



A conceptual model of community dynamics during the transport stage of the invasion process: a case study of ships' ballast

Elizabeta Briski^{1*}, Farrah T. Chan², Hugh J. MacIsaac² and Sarah A. Bailey¹

¹Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries and Oceans Canada, 867 Lakeshore Road, Burlington, ON, Canada L7R 4A6, ²Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON, Canada N9B 3P4

ABSTRACT

Aim After J. L. Lockwood, P. Cassey and T. Blackburn (2009, *Diversity and Distributions*, 15, 904–910) first described a theoretical relationship between propagule pressure and colonization pressure, two empirical studies demonstrated that the transport stage of the invasion process can profoundly influence the strength of the relationship among multiple events, as well as predictions of introduction risk. However, studies exploring dynamics of transported communities are rare, as repeated-measures sampling during transportation by any vector is logistically difficult. We constructed a conceptual model of community dynamics during transportation and supported it by empirical data for propagule pressure and colonization pressure of plankton.

Location Global.

Methods A conceptual model of community dynamics was developed based on lognormal species abundance distribution and the simulation model of J. L. Lockwood, P. Cassey and T. Blackburn (2009, *Diversity and Distributions*, 15, 904–910). We considered four cases: case 'A' – no reduction in propagule nor colonization pressure; case 'B' – strong reduction in propagule and mild reduction in colonization pressure; case 'C' – mild reduction in propagule and strong reduction in colonization pressure; and case 'D' – strong reduction in both propagule and colonization pressures.

Results The cases 'B', 'C' and 'D' were supported by empirical data for invertebrates, dinoflagellates and diatoms from ships' ballast tanks, respectively. Propagule pressure of invertebrates, dinoflagellates and diatoms decreased 99.95%, 80% and 94% in 25 days, respectively, while colonization pressure decreased 34%, 57% and 64%.

Main conclusions Transport affects both propagule pressure and colonization pressure of taxa, with the magnitude of change dependent on length of transport and taxon-specific survival and reproduction. Our model demonstrates that introduction risk varies substantially across and within taxa depending on the occurrence and severity of selection pressures during transportation which serve to change species abundance distributions.

Keywords

Biological invasion, colonization pressure, introduction risk, propagule pressure.

*Correspondence: Elizabeta Briski, Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries and Oceans Canada, 867 Lakeshore Road, Burlington, ON, Canada, L7R 4A6.
E-mails: elizabeta.briski@dfo-mpo.gc.ca; elzabriski@yahoo.com

INTRODUCTION

Human-mediated invasions by non-indigenous species are a profound agent of evolutionary and ecological changes (Carlton & Geller, 1993; Olden *et al.*, 2004). Any mechanism capable of rapid translocation of large numbers of species has the potential to facilitate mass invasions (Olden *et al.*, 2004). Whole communities can be transported incidental to commercial travel and trade, including *via* ships' ballast water or hull fouling, in wood packing materials (i.e. dunnage), livestock feed or horticultural soils, or on or in livestock (Lockwood *et al.*, 2007; Hulme *et al.*, 2008; Seebens *et al.*, 2013). Prevention is widely regarded as the most effective management strategy; however, invasion ecology is a relatively young field (Lockwood *et al.*, 2007), and researchers are still struggling to develop predictive, quantitative models that may inform policy and management. Nevertheless, the invasion process itself has been well described as a series of stages, including transport, introduction, establishment and spread (Kolar & Lodge, 2001; Colautti *et al.*, 2006; Blackburn *et al.*, 2009; Simberloff, 2009). The transition between stages is affected by three factors: propagule pressure (i.e. number of individuals), physiological tolerance of individuals to ambient physical and chemical conditions, and biological community interactions (Kolar & Lodge, 2001; Colautti & MacIsaac, 2004; Lockwood *et al.*, 2007). Empirical and statistical evidence suggest that propagule pressure is of vital importance to introduction success (Colautti *et al.*, 2006; Hayes & Barry, 2008; Lockwood *et al.*, 2009; Simberloff, 2009). In addition, the number of established species in an ecosystem may reflect the number of species introduced (i.e. colonization pressure) (Chiron *et al.*, 2009; Lockwood *et al.*, 2009). Both factors may independently affect invasion success, as high propagule pressure reduces the intensity of Allee effects and increases establishment success of individual species, while high colonization pressure increases the chance that at least one species may tolerate the new environment and become established (Lockwood *et al.*, 2009).

Based on random sampling theory, where larger sample sizes increase the probability of sampling rare species (Preston, 1948), Lockwood *et al.* (2009) described the relationship between propagule pressure and colonization pressure by simulating the random selection of organisms from a hypothetical community with log-series species abundance distribution. Ballast water is an ideal vector to characterize this relationship as it regularly includes hundreds of species (Carlton, 1985; Olenin *et al.*, 2000; Briski *et al.*, 2013). Since then, two empirical studies demonstrated that the transport stage of the invasion process can profoundly influence the strength of the relationship among multiple events, as well as predictions of introduction risk (Briski *et al.*, 2012a, 2013). Transport conditions within vectors are often hostile; for example, drastic changes measured in ballast tanks during single voyages include differences in temperature up to 20 °C, dissolved oxygen up to 6 mg L⁻¹ and salinity up to 15‰ (Klein *et al.*, 2010; Seiden *et al.*, 2011; Simard *et al.*, 2011). Furthermore,

horticultural soil and dunnage are exposed to high temperatures or fumigation with methyl bromide to remove unwanted hitchhikers (European Commission, 2005). However, some vectors, such as intentional transport of livestock, aquaculture species or aquarium species, provide optimal environments during transportation for diversified contaminants, parasites or stowaways. In these cases, transportation may not have much influence on the propagule pressure–colonization pressure relationship and introduction risk of those species.

Studies exploring the dynamics of communities by repeated sampling during transportation are rare, to our knowledge conducted primarily for the shipping vector, and have yielded variable results (Olenin *et al.*, 2000; Klein *et al.*, 2010; Seiden *et al.*, 2011; Simard *et al.*, 2011). Conducting time-point sampling during transportation by any vector is logistically and practically difficult. To bridge this gap in research and to provide managers and policy-makers with information about changes in introduction potential of diversified taxa, we constructed a conceptual model of community dynamics during the transportation stage of the invasion process and supported it by observed community dynamics of three taxonomic groups (i.e. invertebrates, dinoflagellates and diatoms) commonly transported in ships' ballast water. While propagule pressure is strictly defined as the number of individuals of one species that are released (Lockwood *et al.*, 2009), in this study, we examine propagule pressure of whole taxonomic groups (i.e. invertebrates, dinoflagellates and diatoms), unless otherwise stated.

METHODS

Developing the conceptual model

Previous analyses of the empirical species abundance distributions for invertebrates in ballast water (Drake *et al.*, 2013) and the Lockwood *et al.* (2009) simulation model served as the foundation for our conceptual model. We selected four distinct empirical species rank-abundance distributions from Drake *et al.* (2013) (Fig. 1a) and conducted random sampling of 1:1000 organisms within each to construct propagule pressure–colonization pressure relationships (Fig. 1b). For the curves representing the beginning of transportation (T_b) in our conceptual model, we chose the middle curve from Fig. 1b (solid line). Considering the diversified vectors and environmental conditions involved in species transport, we then constructed four distinct hypothetical cases of community dynamics during transport (hereafter, case 'A', 'B', 'C' and 'D') with intentionally emphasized combinations of reduction in propagule pressure and colonization pressure: case 'A' – no reduction in propagule pressure nor colonization pressure; case 'B' – strong reduction in propagule pressure and mild reduction in colonization pressure; case 'C' – mild reduction in propagule pressure and strong reduction in colonization pressure; and case 'D' – strong reduction in both propagule pressure and colonization pressure (Fig. 2a). While the exact shape of the curves, particularly the slope and saturation

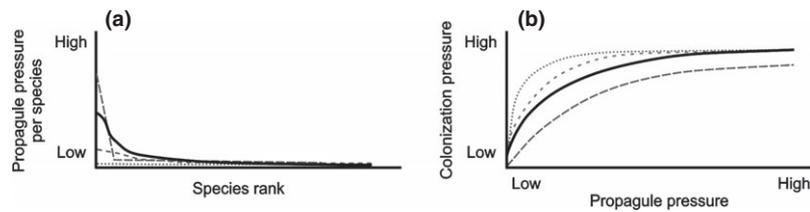


Figure 1 Four distinct empirical species rank-abundance distributions for invertebrates in ships ballast water from Drake *et al.* (2013) (a), and propagule pressure–colonization pressure relationships following random sampling of 1:1000 organisms within each distribution (b).

points, may vary depending on the species rank-abundance distributions (Fig. 1), only the endpoints of the curves were considered here. Nevertheless, curves were added to our model for better visualization; the curves representing short (T_s), medium (T_m) and long (T_l) transportation were arbitrarily drawn without conducting simulations to demonstrate our four hypothetical reductions in propagule and colonization pressures (cases 'A', 'B', 'C' and 'D'; Fig. 2a). We acknowledge that transitional combinations of reduction are possible and that propagule pressure may increase in some cases, but we cannot discuss all possible scenarios.

To determine changes in species rank-abundance distributions resulting from our four case scenarios, we first constructed a hypothetical community consisting of abundant and rare species as commonly described from nature and from ballast tanks immediately after ballast water uptake (e.g. Hoffmeyer, 2004; Dermott *et al.*, 2007; Zervoudaki *et al.*, 2009; Briski *et al.*, 2012b; Michaloudi *et al.*, 2012). Our hypothetical community was based on the empirical ballast tank community (solid line in Fig. 1a) from which our chosen propagule pressure–colonization pressure relationship curve was derived (solid line in Fig. 1b). Considering our four case scenarios, we then determined the number of species truncated and the area of the species abundance distribution truncated at different time points as transport progresses (Fig. 2b).

Supporting the conceptual model with real data

We examined empirical data from a recent, comprehensive study of ballast water sampled from ships operating on international and domestic routes in Canada (Briski *et al.*, 2012a, 2013) with the aim to support our conceptual model. The studies determined propagule and colonization pressures of invertebrates, dinoflagellates and diatoms for more than 150 ballast samples, and Briski *et al.* (2013) conducted regression analyses to examine the influence of voyage length on propagule and colonization pressures (Fig. 3). These regression equations were used in this study to set the endpoint values for the three taxa, at different time points during transportation (Fig. 4). The intercepts on the y -axis in Fig. 3 were set as total (100%) propagule pressure and colonization pressure entrained into tanks immediately after ballasting (T_0), while the empirical values at days 5, 15 and 25 were used to set the endpoints of curves T_5 , T_{15} and T_{25} , and to calculate the corresponding percentage reduction in

propagule pressure and colonization pressure for individual days during voyage (Table 1, Fig. 4).

We again chose the middle curve from Fig. 1 (solid line) to illustrate the relationship between propagule pressure and colonization pressure. While the exact shape of the curves has no importance for our model, when considering multiple transport events over time it is important to consider the variability in the shape of the curves across events. Briski *et al.* (2012a) used model II regression analyses to demonstrate relationships between propagule pressure and colonization pressure which showed to be consistent across ships with longer and shorter voyages for dinoflagellates and diatoms, but only in ships with longer voyages for invertebrates. Taking this into consideration, we used dashed lines to emphasize possible variability of curve shapes for propagule pressure–colonization pressure relationship, making our model representative of multiple events (Fig. 4).

RESULTS

Conceptual model of community dynamics

Our four hypothetical cases of community dynamics during transport resulted in four distinct species abundance distribution outcomes (Fig. 2b). In case 'A', there was no reduction either in propagule or colonization pressure, resulting in no changes in species abundance distribution. Similarly, there would be no meaningful changes in species abundance distribution if propagule and colonization pressures are only mildly reduced, even though there would be slightly fewer species and a lower abundance of each. In case 'B', when propagule pressure was drastically reduced, but colonization pressure decreased only slightly, the species abundance distribution changed from one consisting of dominant and rare species to one dominated by rare species (nearly even abundance across taxa). In contrast, in case 'C', when reductions were mild for propagule pressure but strong for colonization pressure, the species abundance distribution became dominated by abundant species with a small number of species having intermediate abundance, while rare species were lost. In case 'D', where both propagule and colonization pressures were strongly reduced, the shape of the species abundance distribution did not change a lot and consisted of abundant and rare species similar to case 'A' but with fewer species and much lower abundance per species.

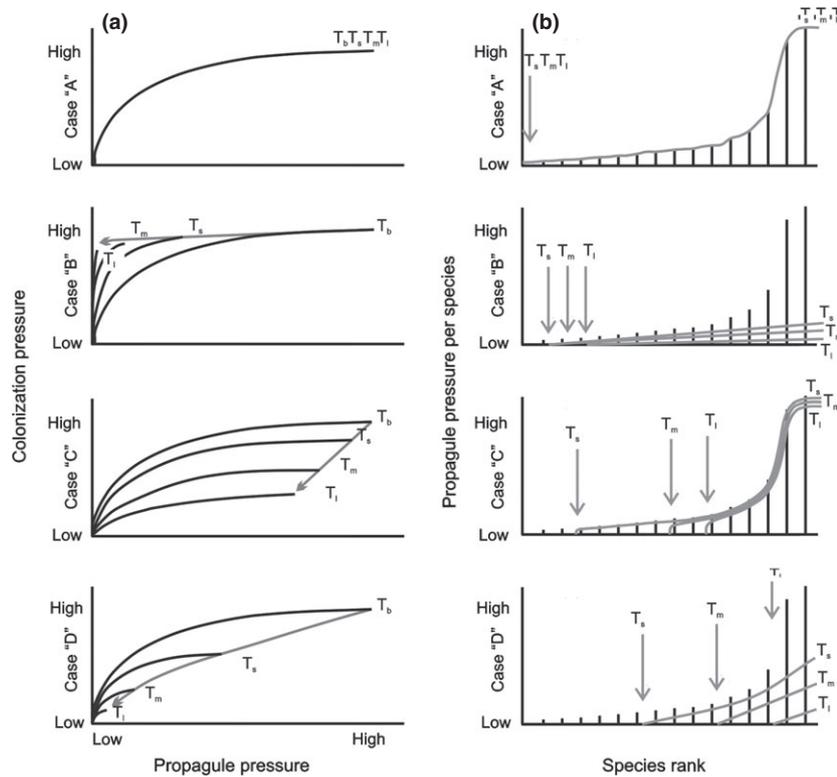


Figure 2 Conceptual model of community dynamics during the transportation stage of invasion process for four different cases: case 'A' – no reduction in either propagule pressure nor colonization pressure, case 'B' – strong reduction in propagule pressure – mild reduction in colonization pressure, case 'C' – mild reduction in propagule pressure – strong reduction in colonization pressure, and case 'D' – strong reduction in both propagule pressure and colonization pressure. Propagule pressure–colonization pressure relationships of our four cases (a) and species rank–abundance distributions resulting from our four case scenarios (b) are shown. In panel (a), grey arrows denote reduction in propagule and colonization pressures at the beginning (T_b), after short (T_s), medium (T_m) and long (T_l) transport. In panel (b), every bar represents one species, grey lines represent reduction in propagule pressure after short, middle and long transport, and species to the left of grey arrows are those that disappeared after short, middle and long transport.

Observed community dynamics in ships' ballast water

The empirical community dynamics supported the conceptual model cases 'B', 'C' and 'D'. Interestingly, the taxa differ in which general form is taken. Similar to case 'B', invertebrate communities in ballast water showed a marked decrease in propagule pressure during the first 5 days of transportation, but almost no decrease in colonization pressure until day 15; by day 25, the decrease in colonization pressure was 34% of all species entrained in the vector (Table 1, Fig. 4). While this pattern could be attributed to nearly even initial abundances across taxa, such that the total number of individuals must be drastically reduced before there is loss of species richness, natural zooplankton communities – and those in ballast water immediately after entrainment into tanks – do not exhibit uniform abundances across taxa (Hoffmeyer, 2004; Dermott *et al.*, 2007; Zervoudaki *et al.*, 2009; Briski *et al.*, 2012b; Michaloudi *et al.*, 2012). The observed community dynamics indicate that mortality was selectively high for abundant species of invertebrates, but that both abundant and rare species remained at the end of the voyage. Consequently, the species

abundance distribution changed markedly during the first 5 days – from one consisting of abundant and rare species to one with a nearly even but relatively low abundance of taxa (Fig. 5) – resulting in no propagule pressure–colonization pressure relationship among multiple transport events for short transport time (Ugland & Gray, 1982; Briski *et al.*, 2012b). However, after day five, the species abundance distribution became more stable, resulting in the establishment of a propagule pressure–colonization pressure relationship with longer transport time (Briski *et al.*, 2012a). Thus, as time since entrainment increased, the relationship strengthened (F.T. Chan, unpublished data).

In the case of dinoflagellates, empirical data showed a mild decrease in propagule pressure through time, but strong decline in colonization pressure (Table 1, Fig. 4). The pattern of dinoflagellates was similar to our model case 'C', but with slightly greater reduction in propagule pressure. Dinoflagellate mortality during transport appeared to affect all species equally; consequently, rare species were lost quite rapidly. Equal mortality of all species across time maintained the propagule pressure–colonization pressure relationship independent of transport duration (Briski *et al.*, 2012a).

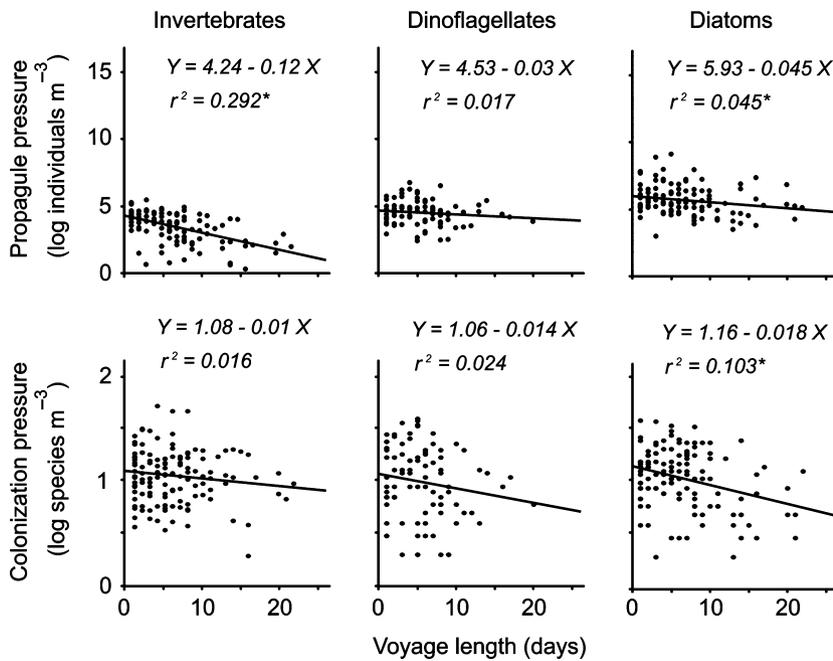


Figure 3 Scatterplots and fitted regression lines with the propagule pressure and colonization pressure as dependent variables and voyage length as the independent variable for invertebrates, dinoflagellates and diatoms collected from 154 ballast tanks of ships arriving at Pacific and Atlantic ports in Canada and Laurentian Great Lakes ports. All data are log-transformed. Asterisks denote significance at 0.05. Modified from Figs 3 and 4 in Briski *et al.* (2013) – Copyright 2013 by the Association for the Sciences of Limnology and Oceanography, Inc.

Considering diatoms, empirical data indicated that propagule pressure decreased almost twice as fast as for dinoflagellates, but at only half the rate of invertebrates (Table 1, Fig. 4). The decrease in colonization pressure of diatoms was similar to that of dinoflagellates for the first 5 days; however, as transport progressed, colonization pressure decreased faster than for dinoflagellates, reaching the greatest decrease in all three taxa examined. The pattern of diatoms was similar to our model case 'D'. Mortality during transport resulted in loss of individuals of all species equally, and due to a rapid decrease in propagule pressure, many species of both rare and intermediately abundant taxa disappeared. Following this trend of accelerated, but not uniform decline in propagule pressure and colonization pressure of taxa with time, longer transport duration may lead to loss of the propagule pressure–colonization pressure relationship among multiple transport events for diatoms (dashed T_{25} line, Fig. 4); a strong relationship has been observed empirically for short but not for long voyages * (Briski *et al.*, 2012a).

DISCUSSION

Environmental tolerance of different taxa and their species diversities

Environmental conditions during transport may vary (European Commission, 2005; Klein *et al.*, 2010; Seiden *et al.*, 2011; Simard *et al.*, 2011), and empirical data from ballast water indicate that different taxa have different environmental (i.e. physical, chemical and/or biological) tolerances (Briski *et al.*, 2012a, 2013). In our model case 'B', which is supported by data for invertebrates, most species have a relatively wide range of environmental tolerance at the population level,

although many individuals within a population have low tolerance (particularly evident in highly abundant species). Taxa might encounter unsuitable microsites inside ballast tanks that cannot support high abundances (Snell *et al.*, 2001; Yoshinaga *et al.*, 2001; Ricklefs, 2008; Zervoudaki *et al.*, 2009). Seasonal or temporal succession of zooplankton, where the relative abundance of individual species changes over time, is commonly observed in nature (Hoffmeyer, 2004; Dermott *et al.*, 2007; Zervoudaki *et al.*, 2009; Michaloudi *et al.*, 2012), and may be accompanied by the production of dormant stages resistant to unfavourable conditions (Cáceres, 1997). While we expect initial zooplankton communities entrained in a vector to resemble natural communities, with a mixture of common and rare species (Hoffmeyer, 2004; Dermott *et al.*, 2007; Zervoudaki *et al.*, 2009; Michaloudi *et al.*, 2012), our model and empirical data for invertebrates indicate that population abundances often became more evenly distributed as transport progresses.

In contrast, our model indicated that environmental tolerance in cases 'C' and 'D', supported by data for dinoflagellates and diatoms, appeared to vary by species, with tolerance being directly proportional to the number of individuals comprising the population (i.e. little decrease in propagule pressure accompanied by relatively high decrease in colonization pressure for dinoflagellates); rare species typically have a relatively narrow tolerance as a population, while abundant species have a wider population tolerance including sensitive to broadly tolerant individuals. Consequently, due to even mortality across all species, populations of dinoflagellates and diatoms in ship ballast tanks had similar population structure as in nature, consisting of abundant, less abundant and rare species (Graham *et al.*, 2004; Anderson & Rengefors, 2006; Dermott *et al.*, 2007).

Changes in introduction and establishment risk

Differing environmental tolerances translate into variable risk of introduction among different taxonomic groups. Introduction risk of taxa such as invertebrates (case 'B') dropped rapidly as transport duration increased, because most species experienced dramatic decreases in propagule pressure.

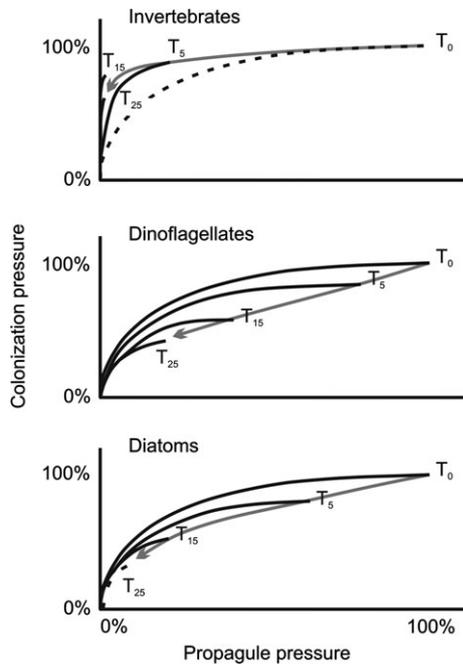


Figure 4 Observed community dynamics during the transportation stage of invasion process for invertebrates, dinoflagellates and diatoms. T_0 , T_5 , T_{15} and T_{25} represent transport duration of 0, 5, 15 and 25 days, respectively. Dashed line denotes no relationship between propagule and colonization pressures when multiple events were considered. Grey arrow denotes reduction in propagule and colonization pressures.

Although colonization pressure of invertebrates may remain high even after 15 or 25 days, propagule pressure of many species may, by that time, be too low to overcome Allee effects and demographic stochasticity after introduction (Lockwood *et al.*, 2007, 2009). The International Maritime Organization proposed invasions by organisms $\geq 50 \mu\text{m}$ (i.e. invertebrates and large algae) would be reduced for ballast water having propagule pressure of <10 individuals per 1 m^3 (IMO, 2004); propagule pressure of invertebrates in our study was 316 and 16 individuals per m^3 for day 15 and 25, respectively (Table 1). In contrast, introduction risk of taxa such as dinoflagellates (case 'C') changed little, if at all, with increasing voyage length. Colonization pressure of dinoflagellates decreased with voyage length, indicating lost species had very specific environmental requirements; these species likely would also have poor prospects for survival upon introduction to the new habitat. Species that survived the transport stage likely had broader environmental tolerance, representing a higher establishment risk for recipient areas as their propagule pressure was still relatively high. Still, very different abiotic factors between donor and recipient areas may prevent establishment following introduction. Establishment by strictly marine species in freshwater systems is highly unlikely. Finally, introduction risk of taxa such as diatoms (case 'D') initially dropped a little, but then started to decrease severely after the fifth day of transport. Low propagule pressure of diatoms after longer voyages might not result in demographic limitations as diatoms reproduce asexually (Lee, 2008), but low colonization pressure might lower establishment potential in the new habitat by decreasing the chance that at least one of the species will tolerate the environment of the new area. Even though events with high propagule pressure and high colonization pressure represent the highest introduction and establishment risk, our model demonstrated that in the case where transport conditions decrease propagule pressure and/or colonization pressure, introduction and establishment risk of high propagule pressure–low colonization pressure events is almost the same

Table 1 Propagule (PP) and colonization pressures (CP) calculated for T_0 (intercept), T_5 , T_{15} and T_{25} , which represent 0, 5, 15 and 25 days of transport, respectively, based on best-fit regression line equations and empirical data in Briski *et al.* (2013). The percentages of propagule and colonization pressures remaining for individual days during the voyage are included in brackets. Case description for each taxon is also included

Taxa	Observed propagule and colonization pressures (percentage remaining from T_0 , %)				Case description	
	T_0	T_5	T_{15}	T_{25}	Reduction	Case
Invertebrates						
PP	31,622	6309 (20)	316 (1.00)	15 (0.05)	Strong	
CP	12	11 (93)	10 (81)	8 (66)	Mild	Case 'B'
Dinoflagellates						
PP	63,095	50,118 (79)	25,118 (40)	12,589 (20)	Mild	
CP	12	10 (83)	7 (60)	5 (43)	Strong	Case 'C'
Diatoms						
PP	1,584,893	1,000,027 (63)	316,227 (20)	100,516 (6)	Strong	
CP	13	11 (83)	7 (55)	5 (36)	Strong	Case 'D'

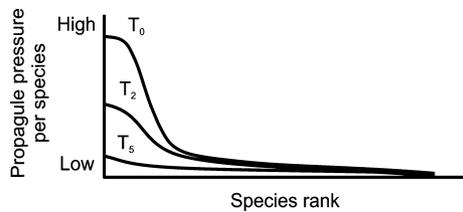


Figure 5 Hypothetical change in species rank-abundance distribution of invertebrates from uptake of ballast water to the fifth day of voyage. T_0 , T_2 and T_5 represent 0, 2 and 5 days of transport, respectively.

as that of high propagule pressure–high colonization pressure (i.e. case ‘C’).

Can we predict introduction risk?

The risk of introduction posed by a particular vector should be examined for individual taxonomic groups. Knowing the propagule pressure–colonization pressure relationship of a particular taxonomic group allows estimates of total abundance being transported to be used as a proxy for species richness without time-consuming species identifications. However, Briski *et al.* (2012a) demonstrated that when multiple events are taken into account (i.e. across 176 ship samples), the relationship may not exist for some taxonomic groups during some time periods (e.g. invertebrates transported <5 days in ballast water). Previously, Briski *et al.* (2012a) suggested that taxa may not be randomly entrained in the transport vector, thereby violating a key assumption of the expected relationship between propagule pressure and colonization pressure. However, this study revealed that this pattern may be due to extremely rapid changes in species abundance distributions in a short transport time. Indeed, in the case of invertebrates, it is possible that every day has its own distinct propagule pressure–colonization pressure relationship. Consequently, separate propagule pressure–colonization pressure relationships may need to be developed for each of the first 5 days of transport if we wish to predict introduction risk of invertebrates in ‘young’ ballast. As transport progressed and ballast aged, species abundance distributions became more similar across events, resulting in the expected relationship between these variables and making introduction risk by invertebrates easier to predict. However, by the time the relationship becomes strong, propagule pressure per species may be too low for many taxa to establish if discharged into a new habitat. In contrast, dinoflagellate introduction risk was highly predictable, independent of ballast water age because species abundance distributions did not change much through time. Finally, diatom introduction risk was highly predictable for ballast during short voyages, but became less so with longer transport as species abundance distributions became more distinct with time. Consequently, our study indicates that it is necessary to explore different taxonomic groups and transport vectors separately to be able to construct propagule pressure–colonization pressure relationships to predict introduction risk.

Comparison with other vectors

Transport conditions, such as those in ballast tanks, horticultural soil or dunnage, are often hostile (European Commission, 2005; Klein *et al.*, 2010; Seiden *et al.*, 2011; Simard *et al.*, 2011), whereas other vectors may provide a relatively benign or even favourable environment. For example, the aquarium and aquaculture industries optimize transport conditions to minimize losses of desirable, marketable species being transported (Lim *et al.*, 2003; Harmon, 2009). Accordingly, we assume that neither propagule nor colonization pressure of aquarium or aquaculture species would decrease very much. Still, we expect that both propagule and colonization pressures of parasites or other stowaways on aquarium and aquaculture species may be reduced severely if those species has been treated against parasites. Consequently, we expect that introduction risk of aquarium or aquaculture species would not decrease a lot through time, but that of parasites or stowaways might. We are not aware of studies on community dynamics of taxa transported in vectors other than shipping; however, we assume that introduction risk vary among vector and taxa depending on the type of vector and species’ environmental tolerance.

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*[Correction added on 3 December 2013 after first online publication on 25 November 2013 in *Diversity and Distributions*: The last part of the sentence should read ‘...has been observed empirically for short but not for long voyages’. The error has been corrected in this version of the article.]

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BIOSKETCH

Elizabeta Briski studies transport patterns and survival of plankton and their dormant stages in the hostile environment of ships' ballast tanks. Elizabeta also works on the ecological theory regarding propagule and colonization pressures, two factors identified as the key determinants of whether introduced species survive in new environments. All authors are interested in invasion ecology, particularly in vectors and pathways by which non-indigenous species are introduced.

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