

Variation in propagule and colonization pressures following rapid human-mediated transport: Implications for a universal assemblage-based management model

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Abstract

Recent studies have recognized the importance of propagule pressure (number of individuals) and colonization pressure (number of species) for explaining establishment success of nonindigenous species. However, the International Ballast Water Management Convention, when ratified, will require ships to satisfy a numeric discharge standard that focuses only on cumulative propagule pressure of all individuals released. Because of practical constraints, the standard does not differentiate between discharges of single vs. multiple species. The assemblage-based approach, which uses rank-abundance gradients to quantify and manage introduction risk, may compensate for this limitation (e.g., even gradient [relatively consistent propagule pressures among n transported species] or uneven gradient [uneven propagule pressures among n transported species]). Here we explore species abundance distributions of zooplankton during transportation in ballast water to assess variability in the structure of assemblages, with implications for the potential development of an assemblage-based management model. Specifically, we explored species abundance distributions for voyages that lasted < 24 h, those from 24 to 48 h, and those from 48 to 72 h (i.e., three time scales). Species abundance distributions within and across transit time scales were highly variable. As transport time increased, we observed a shift from uneven to even rank-abundance gradients. Owing to variation in assemblage structure, the number of organisms necessary to quantify colonization pressure exhibited similarly strong variation within and across time scales. Our study indicates that assemblage-based approaches to estimate introduction risk are warranted, yet the variation inherent in transported assemblages will induce substantial uncertainty within management models.

Ecosystems globally have been altered by the introduction and establishment of nonindigenous species (NIS). Some NIS that establish in new environments pose strong ecological and economic effects; thus, management efforts to reduce the risk of new introductions provide realistic opportunities to mitigate the ecological and economic uncertainty imposed by NIS (Lodge et al. 2006; Lockwood et al. 2007; Hulme et al. 2008). NIS have been introduced by various vectors, including authorized stocking, recreational activities, and commercial travel and trade, including via ships' ballast water or hull fouling, in wood packing materials (i.e., dunnage), in livestock feed or horticultural soils, or on or in livestock (Lockwood et al. 2007; Hulme et al. 2008; MacIsaac 2011). Many vectors have the potential to spread entire species assemblages because physical uptake mechanisms allow multiple species to become entrained in a single human-mediated movement (Lockwood et al. 2007; Hulme et al. 2008; Briski et al. 2013). Of the relevant unintentional vectors, shipping dominates introduction of aquatic NIS because it provides an effective mechanism for uptake, transport, and introduction of a diverse array of species (Ricciardi 2006; Hulme 2009).

Experimental and theoretical evidence suggest that propagule pressure (i.e., number of individuals released) and colonization pressure (i.e., number of species released) are important null models to explore the establishment success of introduced species (Hayes and Barry 2008;

Lockwood et al. 2009; Simberloff 2009). High propagule pressure diminishes the properties of small populations, such as low genetic variation and vulnerability to Allee effects, while high colonization pressure increases the chance that at least one species may tolerate the new environment (Lockwood et al. 2009; National Research Council 2011). Recent studies have recognized the significance of the relationship between propagule pressure and colonization pressure, as well as of the structure of species assemblages, as factors that contribute to species establishment (Lockwood et al. 2009; Briski et al. 2014; Drake et al. 2014). However, the International Ballast Water Management Convention, when ratified, will require ships to meet a numeric performance standard that focuses only on cumulative propagule pressure (i.e., the cumulative number of individuals released irrespective of taxonomic identity; International Maritime Organization [IMO] 2004). Such an approach disregards the importance of the underlying species abundance distribution of transported assemblages, in which the number of species will vary and each transported species exhibits its own abundance and potential for establishment.

While these regulations exist for practicality and ease of monitoring and enforcement, assessing the species abundance distribution of introduced assemblages is important to quantify establishment probabilities among n transported species during a single human-mediated movement (Drake et al. 2014). For example, for a given sample of 1000 total organisms transported and discharged into a novel environment, a highly skewed species abundance

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distribution could occur with relatively few species, though with dominant ones occurring at high abundance. Establishment of each species in the new environment can be considered as a probability trial, with the success of each trial dependent on the abundance of each species. Alternatively, a strongly even species abundance distribution for the same sample of 1000 organisms would exhibit many species but with low abundance, each with a relatively low chance of success because of a dearth of individuals (Drake et al. 2014). Environmental conditions in the new habitat may further obscure the probability of establishment.

Theoretically, the existence of a consistent underlying species abundance distribution for a transported taxonomic group (e.g., zooplankton) would allow estimating a species abundance distribution for a given abundance of organisms. This would provide attributes of the assemblage relevant to establishment risk, such as colonization and propagule pressures among n species, without the need for detailed empirical sampling and species-level identifications. A consistent species abundance distribution would also lead to greater consistency in establishment risk for a given concentration-based discharge standard. However, uncovering a universal relationship between propagule pressure, colonization pressure, and a given abundance of organisms may be unlikely because of stochasticity of the species transport process that spans multiple source communities and vector characteristics.

Despite the theoretical and practical importance of quantifying characteristics of transported assemblages, there exist very few studies pertaining to species assemblages immediately after their entrainment into a vector (e.g., ships' ballast; Briski et al. 2014). Variation among transported assemblages appears to be common across taxonomic groups and related to voyage length. Briski et al. (2014) reported greatest changes for zooplankton during short voyages lasting less than 5 d; those voyages are the most frequent ones in certain high-intensity shipping networks (Kaluza et al. 2010; Rup et al. 2010). Furthermore, based on species communities in nature, shipping data, and the study of Drake et al. (2014), Briski et al. (2014) assumed that species form uneven log-normal species abundance distributions immediately after uptake, with the possibility of different species being abundant among species assemblages due to seasonal and spatial variability of ballast uptakes (Hoffmeyer 2004; Zervoudaki et al. 2009; Hansen et al. 2013). If species abundance distributions of the same age (i.e., assemblages at time, t) are similar, despite rapid changes among species assemblages of different ages (e.g., from day 1 to day 5), predicting introduction potential at time t may be possible by incorporating voyage length as a management variable.

To compensate for the lack of emphasis of multiple transported species within the International Ballast Water Management Convention and to explore the potential for an assemblage-based management model, we explore the assemblage structure of zooplankton during human-mediated transport at rapid time scales. For this purpose, we explored species abundance distributions of zooplankton in ballast water that was < 24 h old as well as 24–48 h and 48–72 h old and determined variability within and among

samples of different ages. Next, we conducted stochastic simulations within each species abundance distribution (i.e., sample) to interpret how colonization pressure changes with increasing propagule pressure and to understand the variability of transported assemblages across multiple human-mediated events and transportation time scales (i.e., < 24, 24–48, and 48–72 h). We tested three hypotheses: (1) species abundance distributions of zooplankton within the same time scale (e.g., < 24 h) will exhibit low variation across different events or samples, and if low variation exists, the number of organisms necessary to document colonization pressure among samples will be relatively consistent; (2) despite similar underlying species abundance distributions, the abundant (dominant) species in each sample may differ; and (3) species abundance distributions of zooplankton across time scales will differ.

Methods

Sample collection, taxa enumeration, and identification—In 2007 and 2008, as a part of a broader study (Briski et al. 2012b), we collected 22 ballast water samples from domestic vessels operating between Great Lakes ports in Canada and the United States. Vessels were boarded opportunistically at cargo or fuel docks in Corunna, Goderich, Sarnia, or Windsor, Ontario, or Superior, Wisconsin, throughout the shipping season. Ballast history for each vessel, including date and location of ballast uptake, was obtained from vessel personnel (Table 1). Eight samples were collected < 24 h after water was pumped into ballast tanks, while eight others were collected 24–48 h after pumping and six more 48–72 h after pumping. Every sample, independent of ballast age, was collected from a different ship. Tanks were sampled by lowering a 30-cm-diameter, 53- μ m-mesh plankton net to the lowest accessible point of the ballast tank through an opened tank access hatch. One to five net hauls were taken, depending on depth, totaling at least 1000 liters of water filtered. The exact amount of water collected per sample was calculated by multiplying the area of the net opening by haul depth and number of hauls. Samples were preserved in ethanol and sent to taxonomic experts for enumeration and identification based on morphological characteristics.

Construction of species rank-abundance and saturation plots—Species rank-abundance plots were constructed for each sample by plotting the species rank (ordered index of n species) on the x-axis and the abundance of each species on the y-axis. To determine colonization pressure variability within each time scale (i.e., < 24, 24–48, and 48–72 h), we sampled organisms contained in each sample as follows: (1) a single individual was randomly selected from a sample, and the number of individuals (i.e., one for the initial draw) and number of species (i.e., one for the initial draw) were recorded; (2) this individual was returned, and then two individuals were randomly selected, again recording number of individuals and number of species; (3) the number of individuals sampled continued until a grab of 1000 individuals was made; (4) the process of (1) through (3) was repeated 100 times; and (5) the outcome of the simulation

Table 1. Descriptive statistics, date of sampling, and ballasting location for samples collected at different time scales (i.e., < 24, 24–48, and 48–72 h). CP and PP represent colonization pressure and propagule pressure per m³, respectively.

Ballast age	Sample	CP	Minimum PP	Median PP	Maximum PP	Mean PP	Total PP	Sampling date	Ballast source
< 24 h	A	15	500	1500	83,476	7165	107,470	11 Jul 2007	Cleveland, Ohio
	B	17	19	77	2538	409	6957	17 Jul 2007	Courtright, Ontario
	C	9	108	3555	89,404	13,596	122,364	11 Oct 2007	Nanticoke, Ontario
	D	17	276	3310	21,238	5549	94,329	17 Oct 2007	Toledo, Ohio
	E	18	582	1456	53,577	10,256	184,606	18 Oct 2007	Kingsville, Ontario
	F	17	24	195	23,000	1794	30,501	22 Oct 2007	Toledo, Ohio
	G	13	73	585	51,750	4852	63,080	06 May 2008	Ashtabula, Ohio
	H	16	135	541	36,663	4511	72,175	16 Jun 2008	Rouge River, Michigan
24–48 h	I	17	77	538	10,916	2286	38,868	25 Jun 2007	Port Colborne, Ontario
	J	14	61	338	7000	1183	16,558	16 Jul 2007	Clarkson, Ontario
	K	11	9	104	65,000	6014	66,157	12 Oct 2007	Detroit, Michigan
	L	9	220	1322	86,354	12,385	111,468	15 Oct 2007	Parry Sound, Ontario
	M	8	58	105	2167	463	3701	22 May 2008	Windsor, Ontario
	N	12	2	29	972	213	2556	24 Oct 2007	Sarnia, Ontario
	O	22	225	899	104,307	6802	149,641	09 Jun 2008	Toledo, Ohio
	P	14	25	190	8400	1416	19,827	27 Aug 2008	Sarnia, Ontario
48–72 h	Q	18	3	383	4251	975	17,559	06 Jun 2007	Sault Saint Marie, Ontario
	R	16	146	365	16,809	2677	42,826	10 Sep 2007	Thunder Bay, Ontario
	S	19	5	1729	20,401	5114	97,171	12 Oct 2007	Toledo, Ohio
	T	16	51	255	7306	977	15,634	01 Nov 2007	Toledo, Ohio
	U	18	38	401	6871	1004	18,067	09 Jun 2008	Toronto, Ontario
	V	9	172	1856	17,874	3665	32,981	29 Aug 2008	Ashtabula, Ohio

was plotted as the cumulative number of individuals (x-axis) vs. number of species (y-axis). Finally, we plotted bootstrap confidence intervals ($\alpha = 0.05$) of the number of individuals necessary to reach the 95th and 99th percentiles of colonization pressure. Saturation plots were used to determine variability among colonization pressures for a given cumulative abundance of organisms.

Statistical analyses—To determine differences among species abundance distributions for samples within the same time scale, we conducted Kruskal–Wallis tests using Monte Carlo simulations with 10,000 iterations and a confidence level of 95% (Yau 2013). Three different Kruskal–Wallis tests were conducted, each of them for ballast water at < 24 h (samples A–H), 24–48 h (samples I–P), and 48–72 h time scales (samples Q–V). Furthermore, we conducted a fourth Kruskal–Wallis test to compare differences among species abundance distributions for different time scales. Pairwise comparisons between different time scales were conducted by Kolmogorov–Smirnov Z-tests, again using Monte Carlo simulations with 10,000 iterations and a confidence level of 95% (Press et al. 2002; Crawley 2007). All statistical analyses were performed in R, version 2.12.1 (R Development Core Team 2008).

Results

Species rank-abundance distributions within and among samples at different time scales—Species abundance distributions of ballast samples collected < 24 h after entrainment ranged from steep rank-abundance gradients (i.e., uneven propagule

pressures among n transported species; Fig. 1, A1 and C1), through those with moderate unevenness of propagules (Fig. 1, D1, E1, F1, G1, and H1), to those with shallow rank-abundance gradients in which propagule pressures were relatively consistent among n transported species (Fig. 1, B1). Statistical comparison revealed significant differences among distributions ($p < 0.05$; Table 2). Species abundance distributions of samples collected within 24–48 h exhibited high and significant variability ($p < 0.05$; Table 2; Fig. 2), as were distributions for samples collected < 24 h after entrainment; however, many distributions collected within 24–48 h had relatively even propagule pressures among n transported species (Fig. 2, I1, J1, M1, N1, and P1). Three distributions had steep gradients and highly uneven propagule pressures (Fig. 2, K1, L1, and O1), while there were no transitional distributions. Species abundance distributions collected within 48–72 h revealed less variability than the other two time scales, with rank-abundance gradients becoming shallower and more even among n transported species (Fig. 3). Still, a few transitional distributions (Fig. 3, R1, S1, and V1) exhibited significant differences due to the variability in assemblage shape ($p < 0.05$; Table 2). When species abundance distributions of different time scales were compared, those collected < 24 h after ballasting were significantly different from those collected within 24–48 h ($p < 0.05$; Table 2). Samples collected within 48–72 h after ballasting did not differ significantly from either of the other two time scales ($p > 0.05$; Table 2).

Propagule and colonization pressure variation at similar time scales—Modeled saturation of colonization pressure for samples collected < 24 h after ballasting were highly variable

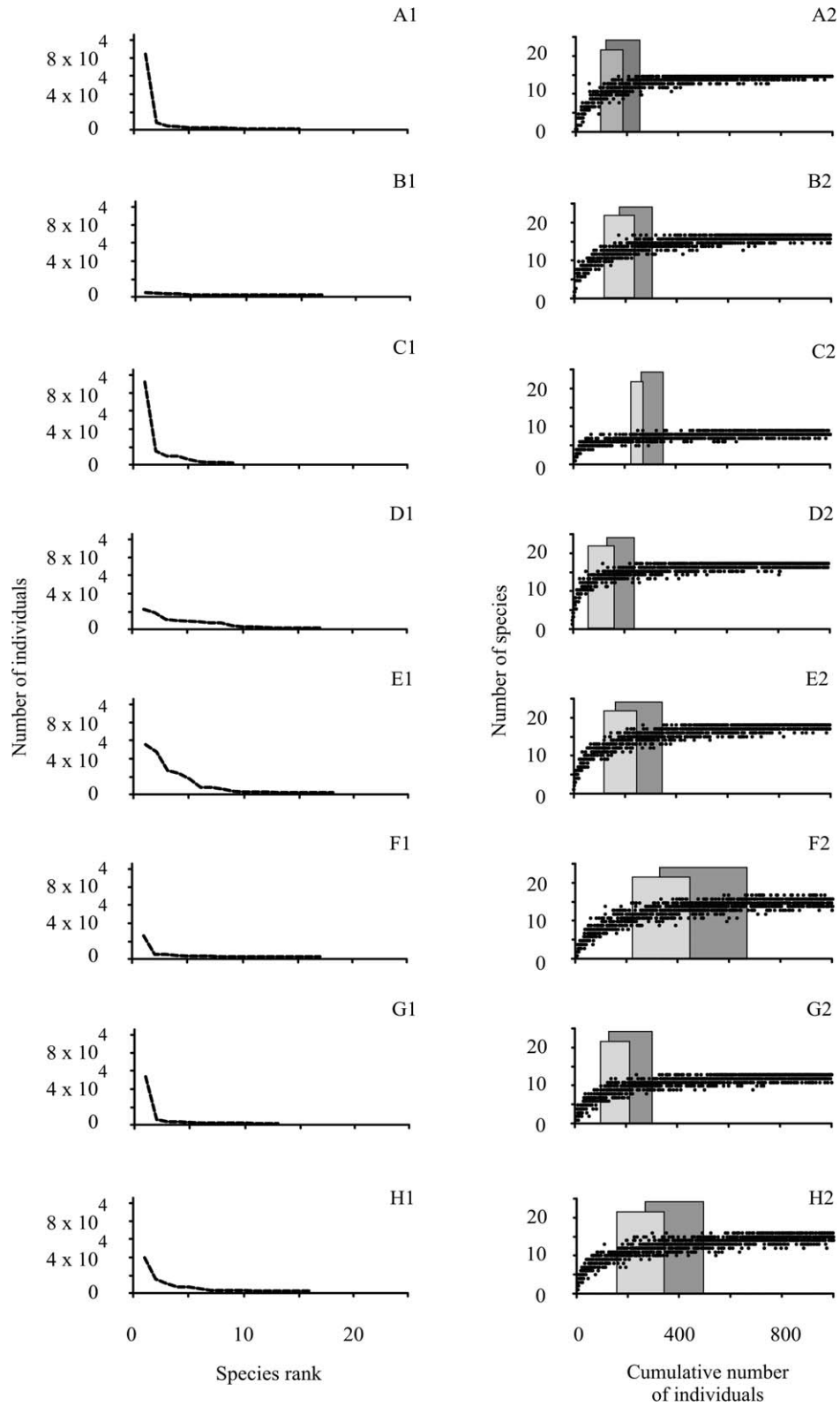


Fig. 1. Species rank-abundance plots (panels A1–H1) and their corresponding propagule pressure–colonization pressure relationships following random sampling of 1000 organisms (panels A2–H2) for samples from < 24-h-old ballast water. Shown are the lower and upper confidence intervals (error rate = 0.05) for the 95th (light gray box) and 99th (dark gray box) percentiles of colonization pressure saturation.

Table 2. Statistical comparisons of species abundance distributions within different time scales (< 24 h [samples A–H], 24–48 h [samples I–P], and 48–72 h old ballast [samples Q–V]) as well as of species abundance distributions among different time scales (< 24, 24–48, and 48–72 h). Pairwise comparisons between different time scales are also included. The comparisons were conducted using Monte Carlo simulations with 10,000 iterations and a confidence level of 95%. The lower and upper bounds represent the 95% confidence intervals for the exact *p*-values. Significant *p*-values are presented in bold.

	Lower bound	Upper bound	<i>p</i>
Within different time scales			
< 24 h	< 0.001	< 0.001	< 0.001
24–48 h	< 0.001	< 0.001	< 0.001
48–72 h	0.003	0.006	0.005
Among different time scales	0.036	0.043	0.04
< 24 h vs. 24–48 h	0.006	0.009	0.008
< 24 h vs. 48–72 h	0.479	0.498	0.488
24–48 h vs. 48–72 h	0.248	0.265	0.257

due to variation in underlying species abundance distributions (Fig. 1). Colonization pressure of samples ranged from 9 to 18 species, with bootstrap confidence intervals necessary to reach the 95th and 99th percentiles of colonization pressure ranging from 67 to 454 and 120 to 670 individuals, respectively. Corresponding species abundance distributions for samples collected within 24–48 h were even more variable. Colonization pressures ranged between 8 and 22 species, while the number of organisms necessary to reach the 95th and 99th percentiles ranged from 21 to 901 and 21 to 928 individuals, respectively (Fig. 2). Finally, species abundance distributions and corresponding colonization pressure saturation points of samples collected within 48–72 h were also variable (Fig. 3). Colonization pressures of those samples ranged from 9 to 19 species, with the number of organisms necessary to reach the 95th and 99th percentiles varying between 31 to 354 and 31 to 608 individuals, respectively (Fig. 3). Our bootstrap confidence intervals indicated significant variability among colonization pressures within samples of the same age for all three ballast water ages (Figs. 1–3).

Species assemblage variability within samples at similar time scales—Species assemblages of samples collected < 24 h after ballast entrainment exhibited the highest abundance among all time scales, averaging 85,185 individuals m^{-3} (Table 1). Minimum propagule pressure per species ranged from 19 to 582 individuals m^{-3} , while maximum values ranged from 2538 to 89,404 individuals m^{-3} . All four taxonomic groups were represented by species with very high numerical abundances, that is, propagule pressure higher than 10,000 individuals m^{-3} : Cladocera (*Bosmina longirostris* and *Eubosmina coregoni*), Copepoda (*Leptodiptomus sicilis*), Rotifera (*Brachionus calyciflorus*, *Polyarthra remata*, *Polyarthra vulgaris*, *Synchaeta kitina*, and *Synchaeta pectinata*), and Mollusca (*Dreissena polymorpha* and *Dreissena rostriformis bugenensis*; Web Appendix, Table A1, http://www.aslo.org/lo/toc/vol_59/issue_6/2068a.pdf). The average number of

organisms in samples collected within 24–48 h was 51,097 individuals m^{-3} , with minimum and maximum propagule pressure per species ranging from 2 to 225 and from 972 to 104,307 individuals m^{-3} , respectively (Table 1). However, few species had propagule pressure higher than 10,000 individuals m^{-3} when compared to samples collected from < 24-h-old ballast (10 vs. 5 species); those species also belonged to all four taxonomic groups observed in samples: Cladocera (*B. longirostris* and *Daphnia retrocurva*), Copepoda (*Leptodiptomus ashlandi*), Rotifera (*P. remata*), and Mollusca (*D. rostriformis bugenensis*; Web Appendix, Table A2). Finally, 48–72-h-old samples had lowest abundance of all three ballast water ages (Table 1). Average number of organisms in those samples was 37,373 individuals m^{-3} , while minimum and maximum propagule pressure per species ranged from 3 to 172 and 4251 to 20,401 individuals m^{-3} , respectively (Table 1). Only two taxonomic groups had species with propagule pressures higher than 10,000 individuals m^{-3} : Copepoda (*Skistodiptomus oregonensis*) and Rotifera (*Brachionus angularis*, *Keratella cochlearis tecta*, *P. remata*, and *S. kitina*); none of those species exceeded 50,000 individuals m^{-3} as was observed in samples collected from < 24 h or those from 24–48-h-old ballast (Web Appendix, Tables A1–A3).

Discussion

Species abundance distributions were highly variable within and across time scales. High variability within distributions of samples after entrainment may result from several factors, including temporal and spatial variability of source communities and consequent nonrandom uptake of taxa prior to transport (Briski et al. 2012a; Drake et al. 2014). Seasonal and temporal succession of zooplankton and spatial variability are frequently observed in nature (Hoffmeyer 2004; Zervoudaki et al. 2009; Hansen et al. 2013). However, most zooplankton communities consist of a mixture of common and rare species. We expected numerically dominant species to differ among ballast samples but to exhibit a fairly constant distribution shape after entrainment. The joint variability of zooplankton in nature and nonrandom uptake of taxa into dispersal vectors may lead to high variability in the composition of communities originally entrained. Stochasticity within each of these processes may further complicate between-sample variation. To resolve the roles of donor ecosystem variability vs. selection mechanisms during the uptake into transport vector, species composition and abundance distributions in port waters should be compared to those in the entrained assemblage immediately after ballast is loaded. Such a study would also identify taxonomic groups (if any) that consistently fail to be transported despite their occurrence in source localities.

Following Briski et al. (2014) and the results of this study, we hypothesize that shifting rank-abundance gradients during transport result from the combined effects of density dependence and fluctuating environmental conditions that favor certain zooplankton species. For example, Declerck et al. (2003) stated that strong intra- and interspecific chemical interference controls zooplankton population abundances. As many zooplankton populations decrease with an increase in abundance of con- or heterospecific zooplankton (Mateev

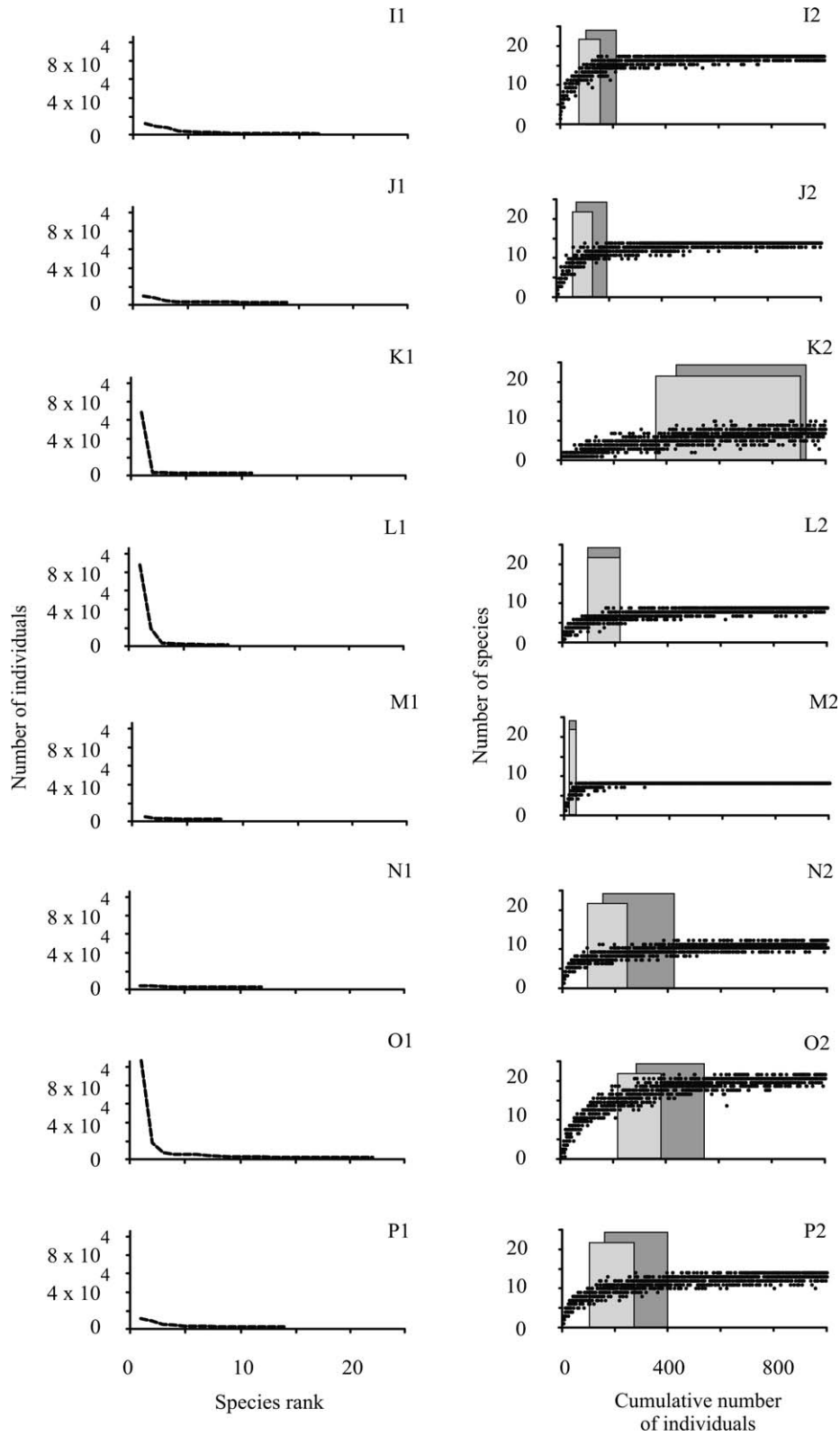


Fig. 2. Species rank-abundance plots (panels I1–P1) and their corresponding propagule pressure–colonization pressure relationships following random sampling of 1000 organisms (panels I2–P2) for samples from 24–48-h-old ballast water. Shown are the lower and upper confidence intervals (error rate = 0.05) for the 95th (light gray box) and 99th (dark gray box) percentiles of colonization pressure saturation.

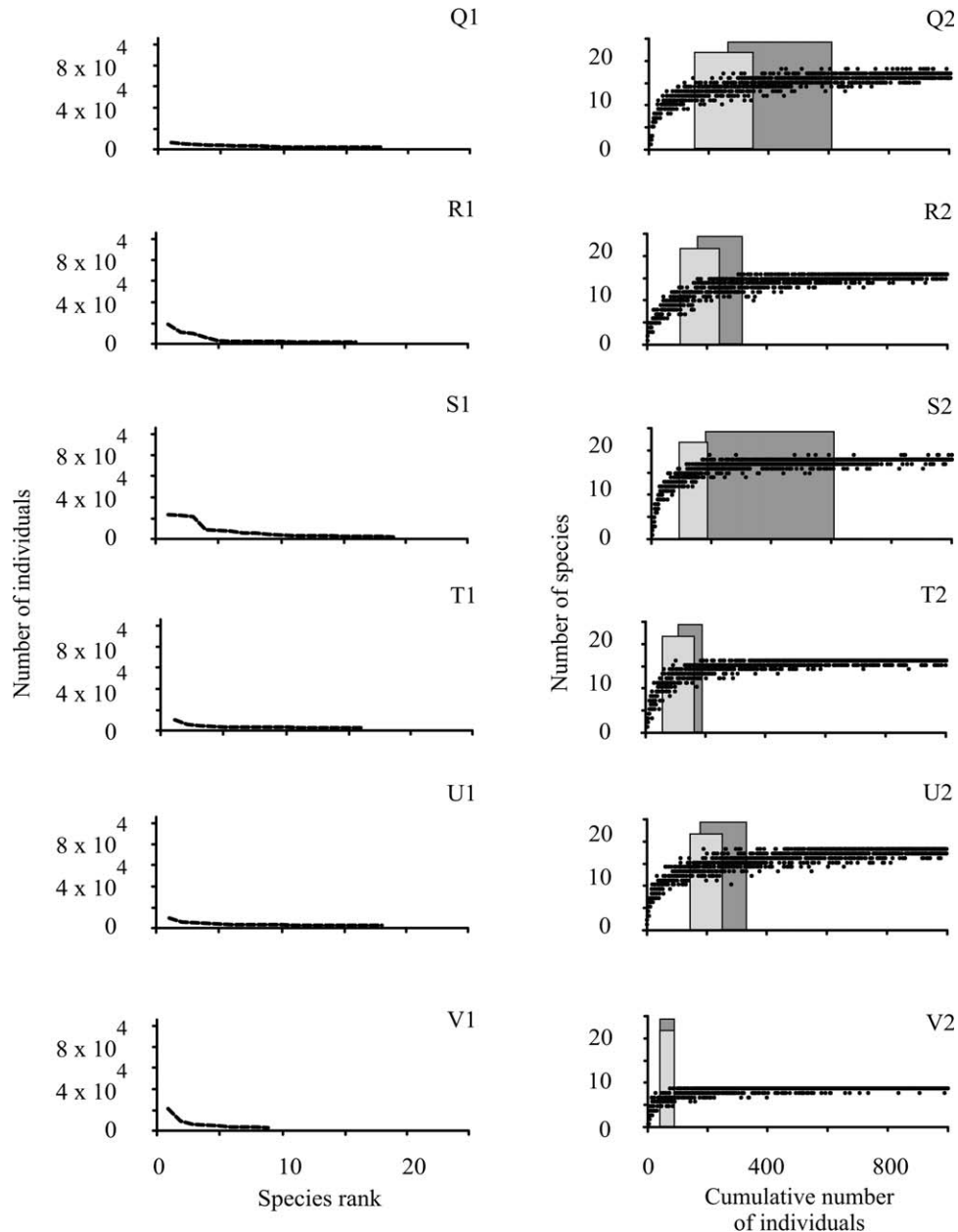


Fig. 3. Species rank-abundance plots (panels Q1–V1) and their corresponding propagule pressure–colonization pressure relationships following random sampling of 1000 organisms (panels Q2–V2) for samples from 48–72-h-old ballast water. Shown are the lower and upper confidence intervals (error rate = 0.05) for the 95th (light gray box) and 99th (dark gray box) percentiles of colonization pressure saturation.

1993), confined areas of ballast tanks may artificially increase predation intensity or interference chemical concentrations (First et al. 2013) that would drive population declines. Also, photoperiod is an important environmental variable affecting zooplankton dynamics, and many taxa suppress population growth under shorter photoperiods (Stenseth et al. 2006). The absence of photoperiods in ballast tanks, in combination with reduction in feeding rate due to increased predation risk (Mateev 1993; Declerck et al. 2003), could lead to increased mortality and population declines. These changes in numerically dominant populations would

cause the progression from uneven to even rank-abundance distributions as transport progresses (Briski et al. 2014).

Further implications of the introduction risk posed by zooplankton relate to the unpredictability of abundant species in uneven species distributions. As species-based propagule pressure is an important factor determining establishment success (Hayes and Barry 2008; Lockwood et al. 2009; Simberloff 2009), it would be beneficial to know which species are highly abundant. Our study demonstrates that those species may belong to any of the major taxonomic groups that are typically transported by ships. Also, the

International Ballast Water Management Convention, when ratified, will permit discharge of treated ballast water only if organisms larger than 50 μm (most zooplankton) are present with a collective abundance of < 10 viable individuals m^{-3} (IMO 2004). Extrapolating our results to the average ship ballast capacity ($\sim 20,000 \text{ m}^3$; Briski et al. 2011) indicates that the nature of the underlying species abundance distribution will strongly dictate the per-species propagule pressure discharged to recipient ecosystems. For example, ships with strongly uneven species abundance distributions (i.e., on short voyages) may have high abundances of the most dominant species. Dominant species from more evenly distributed communities should have lower volumetric abundances; however, even this can be offset somewhat if total ballast release volume is high.

Understanding the variation in propagule pressures among ships and species provides insight into the potential for NIS establishment. Assemblages with uneven rank-abundance distributions were characterized by species of varying propagule pressures. At the extreme, the highest-ranked species were > 820 times more abundant than the least abundant species, signifying a strong disparity in the corresponding probabilities of establishment for a given human-mediated movement. In contrast, even rank-abundance gradients existed with propagule pressures and potential for establishment, exhibiting greater consistency between common and rare species. When total propagule pressure of a transported community is high, both uneven and even rank-abundance distributions may pose a relatively high establishment risk. However, as total propagule pressure decreases, uneven distributions should pose higher risk, as they would still contain some species with relatively high propagule pressure. Given that rank-abundance gradients become more even as transport progresses due to a strong reduction in propagule pressure of dominant taxa (this study; Briski et al. 2014), the establishment risk posed by these communities also decreases through time. Even though most zooplankton species survive transport and surviving individuals likely have broad environmental tolerance (Briski et al. 2014), these small populations may suffer from reduced genetic diversity and low adaptability following introduction to new habitats (Kolbe et al. 2004, 2012; Roman and Darling 2007). On the other hand, uneven distributions, which are common during the first 2 days of transport, represent a higher establishment risk, as some species are abundant and less likely to suffer from Allee effects. Consequently, ships on short voyages pose a greater risk, as they release communities more likely to contain species not affected by Allee effects (Kolbe et al. 2004, 2012; Roman and Darling 2007). Ultimately, our results highlight strong disparity among ships, species, and time scales (Drake et al. 2014). While the exact implications of this disparity are difficult to ascertain without working knowledge of extinction risk of transported species, these results provide insight into the inconsistent predictive success of certain proxy variables that treat human-mediated movements equally (reviewed in Wonham et al. 2013).

Management efforts focused on preventing new introductions and early detection of introduced NIS are of great importance, as they are more effective and less costly than eradication or curtailment of the spread of established populations (Lodge et al. 2006; Lockwood et al. 2007; Hulme et al. 2008). Discharge performance standards imposed by

the International Ballast Water Management Convention represent a positive step toward risk reduction, as the policy implicitly recognizes the importance of propagule pressure to invasion success. However, the policy does not recognize inherent variation in plankton species abundance distributions. Each transported species effectively represents a probability trial for establishment in the new environment, and strong variability in species abundance distributions of transported assemblages dictates a range of propagule and colonization pressures for a given sample of n organisms. Therefore, for a given organism discharge standard, the number of species and propagules per species discharged to recipient ecosystems will vary; thus, invasion risk is not created equally for a given management model. Disentangling the relative influence of skewed vs. even assemblages and identifying those posing greatest establishment potential under a given discharge standard is difficult without a better understanding of species population viability estimated under a range of environmental conditions.

In summary, our study demonstrates that a universal species abundance distribution of transported assemblages does not exist. Therefore, any attempt to incorporate assemblage-based parameters when estimating risk or within a general management framework will induce substantial error or require large confidence limits. Both approaches will introduce substantial uncertainty, such as poor ability to discriminate, a priori, a given human-mediated movement as species rich or otherwise. Because these differences have potentially strong ecological consequences, comprehensive species-based sampling initiatives involving morphological or molecular species identification are still warranted to document the range and identity of transported assemblages. Species identification by next-generation sequencing or by automated counting systems (such as FlowCam) may enhance inspection quality. However, these methods are time consuming, costly, and not yet possible to conduct in real time. After ratification of the International Ballast Water Management Convention, ships will use commercial ballast water treatment systems to treat the ballast, which should be certified to reduce total propagule pressure to < 10 individuals m^{-3} . Nevertheless, ships on short voyages and those exempt from regulation may pose a greater risk and thus warrant increased attention.

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