first review the classical dispersal invasion models, as well as more recent, risk-based ones that have been applied to inland lakes. Finally, we develop a simple model that considers invasions mediated by ballast water from commercial ships.

Invasion models

Early invasion models assumed well-connected, homogeneous environments in which individual organisms reproduced and dispersed. Here, assumptions of diffusion and logistic population growth yielded a simple compact formula for the rate of spatial spread of the invader that was supported by data from a variety of terrestrial studies. Extensions of this model allow individuals to make long-distance (nondiffusive) jumps. These stratified diffusion models recognized that rare, long-distance dispersal could greatly increase the spread rate of an invading species and the variability in this rate. Aquatic ecologists have further extended the idea of stratified diffusion models to focus only on long-distance jumps, based upon frequency of vector movement among invaded and non-invaded lakes. These models may have application to long-distance dispersal mediated by ships.

The first biological invasion model described the wave-like spread of a mutant allele in a population (Fisher 1937). The frequency of allele p in a homogeneous environment would change at a rate defined by:

$$(1) \qquad \frac{\partial p}{\partial t} = D\frac{\partial^2 p}{\partial x^2} + mpq$$

where x is a spatial location, t is time, D is a diffusion coefficient, m is the selection coefficient favouring allele p, and $q = 1-p$ is the frequency of the wild-type allele. The diffusion coefficient describes random, 'Brownian' movement of the mutant allele, and is estimated in terms of the squared displacement per unit time (MSD) by D = MSD/2.

This genetic model was recast in an ecological context to predict the spread of individuals in an invading, logistically-growing population from a central colonization source as:

(2) $$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + ru\left(1 - \frac{u}{K}\right)$$

where *u* is local population density at spatial coordinate *x* and time *t*, and *m* is replaced by *r*, the intrinsic rate of growth (with units time^{-1}) (Skellam 1951). Analysis of equation (2) yields a simple formula, *c* = $2\sqrt{rD}$ (Fisher 1937; Skellam 1951), for the eventual speed *c* at which the introduced species spreads (Figure 1a). This model was used to assess rates of spread of terrestrial species including weeds, butterflies, sparrows, thar, squirrels, and sea otters) (see Grosholz 1996; Shigesada and Kawasaki 1997). Equation (2) can be modified to yield the same asymptotic spread rate in two or more as in one spatial dimension. However, it seriously underestimates the rate of spread of other terrestrial species including beetles, gypsy moths, and starlings (Grosholz 1996) because the simple diffusion assumption in Equation (2) requires that distances moved by an individual in a fixed length of time follow a Gaussian distribution. This assumption is not satisfied for many species with 'Leptokurtic' dispersal kernels, in which there exist more short- and more long-distance dispersers than a Gaussian with the same variance (Figure 1b). This discrepancy results in an underestimate of the true spread rate. Simple reaction-diffusion models have failed to predict rate of spread for invading invertebrate species in marine systems owing to difficulty in establishing the diffusion coefficient (Grosholz 1996).

Advection influences dispersal of many aquatic taxa. For example, lake currents and flowing river disperse water zooplankton and benthic insects downstream. In these cases, population range expansion in two spatial dimensions is determined by a combination of diffusion, logistic growth and advection as:

$$(3) \qquad \frac{\partial u}{\partial t} = D\left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}\right) + ru\left(1 - \frac{u}{K}\right) - a\frac{\partial u}{\partial x},$$

where *a* describes current speed along the x-axis (Shigesada and Kawasaki 1997). Population density radius expands asymptotically at a rate $2\sqrt{rD}$ with the population centroid displaced downstream at rate *a* (Shigesada and Kawasaki 1997). Initial dispersal of zebra mussels in the Great Lakes essentially conformed to this model, as spread occurred much more rapidly downstream than upstream (Griffiths et al. 1991).

Dispersal patterns may not conform with assumptions implicit to Skellam's (1951) model, specifically with the assumptions that individuals move randomly and that dispersal distances are normally distributed. Dispersal redistribution 'kernels' describe the probability distribution that individuals will be found at specific spatial coordinates relative to their original location (Kot et al. 1996; Neubert and Caswell 2000). Dispersal functions are typically characterized by a leptokurtic distribution, in which more individuals are found in both the central and tail regions of the curve relative to the normal distribution (Kot et al. 1996; Figure 1b). Tail regions of distribution functions are particularly important to models of species range expansions, as a few individuals dispersing long distances can profoundly affect invasion speed (Kot et al. 1996; Lewis 1997; Higgins and Richardson 1999). Kot et al. (1996) assessed invasion dynamics of *Drosophila* using integrodifference equations and five different redistribution kernels. A parametric form of the Normal redistribution kernel yielded the poorest fit of observed dispersal distances, and a low but constant rate of radial expansion. By contrast, the redistribution kernel with the 'fattest' tail (i.e., the curve with individuals dispersing farthest from the parental colony) fit the observed dispersal pattern best and resulted in an accelerating rate of invasion (Kot et al. 1996; Lewis 1997). Leptokurtic and 'fat tail' dispersal curves result in greater spatial variability in invader density at the wave front (Figure 1b) (Lewis 1997).

Hengeveld (1989) referred to the combined effects of neighbourhood diffusion and distant but infrequent dispersal as 'stratified’ diffusion (Figure 1b). Shigesada and Kawasaki (1997) described a stratified, scattered colony model in which a core population increased its range by neighbourhood diffusion as well as by producing long-distance dispersers that created new population nuclei. Here the spread rate depends crucially upon how many individuals in the colonies produce long-distance dispersers (Shigesada and Kawasaki 1997).

Examination of plant invasions illustrates the importance of rare, long-distance dispersal events to overall invasion velocity. Neubert and Caswell (2000) found that invasion velocity of an herbaceous perennial plant was determined almost completely by dispersal associated with an ant species that accounted for only 7% of all seeds dispersed. Higgins and Richardson (1999) simulated dispersal of invasive pine trees in

South Africa using a three-component, Weibull distribution models. Rate of population spread increased by up to an order-of-magnitude when even a very small proportion (0.001) of seeds were moved long distances. Clark (1998) utilized 'fat-tailed' dispersal functions to reconcile Holocene dispersal of trees with empirical seed dispersal distances.

Numerous other invasion models have been developed. For example, Case (1990) assembled stable Lotka-Volterra, multi-species communities, and then subjected these communities to introductions by 'invading' species. Invasion success was limited when communities were comprised of many strongly interacting species, indicating that invasibility was determined by community rather than by invading species attributes (Case 1990). Priority effects, whereby the sequence in which species assemble to a community, have also been reported to influence invasion success (Drake 1993). These conditions may not apply universally, however, as under some circumstances establishment of invading NIS may be facilitated rather than retarded by resident native or previously established NIS (see Ricciardi 2001).

Invasion models for lakes

Zebra mussels (*Dreissena polymorpha*) and spiny waterfleas (*Bythotrephes longimanus*) have invaded ecosystems throughout temperate, eastern North America. These invasions have provided ecologists with opportunities to develop invasion models to predict spread of these species in particular and NIS in general. MacIsaac et al. (2000) predicted the distribution of *Bythotrephes* in European lakes with 92% accuracy using water transparency, lake area, chlorophyll concentration and maximum depth. Application of the same model to the Great Lakes basin correctly identified 82%

of invaded lakes but incorrectly classified 74% of noninvaded lakes, indicating that *Bythotrephes* has the potential to establish in many lakes in the region if introduced by human or other vectors (MacIsaac et al. 2000).

While distribution patterns of *B. longimanus* (MacIsaac et al. 2000) have been modeled using only physical and chemical parameters, spatial analysis of propagule dispersal may afford unique insights into the invasion process. For example, a parallel may be drawn between 'fat-tailed' redistribution kernels of plants dispersed by winds or animals (described above) and dispersal of aquatic taxa by human vectors. Introduction of NIS *via* discharge of ballast water releases large numbers of propagules of multiple species to areas where they were unlikely to reach using natural dispersal mechanisms, a process Carlton and Geller equated with 'ecological roulette' (Carlton 1985; Carlton and Geller 1993). In essence, dispersal of species by human vectors transforms what were once local dispersal kernels into leptokurtic or 'fat-tailed' distributions (Figure 1b) (see Lewis 1997). A key difference between human-vectored dispersal of freshwater taxa and natural, stratified dispersal is that no assumptions need to be drawn regarding diffusion probabilities and patterns. In addition, while establishment of new colonies on the invasion front is difficult to predict with classical stratified diffusion, analysis of human vector patterns may afford a clear opportunity to predict new invasions.

In this section we address two classes of models to describe human dispersal of species in aquatic ecosystems: regional dispersal associated with activities including but not limited to movement of boats and their trailers; and intercontinental movement of ballast water contaminated with NIS. For the former class, we review gravity models that have been used to describe spread of *D. polymorpha* and *Bythotrephes* to inland lakes bordering the Great Lakes, while for the latter we develop a simple ballast water model to predict the number of propagules arriving to the Great Lakes from European ports in different ballast water classifications (i.e. ships with no declarable ballast on board, and those with exchanged or unexchanged ballast).

Regional dispersal models

Zebra mussels (*D. polymorpha*) spread rapidly to inland lakes subsequent to invasion of the Great Lakes. Padilla et al. (1996) first explored aspects of these invasions by relating pleasure boat census data from invaded Great Lakes sources to inland lakes in Wisconsin. Schneider et al. (1998) developed a production-attraction constrained transportation (i.e., gravity) model to assess the relationship between boater activity in Illinois and dispersal of zebra mussels in the state. Gravity models, unlike their diffusion counterparts, estimate the 'force of attraction' between an origin and a destination, with movement rates indicative of the strength of the force (Schneider et al. 1998). Because boaters are assumed to be the primary vector of dispersal of zebra mussels to inland lakes (Johnson and Padilla 1996; Johnson and Carlton 1996), analysis of boat movement among lakes can be used to estimate invasion risk (Schneider et al. 1998). Due to the absence of specific traffic intensity patterns between individual lakes, Schneider et al. (1998) estimated the likelihood of boat movement between pairs of lakes as:

$$(4) \qquad T_{ij} = \frac{A_i O_i B_j D_j}{c_{ij}{}^{\alpha}} ,$$

where T_{ij} is the relative traffic between origin and destination lakes, A_i and B_j are scaling constants that ensure that all boats entering a lake also leave it, O_i and D_j are the total number of boats leaving the origin and arriving at the destination lake, respectively, c_{ij} is the distance between origin and destination lakes, and α is a measure of the force of attraction for boaters moving between particular source and destination lakes (Schneider et al. 1998). T_{ij} values for individual source-destination lakes were multiplied by the probability (P_i) that a boat traveling from the origin to the destination lake would be infested with live zebra mussels. Probability of transfer of live zebra mussels was set at 0.01 for infected origin lakes. $T_{ij}P_i$ values for all different source lakes were then summed to estimate the total number of boats that could infect a particular destination lake. Schneider et al. (1998) determined that the initial spread of zebra mussels was expected to be most acute in high-usage lakes in the heavily populated northern portion of the state, in close proximity to infested waters. Moreover, some of the reservoirs in the central part of the state were expected to serve as stepping-stones for secondary invasions elsewhere in the state.

Bossenbroek et al. (2001) also used boater traffic patterns to predict spread of zebra mussels in inland lakes around the Great Lakes. Bossenbroek et al. (2001) used a production-constrained gravity model similar to that used by Schneider et al. (1998) to forecast overland dispersal of zebra mussels into inland lakes in Illinois, Indiana, Wisconsin and Michigan. While Schneider et al. (1998) used information on boater activity for specific lakes, Bossenbroek et al. (2001) utilized the number of registered boaters in state counties as an input parameter for boater activity. Bossenbroek et al. (2001) developed deterministic and stochastic versions of their gravity model, both of which successfully predicted the number of infected lakes in different counties. Buchan and Padilla (1998) found that Skellam's diffusion model (see Equation 2) overestimated occurrence of invasions in local lakes in Wisconsin but underestimated invasions of distant lakes. Long-distance invasions were, however, consistent with boat traffic patterns in the state (Buchan and Padilla 1999).

Borbely (2001) utilized a doubly-constrained gravity model to predict invasions by *Bythotrephes* in inland lakes in Ontario. Unlike their production-constrained analogues, doubly-constrained gravity models are capable of assessing invasion risk between individual invasion source-destination lake pairs. This higher degree of spatial resolution comes at the expense of generality, however. Borbely’s (2001) model successfully backcasted the invasion sequence of inland lakes from the Great Lakes, and successfully forecasted invasion risk of noninvaded lakes that were invaded during 2001.

Bossenbroek et al. (2001) argued that gravity models are better suited to explain invasions of species into lakes than either classical or stratified diffusion models. Gravity models are superior to simple diffusion models because they allow invasions of isolated habitats (i.e., lakes) in heterogeneous landscapes. They are also superior to stratified diffusion models because they allow invading species to 'leap-frog' unsuitable habitat and dispersal barriers (Bossenbroek et al. 2001). Because it is relatively simple to quantify boater activity and vector strength, it may be possible to identify 'gateway' lakes, that, if invaded, can act as foci for secondary invasions (Johnson and Padilla 1996; Borbely 2001; Johnson and Carlton 2001). Analyses of lake ecosystems may therefore provide unique opportunities to develop and test invasion theory.

Intercontinental dispersal models

The Great Lakes were invaded throughout the twentieth century by NIS species linked to discharge of ballast water from commercial ships (Mills et al. 1993; Ricciardi 2001). Studies have addressed the biological composition of ballast water for ships inbound to the Great Lakes (e.g., Locke et al. 1991, 1993; Aquatic Sciences 1996), while others have attempted to predict potential invaders to the system based on the geographic origin of previous invaders and commercial shipping patterns (Ricciardi and Rasmussen 1998). However no attempts have been made to identify the risk posed by different categories of commercial ships entering the Great Lakes, or to establish the relative risk of invasions by different groups of biota. Below we develop a simple model to assess these questions for commercial ships entering the Great Lakes.

Our model has two objectives. First, we wish to determine exposure risk associated with different ballast management strategies. Specifically, we seek to address the relative risk of invasion to the Great Lakes: 1) posed by ships that comply with extant legislation and exchange ballast while on the high sea and then discharge saline water in the Great Lakes; and 2) posed by ships entering the system with no declarable ballast on board (NOBOB). Most of the vessels (~90%) entering the Great Lakes do so as NOBOBs (Colautti et al. 2002). These vessels typically carry residual water and sediment that may contain live NIS or their resting stages (S. Bandoni, University of Windsor, Windsor, ON; pers. comm.). Many of these vessels load Great Lakes' ballast water during their inbound transit after discharging cargo, and later discharge the mixed ballast water in the Great Lakes, thereby potentially exposing the system to NIS

(Colautti et al. 2002). For comparative purposes, we also consider the number of propagules delivered to the Great Lakes if ballast exchange were not exchanged.

A second objective of our model is to identify which processes and parameters require further quantitative investigation. For example, virtually nothing is known regarding survival functions of most freshwater taxa immersed in either freshwater or saltwater in ballast tanks (but see Wonham et al. 2001). Our model is not species-specific and does not identify absolute risk, as at present we lack the ability to translate the number of introduced organisms to a probability of successful colonization.

Ballast water mediated invasions into the Great Lakes

In our simplest model, we assume that survival of different taxonomic groups, hereafter considered taxa, in ballast tanks follows an exponential decay function. This assumption is consistent with the limited available from information regarding survival rates of plankton in ballast tanks during transoceanic transit (Smith et al. 1999; Wonham et al. 2001). For example, Wonham et al. (2001) reported that abundance of planktonic invertebrates declined between 98.5 and >99% in ballast tanks during a 16-day transoceanic trip. Our model assumes that the mortality rate μ (t^{-1}) is constant, and represents the rate at which organisms die (i.e., there is no reproduction). Mortality rates (μ_{f_i}) of freshwater taxa in freshwater differ among *i* taxonomic groups (e.g. rotifers, cladocerans, copepods, bacteria). All taxa are assumed to live suspended in the water.

The probability of the population of taxon *i* surviving to time *t* is defined as:

(5) $P_r(t) = \exp\{-\mu_{f_i} t\}$.

At time *t* = 0 the probability of survival is unity, and, as *t* increases the probability of survival approaches zero. The number of organisms surviving transit in a ship that does not exchange its freshwater ballast can be related to transit time between the source where ballast was loaded and the destination where it is discharged by:

$$(6) \qquad n_i(t) = n_i(0) \exp\{-\mu_{f_i} t\},$$

where $n_i(0)$ is the number of organisms loaded into the ballast, μ_{f_i} is the mortality rate per day in freshwater, and *t* is the length of the trip in days.

The above model can be extended to incorporate ballast water exchange on the open sea. If the ship loads freshwater ballast at time $t = 0$, discharges it on the open sea at time $t = t_B$, whereupon it loads saltwater that is later discharged in the Great Lakes at time $t = T$, then the number of organisms transferred alive from the source to the Great Lakes can be related to the survival rate in freshwater, exchange efficiency, and survival rate in saltwater. In other words, individuals must survive in freshwater from time $t = 0$ until $t = t_B$, remain in the ballast water during exchange on the ocean (i.e., not be flushed out; probability r_0), and survive in saline water until the water is discharged in the Great Lakes [probability $\exp\{-\mu_{s_i}(T-t_B)\}$], where μ_{s_i} is the mortality rate in saltwater. When the vessel discharges ballast on the Great Lakes, the probability that surviving organisms are flushed out is $1-r_1$. The number of freshwater organisms of taxon *i* transferred alive to the Great Lakes in exchanged ballast water for a ship originating at a freshwater source is estimated as:

(7) $n_i(T) = n_i(0) \exp\{-\mu_{f_i} t_B\} r_0 \exp\{-\mu_{s_i}(T - t_B)\} (1 - r_1)$.

The case where no ballast exchange occurs simplifies to:

(8) $n_i(T) = n_i(0) \exp\{-\mu_{f_i} T\} (1 - r_1)$.

Equation 7 can be used to estimate the yearly number of individuals of taxon *i* transferred alive in exchanged ballast water for all ships entering the Great Lakes as:

(9) $N_i(t) = \sum_{j=1}^{M} n_{i_j}(0)\, r_0\, (1 - r_1) \exp\{-\mu_{f_i} t_{B_j}\} \exp\{-\mu_{s_i}(T_j - t_{Bj})\}$

Here *M* is the number of ships per year entering the Great Lakes, $n_{i_j}(0)$ is the initial number of taxon *i* in ship *j* at the foreign port visited prior to the Great Lakes, t_{Bj} is the time elapsed between leaving the foreign port and ballast water exchange, and T_j is the total time taken to travel from the foreign port to the Great Lakes port. Equation 9 can be applied to all of the different ports from which ships destined to the Great Lakes originate. A simplified form of Equation 9 can also be applied to NOBOB ships or those carrying unexchanged freshwater ballast.

Because no data are available for survival rate of freshwater plankton in ballast tanks, we estimated mortality rate for rotifers (*i* = 1), copepods (*i* = 2), cladocerans (*i* = 3) and bacteria (*i* = 4) using a variety of sources (e.g., Bogosian et al. 1996; Kirk 1997).

We also considered densities of freshwater organisms in ballast tanks of ships sampled while entering the Great Lakes system (i.e., near the end of their voyage; Locke et al. 1991). Mortality rate was estimated from Equation 6 as:

$$(10) \quad \rho(14) = \rho(0) \exp\{-\mu_{f_i} 14\},$$

where $\rho(14)$ is the density (ind $\cdot$ m^{-3}) of taxon *i* after 14 days. Initial densities of rotifers, copepods and cladocerans in ballast water at the source port were $\rho_1(0) = 1.00 \times 10^5$, $\rho_2(0) = 2.00 \times 10^4$ and $\rho_3(0) = 2.00 \times 10^4$ ind $\cdot$ m^{-3}, respectively (Appendix 1a), while final densities were $\rho_1(14) = 2817$, $\rho_2(14) = 3355$ and $\rho_3(14) = 1677$ ind $\cdot$ m^{-3}; these values are characteristic of many freshwater ecosystems and of the biotic composition of ballast tanks of vessels inbound to the Great Lakes (Locke et al. 1991). Resultant mortality rates were $\mu_{f_1} = 0.25$, $\mu_{f_2} = 0.13$ and $\mu_{f_3} = 0.18$ day^{-1} (Figure 2, Appendix 1a). To estimate $n_i(0)$, we considered a ballast volume (V_{bal}) of 8500 m^3. This volume is typical of a mid-size ocean-going vessel. NOBOB vessels carry residual ballast water (V_{NB}), which is estimated to be 1% of the ballast volume, or 85 m^3 (P. Rouderbourg, FedNav Shipping Co., Montreal, PQ). From volumes of ships with full or residual ballast, we respectively estimate $n_i(0)$ as:

$$(11) \quad n_i(0) = \rho(0) V_{bal} \quad \text{or} \quad n_i(0) = \rho(0) V_{NB}$$

The number of rotifers (*i* = 1), copepods (*i* = 2) and cladocerans (*i* = 3) initially loaded in ballast is thus $n_1(0) = 8.50 \times 10^8$, $n_2(0) = 1.70 \times 10^8$ and $n_3(0) = 1.70 \times 10^8$ for fully ballasted ships, and $n_1(0) = 8.50 \times 10^6$, $n_2(0) = 1.70 \times 10^6$ and $n_3(0) = 1.70 \times 10^6$ for NOBOB vessels (Appendix 1a).

We utilized a mortality rate (μ_{f_4}) of 0.49 day^{-1} for bacteria (Bogosian et al. 1996)(Figure 2). Initial bacterial density was estimated as $\rho_4(0) = 1.00 \times 10^{12}$ cells $\cdot$ m^{-3} (F. Dobbs, Department of Ocean, Earth and Atmospheric Sciences, Old Dominion University, Norfolk, VA; pers. comm.). The total number of bacteria initially loaded in ballast was thus $n_4(0) = 8.50 \times 10^{15}$ for fully ballasted vessels and $n_4(0) = 8.50 \times 10^{13}$ for NOBOB ships (Appendix 1a).

In order to estimate the number of organisms arriving alive to the Great Lakes in ships that exchange ballast water, we estimated total transoceanic transit time, and time of ballast exchange, from two major shipping regions, Antwerp and Rotterdam, and the Baltic Sea (P. Roderbourg, FedNav Shipping Co., Montreal, PQ; pers. comm.). The average total transit times (T) were 9.7 and 11.8 days, respectively, from these regions, while time at which ballast exchange commenced (t_B) averaged 3.6 and 7.2 days (Appendix 1b). Duration of the saltwater exposure period for organisms in ballast tanks was thus 6.1 and 4.6 days, respectively (Appendix 1b).

We used two estimates of ballast water exchange efficiency. First, we assumed that ships were 99% ($1- r_0$) efficient at deballasting water and organisms on the open ocean, and that efficiency was the same on the Great Lakes ($1- r_1$) (P. Roderbourg, FedNav Shipping Co., Montreal, PQ; pers. comm.). For NOBOB ships we assumed that, after offloading goods, ships would take up a ⅓ ballast volume before moving to the next site within the Great Lakes to pick up cargo, and then, when picking up cargo, flush the ballast tanks with 99% efficiency. The dilution by the introduction of the ⅓ ballast volume leads to an overall 98% efficiency in flushing (1-r). Thus, probability of discharge into the Great Lakes for organisms surviving the trip to North America is $1- r_1 = 99\%$, and $1 – r_1 = 98\%$ for NOBOBs (Appendix 1c). For comparison, we also utilized an 85% efficiency rate ($1- r_0$) on the ocean and in the Great Lakes ($1- r_1$), as U.S. Coast Guard estimates indicate efficacy of exchange may be substantially lower (U.S. Coast Guard, Massena, N.Y.; Appendix 1c). Our estimates correspond well with field data for an exchange experiment, in which 93 to 100% of coastal water and 80 to 100% of coastal organisms in ballast tanks were removed by ballast exchange on the open ocean (Wonham et al. 2001).

To compute the mortality rate in salt water, we assumed that 5-day survival rate of organisms is 2 orders of magnitude lower than survival in freshwater. While data for most freshwater taxa is unavailable, this assumption is consistent with results for *Escherichia coli* exposed in marine microcosms to saline water (Byrd et al. 1992). If coastal (i.e. estuarine) species are loaded with ballast water at the point of origin, mortality upon exposure to salt water may be reduced (Wonham et al. 2001) although, presumably, it would be elevated when eventually discharged into the Great Lakes. The parameter μ_{s_i} is found by solving the following equation:

$$\exp\{-\mu_{s_i} 5\} = \frac{1}{100} \exp\{- \mu_{f_i} 5\}. \qquad (12)$$

Using the μ_{f_i} values above, computed μ_{s_i} for rotifers, copepods, cladocerans and bacteria are $\mu_{f_1} = 1.18$, $\mu_{f_2} = 1.05$, $\mu_{f_3} = 1.10$, and $\mu_{f_4} = 0.98$ day^{-1} (Appendix 1a, Figure 2).

Using equation 7 for ships that exchange ballast and equation 8 for ships that declare NOBOB or those that have not exchanged ballast, we developed a third model to estimate total number of each group of organisms arriving to the Great Lakes from multiple sources. Here we used previously given shipping and ballast water exchange times, inoculum densities, mortality rates in fresh and salt water, and probabilities of initially surviving ballast exchange and later being discharged into the Great Lakes (Appendix 1). We also used long-term (1986-1998) average vessel traffic from Antwerp/Rotterdam and from various Baltic Sea ports to estimate the number of trips per year. Mean numbers for vessels arriving from these regions ($\hat{S}$) are 120 year^{-1} and 54 year^{-1} (Appendix 1b). We utilized two estimates of the number of these vessels that arrived to the Great Lakes fully ballasted with exchanged water or with unexchanged water, or as NOBOBs. In the basic model, representing most years during the past decade, 90% of the vessels arrived as NOBOBs, 9% loaded with exchanged ballast and 1% loaded with freshwater ballast (Colautti et al. 2002). In the second scenario, representing recent (1997, 1998) shipping years, these values were respectively 74%, 19% and 7% (U.S. Coast Guard, Massena, N.Y.; Appendix 1c).

Results of our simplest simulation, of ships entering the lakes either without having exchanged freshwater ballast water ($V_{bal} = 8500$ m^3) or as NOBOBs ($V_{NB} = 85$ m^3), reveal a very high abundance of bacteria both before and after transit across the ocean (Figure 3). Rotifer and cladoceran zooplankton experienced the greatest declines in abundance during the voyage, and copepods the least. In our second series of simulations, we assessed the importance of ballast water management procedures (i.e., exchange, no exchange, NOBOB), source region and ballast water exchange efficiency (Table 1). Ballast water management procedures have a very pronounced effect on abundances of all taxa carried in ballast tanks. Total abundance of all taxa arriving to the Great Lakes is orders of magnitude lower for ships carrying exchanged ballast water than for those with unexchanged ballast (Table 1), owing both to open-ocean purging and to low survival of species in exchanged water (Table 1). Nevertheless, organisms are expected to arrive alive to the Great Lakes even in vessels with exchanged ballast water. This simulation indicates that the ballast water management strategy currently employed on the Great Lakes provides good but not complete protection against NIS. As Locke et al. (1993) noted, this strategy is intended to serve only as a filter to reduce the abundance and diversity of NIS introduced to the lakes, and not as an impassable barrier. Abundances of all taxa were also orders of magnitude lower for NOBOB vessels than for those carrying unexchanged freshwater ballast (Figure 3), owing to differences in volume of water carried.

Assuming similar initial taxon densities, region of origin had a minor influence on arriving abundance of all taxa, with the lower Rhine River sources (i.e., Antwerp-Rotterdam) always having higher abundances than those from the Baltic Sea (Table 1). This effect was a result of the lower transit time to the Great Lakes from the Rhine region, although it is dwarfed in importance by ballast water management strategy. Purging efficiency had smallest effect on population densities in ballast water upon arrival to the Great Lakes (Table 1).

In our third set of simulations, we assessed total vector strength (i.e., the number of ships arriving from particular sources). Collectively, total abundance of all groups arriving to the Great Lakes is orders of magnitude lower in ships with exchanged ballast water than in NOBOB vessels, reflecting both open-ocean purging and lower survival in exchanged vessels and the numerical dominance NOBOBs among arriving vessels (Table 2). Because of this numerical dominance, the NOBOB fleet may discharge as many propagules as is carried (but not legally discharged) by vessels entering the system with unexchanged ballast water.

When combined with initial densities, survival probabilities and ballast exchange efficiencies, this simulation provides an estimate of the 'propagule pressure' exerted by different taxonomic groups and by different invasion corridors. Propagule pressure is between 7 and 8 orders of magnitude higher for bacteria than for all other groups (Table 2). Despite the numerical importance of microorganisms in ballast water, they have received little attention by invasion biologists and regulators alike.

Model limitations

Our model provides an initial assessment of invasion risk from ballast water in the Great Lakes. Nevertheless, it has a number of limitations and should only be considered as a starting point. First, our model assumes that all invasions occur as a result of inoculation by live, planktonic individuals. This assumption is unlikely to be met in the Great Lakes or elsewhere, as available studies have revealed the presence of resting stages (i.e., spores, resting eggs, cysts) in residual ballast water and associated sediment (e.g. Kelly 1993; Harvey et al. 1999; Hamer et al. 2000). The importance of resting stages may be greatest for NOBOB ships that arrive with only residual ballast water and sediment; these ships load and deballast in the Great Lakes, possibly inoculating the Great Lakes with NIS. Residual sediments may harbour surficial biofilms and be an important habitat of microbes in ballast tanks (F. Dobbs, Department of Ocean, Earth and Atmospheric Sciences, Old Dominion University, Norfolk, VA**;** pers. comm.). Lake Superior appears to be particularly vulnerable, as >70% of discharges by NOBOB vessels on the Great Lakes are made into this system (Colautti et al. 2002).

Second, our results depend critically on the survival function used to describe the transition from living in fresh- to saline ballast water. With the exception of some microbes, little is known regarding survival of freshwater organisms in saline water. The survival rate of freshwater organisms immersed in saline ballast water is almost certainly much lower than that in freshwater, but the nature of time-dependent differences has not been addressed. Available evidence indicates that complete mortality cannot be assumed under these conditions. For example, 61 of 80 ocean-going vessels surveyed entering the Great Lakes had freshwater or estuarine plankton in some of their tanks, including ships that reported ballast exchange on the open ocean or in a salt-water port of call (Aquatic Sciences 1996). Locke et al. (1991, 1993) also found live freshwater zooplankton in some ships that entered the Great Lakes with saline ballast water. Thus, while it is not possible at present to define the survival rate of freshwater species in saline ballast water, it exceeds zero in at least some cases.

Third, we have assumed that all ships undergo nearly complete ballast water exchange. Although our findings were insensitive to ballast exchange efficiency, this parameter could have profound biological significance. Partial ballast exchange may allow survival of some fresh- or brackish water taxa that are unlikely to survive in highly saline water (e.g., *Cercopagis*; Locke et al. 1993; MacIsaac et al. 1999). For example, Wonham et al. (2001) reported that open ocean water was not lethal to 'coastal' marine species.

Fourth, we classified abundances according to broad taxonomic categories. Species within these categories (e.g., rotifers, copepods) display significant divergence with respect to salinity tolerance. Consequently, taxon survival rates in ballast water need to be established. Wonham et al. (2001) determined that survival rates of 'coastal' zooplankton species differed among species and even among flooded cargo holds and deck tanks. Our model also assumed that individuals did not reproduce while resident in ballast tanks. Many of the species in ballast tanks are capable of asexual reproduction, and could produce or release offspring while vessels are underway. Reproduction would result in a larger cohort of individuals to survive ballast exchange and increase the number of potential colonists when ballast water is discharged into the Great Lakes.

Fifth, our analysis explored only those invasions mediated by transfer of species in ballast water. NIS also could be introduced attached to or associated with other ship components, including the sea chest, anchor and anchor chain, seawater piping systems, or fouled to the exterior of the hull (see Carlton 1985; Ruiz et al. 2000). A German study of sea-going vessels estimated that a typical vessel supported 6.2 fouling species at a density of 1.8 ind $\cdot$ cm^{-2} (Gollasch and Leppäkoski 1999). It is improbable that freshwater species could survive prolonged exposure to the open ocean while fouled on the hull of a transoceanic ship, thus this mechanism is almost certainly far less important for introductions to the Great Lakes than to coastal marine environments.

A number of research needs arise from our model. Model predictions are sensitive to transition mortality rates for freshwater species exposed to saline water in ballast tanks. These rates need to be measured carefully. Intensive biological sampling of ballast tanks subjected to mid-ocean exchange is imperative.

NOBOB vessels have been identified as an invasion risk (Locke et al. 1993), although the extent to which they contribute to the NIS problem in the Great Lakes has yet to be determined. This risk stems from three components, each of which requires investigation. First, species resident in residual water could be discharged when ships deballast while operating on the Great Lakes. Second, resting stages in residual sediments in these vessels could become activated (i.e., hatch) if ships load ballast water while on the lower Great Lakes and later discharge it within the system. It is also possible, if unlikely, that viable resting stages could be discharged directly with ballast water, and hatch in the Great Lakes. Each of these mechanisms would serve to enhance the relative importance of NOBOB vessels as a vector of NIS to the Great Lakes.

Ecologists have sought to identify the relationship between 'propagule pressure' and invasion success (see Lonsdale 1999; Smith et al. 1999; Ruiz et al. 2000). Available evidence implicates propagule pressure as a determinant of invasion success in plant communities (e.g., Lonsdale 1999), though evidence from aquatic systems is presently limited to marine systems and to invasions of inland lakes (see above). It may be possible to assess the association between propagule pressure and international shipping activities by tracking sources, destinations and volumes of ballast water discharged into the Great Lakes, particularly if the information deficiencies described above are resolved. Our study indicates that, collectively, NOBOB vessels presently constitute the greatest shipping vector to the Great Lakes today, although even vessels that discharge exchanged ballast water in compliance with existing law pose some risk of new invasions.

Finally, it would be instructive to develop stochastic versions of our model in which uncertainty in input parameters and initial organism densities in tanks were explored to provide confidence intervals for our propagule pressure estimates.

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Table 1. Simulated transfer of rotifers, copepods, cladocerans and bacteria in ballast tanks of ships inbound to the Great Lakes. Output is based on ship transport type upon entry to the lakes (exchanged [EX] or unexchanged [UN] ballast water, or no declarable ballast on board [NOBOB]), ballast source regions (Rotterdam/Antwerp [RA]; Baltic Sea [BS]), and ballast exchange efficiency (High = 99%; Low = 85%). See text for details.

Group	Transport type		Number of propagules delivered			
		Ballast Source	Rotterdam /Antwerp		Baltic Sea	
		Exchange efficiency	High	Low	High	Low
Rotifera	UN		$7.45x 10^7$	6.39×10^7	4.40×10^7	3.78×10^7
	NOBOB		7.37×10^5	6.39×10^5	4.36×10^5	3.78×10^5
	EX		2.56×10^3	3.30×10^4	2.20×10^3	2.83×10^4
Copepoda	UN		4.77×10^7	4.09×10^7	3.63×10^7	3.12×10^7
	NOBOB		4.72×10^5	4.09×10^5	3.59×10^5	3.12×10^5
	EX		1.74×10^3	2.24×10^4	1.92×10^3	2.47×10^4
Cladocera	UN		2.94×10^7	2.52×10^7	2.01×10^7	1.73×10^7
	NOBOB		2.91×10^5	2.52×10^5	1.99×10^5	1.73×10^5
	EX		1.07×10^3	1.38×10^4	1.06×10^3	1.37×10^4
Bacteria	UN		7.26×10^{13}	6.23×10^{13}	2.59×10^{13}	2.23×10^{13}
	NOBOB		7.19×10^{11}	6.23×10^{11}	2.57×10^{11}	2.23×10^{11}
	EX		2.65×10^9	3.42×10^{10}	1.37×10^9	1.76×10^{10}

Table 2. Cumulative abundance of rotifers, copepods, cladocerans and bacteria in ballast tanks of all ships inbound to the Great Lakes. Output is based on ship transport type upon entry to the lakes (exchanged [EX] or unexchanged [UN] ballast water, or no declarable ballast on board [NOBOB]), ballast source regions (Rotterdam/Antwerp [RA]; Baltic Sea [BS]), and ballast exchange efficiency (High = 99%; Low = 85%). Total transit times from RA and BS are estimated as 9.7 and 11.8 days, respectively, while times to ballast exchange are 3.6 and 6.1 days. Total number of arriving from RA as UN, NOBOB and EX are 1.20, 108.00 and 10.8, respectively. Comparable arrivals from the BS are 0.54, 48.60 and 4.86.

Group	Transport type	Cumulative number of propagules delivered				
		Ballast source	Rotterdam / Antwerp		Baltic Sea	
		Exchange efficiency	High	Low	High	Low
Rotifera	UN		8.93×10^7	7.67×10^7	2.38×10^7	2.04×10^7
	NOBOB		7.96×10^7	6.90×10^7	2.12×10^7	1.84×10^7
	EX		2.76×10^4	3.56×10^5	1.07×10^4	1.37×10^5
	TOTAL		1.69×10^8	1.46×10^8	4.50×10^7	3.89×10^7
Copepoda	UN		5.72×10^7	4.91×10^7	1.96×10^7	1.68×10^7
	NOBOB		5.10×10^7	4.42×10^7	1.75×10^7	1.51×10^7
	EX		1.88×10^4	2.42×10^5	9.31×10^3	1.20×10^5
	TOTAL		1.08×10^8	9.36×10^7	3.71×10^7	3.21×10^7

Cladocera	UN	3.52×10^{7}	3.03×10^{7}	1.09×10^{7}	9.33×10^{6}
	NOBOB	3.14×10^{7}	2.72×10^{7}	9.68×10^{6}	8.40×10^{6}
	EX	1.16×10^{4}	1.49×10^{5}	5.16×10^{3}	6.65×10^{4}
	TOTAL	6.66×10^{7}	5.76×10^{7}	2.06×10^{7}	1.78×10^{7}
Bacteria	UN	8.71×10^{13}	7.48×10^{13}	1.40×10^{13}	1.20×10^{13}
	NOBOB	7.76×10^{13}	6.73×10^{13}	1.25×10^{13}	1.08×10^{13}
	EX	2.86×10^{10}	3.69×10^{11}	6.66×10^{9}	8.57×10^{10}
	TOTAL	1.65×10^{14}	1.42×10^{14}	2.65×10^{13}	2.29×10^{13}

Figure Legend

Figure 1. Models for spatial spread. (a) Assumptions of logistic growth and local diffusion (Equation (2)) lead to an expanding wave. The rate of spread, given by the rate of change of the threshold point x*, approaches $c = 2\sqrt{rD}$ as time progresses. See text for further discussion. (b) The local diffusion assumption is consistent with the assumption that the distance traveled by an individual in a fixed length of time is Gaussian (top left panel). By way of contrast, the stratified diffusion assumption is consistent with a leptokurtic dispersal kernel (top right panel). Note that the leptokurtic kernel has more short- and long-range dispersers than the Gaussian with identical variance. Two-dimensional stochastic simulations for population spread show that, unlike Gaussian kernels, leptokurtic kernels predict patchy spread with irregular wave fronts (compare left and right middle panels). Here each dot shows the location of a single individual 40 generations after the release of 10 founding individuals at the origin. The left middle panel uses the Gaussian Kernel and the right middle panel used the leptokurtic kernel. The process by which the patchy spread occurs is sometimes referred to as ‘stratified’ diffusion (bottom right panel), as opposed to ‘classical’ diffusion (bottom left panel). Intercontinental dispersal of organisms via ballast water involves very long distances and stochastic elements, and hence relates to the rare, long-distance dispersal events described by the tails of leptokurtic kernels. Panel (a) is based on Shigesada and Kawasaki (1997), and panel (b) is based on Figure 2 of Lewis and Pacala (2000) and on Hengeveld (1989). Further details of the simulations can be found in this reference.

Figure 2. Survival rate function of freshwater taxa in fresh water and salt water. See text for details.

Figure 3. Expected number of organisms surviving transoceanic transit in ballast water of a ship that does not undergo ballast exchange on the open ocean (a) and in residual water of a vessel declaring 'no ballast on board' (b) upon entry to the Great Lakes.

Appendix 1a. Input parameters for ballast water model, where μ_{f_i} and μs_i are mortality rates of group *i* in fresh and salt water, respectively, $\rho_i(0)$ is density of organisms in source water, and $n_i(0)$ BOB and $n_i(0)$ NOBOB are total inocula of group *i* in ballast tanks at time 0.

Taxon	Group *i*	μ_{f_i} (day^{-1})	μ_{s_i} (day^{-1})	$\rho_i(0)$) ($Ind \cdot m^{-3}$)	$n_i(0)$ BOB (Individuals)	$n_i(0)$ NOBOB (Individuals)
Rotifers	1	0.25	1.18	1.00×10^{5}	8.50×10^{8}	8.50×10^{6}
Copepoda	2	0.13	1.05	2.00×10^{4}	1.70×10^{8}	1.70×10^{6}
Cladocera	3	0.18	1.10	2.00×10^{4}	1.70×10^{8}	1.70×10^{6}
Bacteria	4	0.49	1.41	1.00×10^{12}	8.50×10^{15}	8.50×10^{13}

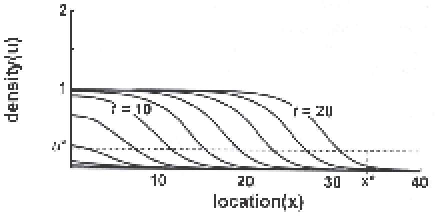
Appendix 1b. Shipping characteristics of vessels bound for the Great Lakes from European sources, including total transit time (T), time at which ballast exchange commences (t_B), duration of interval during which organisms in ballast tanks are exposed to salt water ($T-t_B$) and number of ships from different source regions ($\hat{S}$).

Source region	T (days)	t_B (days)	$T-t_B$ (days)	$\hat{S}$ ($year^{-1}$)
Rotterdam/Antwerp	9.7	3.6	6.1	120
Baltic Sea	11.8	7.2	4.6	54

Appendix 1c. Ballast water exchange efficiency characteristics, including the probability of an organism remaining in a tank during exchange on the open ocean (r_0), and the probability of being expelled during ballast discharge on the Great Lakes (1- r_1).

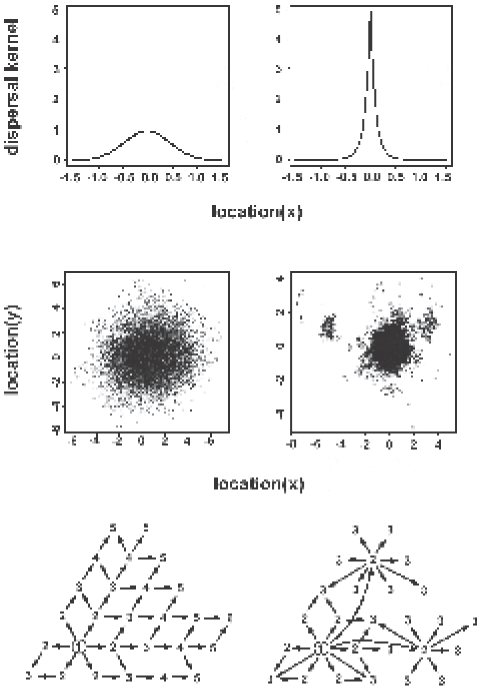
Information source	r_0	1- r_1 (BOB)	1- r_1 (NOBOB)	NOBOB (%)
Ship industry	0.01	0.99	0.98	9
Coast Guard	0.15	0.85	0.85	19

(a)



2
1
density(u)
r = 10
r = 20
u*
10
20
30
x*
40
location(x)

(b)



dispersal kernel
5
4
3
2
1
0
-1.5 -1.0 -0.5 0.0 0.5 1.0 1.5
location(x)
location(y)
6
4
2
0
-2
-4
-6
-6 -4 -2 0 2 4 6
location(x)