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Per capita invasion probabilities: an empirical model to predict rates of invasion via ballast water

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Abstract. Ballast water discharges are a major source of species introductions into marine and estuarine ecosystems. To mitigate the introduction of new invaders into these ecosystems, many agencies are proposing standards that establish upper concentration limits for organisms in ballast discharge. Ideally, ballast discharge standards will be biologically defensible and adequately protective of the marine environment. We propose a new technique, the per capita invasion probability (PCIP), for managers to quantitatively evaluate the relative risk of different concentration-based ballast water discharge standards. PCIP represents the likelihood that a single discharged organism will become established as a new nonindigenous species. This value is calculated by dividing the total number of ballast water invaders per year by the total number of organisms discharged from ballast. Analysis was done at the coast-wide scale for the Atlantic, Gulf, and Pacific coasts, as well as the Great Lakes, to reduce uncertainty due to secondary invasions between estuaries on a single coast. The PCIP metric is then used to predict the rate of new ballast-associated invasions given various regulatory scenarios. Depending upon the assumptions used in the risk analysis, this approach predicts that approximately one new species will invade every 10–100 years with the International Maritime Organization (IMO) discharge standard of <10 organisms with body size >50 μm per m^3 of ballast. This approach resolves many of the limitations associated with other methods of establishing ecologically sound discharge standards, and it allows policy makers to use risk-based methodologies to establish biologically defensible discharge standards.

Key words: aquatic invaders; ballast water discharge; IMO standards; invasion probabilities; propagule pressure.

Introduction

Aquatic invasions are a key factor causing environmental stress on estuarine and marine ecosystems (Ruiz et al. 1999, Occhipinti-Ambrogi and Savini 2003). The primary source for these biological invasions is shipping (Ruiz and Carlton 2003, Molnar et al. 2008). Of the potential shipping vectors, ballast water is one of, if not the, most important (Carlton 1996, Fofonoff et al. 2003). For example, since the opening of the St. Lawrence Seaway in 1959, ballast water is the suspected source for over 70% of the nonindigenous species found in the Great Lakes (Holeck et al. 2004).

In response, agencies at the international, national, and U.S. state level have sought to establish regulations that limit the concentration of organisms in discharged ballast water (Albert et al. 2013). The fundamental assumption behind establishing organism-based ballast water standards is that, all else being equal, invasion risk decreases with decreasing propagule pressure (Lockwood et al. 2009, National Research Council 2011). This assumption is supported by a wide body of evidence showing that the establishment probability for nonindigenous species (NIS) increases with propagule pressure due to either a higher concentration of organisms in an inoculation, and/or an increase in the frequency of inoculations (Kolar and Lodge 2001, Colautti et al. 2006, Simberloff 2009). However, deriving discharge standards that are protective of the environment has been challenging (Lee et al. 2011, National Research Council 2011), and the broad range in proposed discharge standards (Albert et al. 2013) reflects the complexity of this issue.

To address the need for practical approaches of deriving discharge standards, we developed an empiri-

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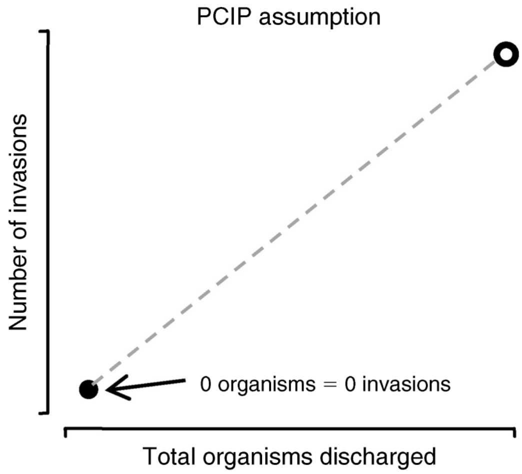

FIG. 1. The per capita invasion probability (PCIP) empirical model assumes a linear relationship between the number of invasions and the total number of organisms discharged into a geographic region. Zero organisms discharged results in zero invasions (solid circle), and the open circle is calculated from historical invasion rates and the total organisms discharged into all ports on a coast annually.

cally based "per capita invasion probability" (PCIP) metric that managers can use to derive environmental-based standards. The PCIP is the likelihood that a unique, nonindigenous organism discharged from ballast water will become established on a coast in a year. Using a linear dose–response model, the PCIP is calculated from the historical number of ballast-mediated invasions on a coast per year, and the approximate total number of organisms discharged annually on that coast. We calculate historical PCIP values for the Atlantic, Gulf, and Pacific Coasts, as well as the Great Lakes. We then demonstrate how PCIP values can estimate future invasion probabilities based on various regulatory scenarios. In theory, this approach could be used for any size class of organisms, however, analyses for smaller size classes are currently limited by data availability. For that reason, we focus on the >50-μm size class of organisms.

Our primary objective was to "cut through" the complexities of invasion biology to develop a method of generating discharge standards that are protective of the environment. The PCIP model is well suited for generating concentration-based discharge standards because it directly relates the risk of invasion to ballast water organism concentrations. Furthermore, the data inputs and assumptions are transparent and the data is relatively easy to obtain. The PCIP model does make several simplifying assumptions, and as with any model, there is some uncertainty in regard to the input parameters. To help ensure that the discharge standards generated by the PCIP approach are adequately protective, despite inherent uncertainty, safety factors can be incorporated in the model. Furthermore, as we gain a better understanding of invasion biology, the PCIP model is flexible enough to accommodate improved data and invasion models.

METHODS

Empirical PCIP invasion model

To predict the potential rate of invasion from ballast water, it is necessary to first estimate the per capita invasion probability (PCIP). The PCIP is the probability that an individual organism in ballast discharge will become established as a new nonindigenous species on a coast (new invading species/organisms discharged). As a starting point, we calculate PCIP using a linear dose–response relationship (Fig. 1) in which the number of invaders is predicted to increase proportionally with the number of organisms discharged in ballast water:

$$\mathrm{PCIP} = \frac{N_\mathrm{h}}{O_\mathrm{h}} \quad (1)$$

where N_h is the historical annual invasion rate of ballast-associated invaders for a coast (new invading species per year), and O_h is the total number of historic organisms discharged into all ports on a coast annually (organisms per year). For example, if one new nonindigenous species became established on a coast in which a total of a million individual organisms were discharged in a year, the per capita invasion probability would equal 10^{-6}.

The historical number of organisms discharged (O_h) is defined as

$$O_\mathrm{h} = \sum_{1}^{n} D_i \times C_i \quad (2)$$

where n is the total number of ships discharging foreign ballast water into ports on a coast annually, D_i is the volume in cubic meters being discharged by ship i, and C_i is the concentration of organisms in the ballast water being discharged (organisms/m^3) by ship i.

The PCIP metric can be used to predict the annual invasion rate of ballast-associated invaders for a coast (where N_p is defined as the number of new invading species/year):

$$N_\mathrm{p} = \mathrm{PCIP} \times O_\mathrm{p} \quad (3)$$

given the predicted total number of organisms in ballast water discharged into ports on a coast (O_p, organisms/year) under different regulatory scenarios.

Estimates of historical invasion rates (N_h)

The total numbers of invaders (N_h) were obtained from the Smithsonian Institution invasive species database (database *available online*).[5] To be included in the analyses, each species had to be considered established and potentially introduced via ballast water. The number of invaders is based on nonindigenous inverte-

[5] invasions.si.edu/nemesis/

TABLE 1. Average annual historical number of invaders (N_h), average annual foreign ballast discharge volumes (D_h), total number of organisms discharged annually (O_h), and per capita invasion probabilities (PCIP) for the Atlantic, Gulf, and Pacific Coasts and the Great Lakes of the United States.

	Mean per year			No. organisms discharged per year		PCIP	
Coast	No invaders	Foreign BW (m^3)	No. ships discharging foreign BW	Estimates using lower 0.025 quantile	Estimates using median	From lower 0.025 quantile estimates	From median estimates
Atlantic Coast	1.6	7 407 832	4287	3.2×10^{10}	3.5×10^{10}	5.0×10^{-11}	4.5×10^{-11}
Gulf Coast	0.72	19 605 340	3940	8.8×10^{10}	9.3×10^{10}	8.2×10^{-12}	7.7×10^{-12}
Pacific Coast	2.68	14 788 369	1999	6.6×10^{10}	7.0×10^{10}	4.1×10^{-11}	3.8×10^{-11}
Great Lakes, macrofauna	0.44	1 395 461	unknown	NA	6.5×10^{9}†	NA	6.8×10^{-11}‡

Notes: The number of coastal invasions is the average annual number of nonindigenous invertebrates and macroalgae >50 μm first reported from 1982 to 2007 that were possibly introduced via ballast water (BW) and are considered established. The total number of invaders includes marine, brackish, and freshwater species. The average annual foreign ballast discharges for a coast and average number of ships discharging annually from 2005 to 2007 and include marine, brackish, and freshwater ports on a coast. Per capita invasion probabilities for each coast are calculated using the lower quantile (0.025) and median (0.5) of probable organisms discharged into the coast. The number of invaders for the Great Lakes is given for macrofauna for the period 1965 to 1990, while the ballast water discharge volume is for 1991. NA stands for not applicable.

† Based on mean IMO organism concentration.

‡ PCIP metric calculated using mean IMO organism concentration.

brates and macroalgae >50 μm; fishes and vascular plants were not included. Because of the poor resolution between native vs. nonindigenous phytoplankton species in coastal waters (Carlton 2009), no attempt was made to estimate the number of invaders in the 10–50 μm size class.

We focus on invasions that occurred prior to the enactment of ballast water exchange (BWE). For the contiguous United States Pacific, Atlantic, and Gulf Coasts, we used the total number of invaders reported from 1982 to 2007 (Table 1). Even though mandatory BWE for United States coasts was enacted in 2004 (Albert et al. 2013), we believe the 25-year span through 2007 helps mitigate effects of the lag between an actual invasion event and when a species is first discovered (e.g., Costello and Solow 2003). A longer time period also helps smooth short term variation in invasion rates as well as variation in monitoring efforts. The majority of the Atlantic, Gulf, and Pacific invaders and their vectors are listed in Appendix A of Ruiz et al. (2000). For the Great Lakes, we used the 1965 to 1990 time period to maintain a consistent 25-year time span prior to the implementation of mandatory ballast water exchange in 1993.

Estimates of foreign ballast water discharge rates (D_i)

Historic foreign ballast discharge volumes (coastal water that was carried through waters outside the U.S. and Canadian exclusive economic zones, D_i) were used to calculate the approximate total number of organisms (O_h) discharged on a coast annually. All reported foreign ballast discharge events for a coast were obtained from the Smithsonian Institution ballast water database (National Ballast Information Clearinghouse; data *available online*).[6] Average yearly foreign discharge volumes (D_i) were calculated for the contiguous Atlantic, Gulf, and Pacific coasts (Table 1) from discharge records for all ships discharging foreign ballast in ports on the respective coasts from 2005 to 2007. These dates were chosen because they occur after the implementation of mandatory ballast water reporting (Albert et al. 2013) and represent the most complete discharge records available. Prior to 2005, ballast water discharge records were voluntary and incomplete. For each discharge event, the data included the type of vessel, whether the last port of call (LPOC) was foreign or domestic, the volume of water discharged and whether the water in the tank being discharged was foreign or domestic. Because foreign ballast was recorded on a per tank basis it was possible to account for foreign ships that initially entered one port but did not discharge their ballast until they visited another port. This allowed us to identify ballast as foreign even if the LPOC was domestic. For the Great Lakes, the National Biological Invasion Shipping Study (Reid and Carlton 1997) reported a total annual foreign ballast water discharge of 1 395 461 metric tons (Mg) in 1991.

Estimates of organism concentrations in ballast discharge (C_i)

Based on four independent studies in which ballast water was sampled using net sizes from 50 μm to 80 μm, average organism concentrations in untreated ballast water ranged from 1004 to 6020 organisms per cubic meter (Table 2). To estimate the total number of organisms discharged on each coast, we used the distribution of organism concentrations (C_i) reported by Minton et al. (2005). Of the studies, these data were the most extensive ($N = 354$ ships) and were collected from international ships docking at U.S. ports, which is regionally consistent with the data in our analyses. Although the Minton data were collected with an 80-μm net, net size does not appear to be the primary source of variation in organism concentration among studies

[6] http://invasions.si.edu/nbic/search.html

TABLE 2. Summary of published ballast water sampling data and organism concentrations in untreated and not-exchanged ballast water.

Source	No. ships sampled	Concentration (no. organisms/m^3)	Net size (μm)	Details
S. Gollasch, *personal communication*	101	1004	55	mostly container ships; long voyages; minimal discharge; European destinations
Gollasch and David (2010)	1†	1718	50	NA
MEPC (2003)‡	429	4640	55–80	all types of ships; global destinations; variable voyage durations
Minton et al. (2005)	354	4768	80	bulkers and tankers; large discharges; U.S. destinations; long voyages
David et al. (2007)	15	6020	50	bulkers, containers, and tankers; short voyages; Mediterranean source and destination

Note: All samples were taken at discharge.
† One ship, 2 test runs × 3 discrete samples = 6 sample average.
‡ Data are not independent of other studies listed.

(Table 2). Thus these data appear to provide a reasonable estimate of the range of organism concentrations discharged by international ships docking at United States ports.

Estimates of total number of organisms discharged on a coast annually (O_h)

The distribution of organism concentrations (Minton et al. 2005) was highly skewed, with a large proportion of ships having relatively low organism concentrations and a long tail of ships with very high organism concentrations. To quantify the probable range in the total number of organisms discharged (O_h) we developed a randomization algorithm using the R statistical package (R Development Core Team 2008). The algorithm randomly assigned each ship discharging foreign ballast on a coast between January 2005 and December 2007 a concentration of organisms, selected from the distribution of values reported by Minton et al. (2005: Fig. 2a). The randomly selected concentration (C_i) was then multiplied by the volume of foreign ballast discharged by that particular ship (D_i). The total organisms discharged ($C_i \times D_i$) from all the ships for a coast were then summed and divided by three (to account for the three years of discharge data) to find the average number of organisms that were discharged on a coast annually (O_h). This procedure was repeated 10 000 times to estimate the range of the total number of organisms discharged on a coast annually from which the lower (0.025) and median quantile values were determined (Table 1, Fig. 2).

The PCIP metric can be derived from different quantiles of estimated total organisms discharged in ballast water (Fig. 2). Although the median value is the most intuitive, it may underestimate the invasibility of species (i.e., a lower PCIP metric), resulting in less protective standards. When possible, we recommend using the lower (0.025) quantile, which is an estimate of the lowest likely number of total organisms discharged into a system, and will result in a higher, but still realistic, estimate of the PCIP. Ultimately this will generate more stringent standards and reduce the possibility of underestimating the risk of invasion. Because we did not have individual ship records for the Great Lakes during 1991, the mean ballast water organism concentration from the IMO baseline study (4640 organisms/m^3; MEPC 2003) was used to calculate the PCIP metric for the Great Lakes.

Spatial scale of analyses

Our original approach was to calculate the PCIP metric for 17 individual ports (Reusser et al. 2011). However, there was considerable range in PCIP metrics across ports that we suspect was due to a suite of nonexclusive factors (Reusser et al. 2011; also see National Research Council 2011). For example, smaller ports tended to have more invaders than expected given the amount of foreign ballast discharged, possibly due to secondary invasions (Simkanin et al. 2009) from larger

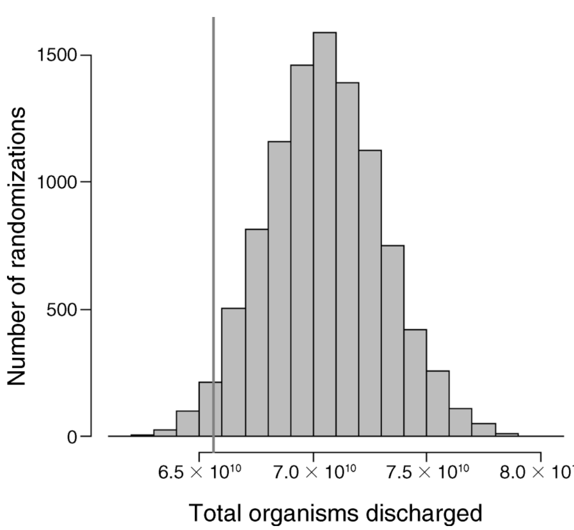

FIG. 2. Histogram of total organisms discharged annually on the Pacific Coast based on 10 000 iterations of the randomization algorithm for organism concentrations among the 5998 ships discharging foreign ballast over three years from 2005–2007. The vertical line indicates the lower 0.025 quantile that was used to estimate the number of organisms discharged into all ports on a coast annually.

TABLE 3. Assumptions and potential sources of error for the per capita invasion probability approach to setting ballast water discharge standards.

Assumption	Effect on estimate of per capita invasion probability	Effect on discharge standard	Mitigation approaches
Linear dose–response between number of invaders and total number of organisms discharged in ballast water	May overestimate invasion probability for many sexual species due to rarefaction and Allee effects at reduced concentrations; potentially under estimates for asexual and parthenogenic species.	Protective against most sexual invaders; possibly under-protective for asexual and parthenogenic species.	Use safety factor >1.
Samples using 80-μm net size provide reasonable estimation of organism concentrations found in ballast water	Underestimates the number of organisms greater than 50 μm in the minimum dimension and will overestimate PCIP.	More protective against invaders.	Use median or upper quantile to estimate total number of introduced organisms when calculating PCIP.
All invaders introduced via foreign ballast water	Overestimates PCIP.	Erroneously makes discharge standard less stringent.	Coastal-scale analysis reduces probable effect of polyvectic invaders.
The number of invaders is accurate	Likely underestimates PCIP given probability that many invaders have not been identified.	Erroneously makes discharge standard less stringent.	Use safety factor >1. Safety factor of 2 would correct for a 50% underestimate of invaders.
Annual volume of discharge between 2005–2007 is comparable to annual discharge between 1982–2004, (i.e. years of invasion data)	Underestimates PCIP if annual discharge volume was less between 1982–2004.	Erroneously makes discharge standard less stringent.	Use safety factor >1. Safety factor of 2 would imply that half as much ballast water was discharged on average in earlier years.
Voyages between 1982–2004 took the same amount of time as between 2005–2007	Overestimates the number of organisms that could have survived in ballast water in vessels between 1982–2004; underestimates PCIP.	Erroneously makes discharge standard less stringent.	Use safety factor >1. Safety factor of 2 would imply that half as many organisms survived earlier voyages.
No change in invasibility of waterbodies on a coast over time or change in the invasion potential of new invaders	Either increases or decreases PCIP depending upon type and magnitude of environmental changes.	Protective or under protective depending upon the type and magnitude of changes.	Use lower bound estimates for input values and/or safety factor to account for changes in environment.

ports such as the San Francisco Estuary, or introductions through vectors other than ballast discharge. Due to the potential for secondary invasions and the uncertainty in estimates derived from any single port, we believe the best strategy for developing discharge standards is to use PCIP metrics derived from the aggregated data for a particular coast. The aggregated data also appears to reduce other sources of variation given the reasonably small range in PCIP values among coastal regions and the Great Lakes (Table 1).

Generating organism-based discharge standards (C_s)

Ballast discharge standards can be generated for a coast by calculating an organism concentration in ballast water (C_s) that would result in a managerially defined acceptable invasion risk, presented as the predicted number of new invaders per year (N_p). The calculation is based on the projected annual total ballast water discharge volume (D), the PCIP values estimated using historical data (Table 1), and a safety factor:

$$C_s = \frac{N_p}{D \times \text{PCIP} \times \text{safety factor}}. \quad (4)$$

There are several sources of uncertainty that could result in underestimating the risk of introducing new invaders through ballast discharges (Table 3). When establishing discharge standards, regulatory agencies might consider applying a safety factor to account for these uncertainties. When a safety factor of 1 is used in Eq. 4, no additional margin of safety is incorporated into the standard. Safety factors >1 will result in more stringent discharge standards. Table 3 and the discussion contain more information on utilizing safety factors to mitigate some of the uncertainties associated with the PCIP metric.

RESULTS

Coastal patterns of invasion risk

The PCIP metrics are based on the aggregation of data for all ports along contiguous coasts. The PCIP values among the four coastal regions ranged from 7.7×10^{-12} to 6.8×10^{-11} (based on a comparison of median values). The differences among the Pacific, Atlantic, and Great Lakes ranged from <20% to about 80% (Table 1). The Gulf Coast is somewhat distinct with a PCIP value about an order of magnitude smaller than the other areas.

Example: Generating organism based discharge standards

To demonstrate the use of Eq. 4, we calculate a discharge standard predicted to reduce ballast mediated invasion rates on the U.S. Pacific Coast to an arbitrarily selected 1 new invader every 1000 years. To achieve this goal, Pacific Coast managers could choose between the more protective PCIP value of 4.1×10^{-11} and the less protective PCIP value of 3.8×10^{-11}. In addition, managers can input an expected discharge volume for a year, depending on general trends in shipping traffic. For a more conservative standard, a safety factor can also be included. For our example, we opted to use the more protective PCIP value of 4.1×10^{-11}, the current average annual ballast water discharged on the Pacific Coast of 15 million cubic meters, and no safety factor. These choices result in a discharge standard of 1.63 organisms/m^3 ballast discharge:

$$C_s = (1 \times 10^{-3} \text{ invaders/yr})/ ([15 \times 10^6 \text{ m}^3 \text{ ballast water/yr}] \times [4.1 \times 10^{-11} \text{ invaders/organism}] \times 1) = 1.63 \text{ organisms/m}^3.$$

To demonstrate how this metric can be used to explore different management options, we generated a "risk diagram" based on ballast water discharge volumes between 0 and 30 million cubic meters and organism concentrations between 0.0001 and 1000 using the conservative PCIP value of 4.1×10^{-11} and no safety factor (Fig. 3). Using these values, the predicted invasion rate for the proposed IMO standard of <10 organisms $>$than 50 μm/m^3 of ballast will be approximately one new species invasion every 10 to 100 years (Fig. 3) depending on the total amount of ballast water discharged per year. The risk diagram also indicates that an increase in the amount of ballast water discharged will require a reduction in the organism concentration standard to avoid an increase in the invasion rate over time. Similar risk diagrams can be generated for less conservative PCIP values with and without safety factors using Eq. 4.

Discussion

In order to estimate invasion probabilities for various regulatory scenarios, we first generated per capita invasion probabilities (PCIP) for the Pacific, Atlantic, and Gulf Coasts, as well as the Great Lakes based on historical invasion rates and estimates of the total number of organisms discharged in ballast. Overall, the variance in PCIP values among the regions was small. Thus, even when comparing across four different regions with different ballast discharge volumes and donor regions, the calculation of the PCIP parameter was fairly robust and the potential uncertainty in this input variable appears relatively small. The largest outlier was the Gulf Coast with a PCIP value approximately one order of magnitude smaller than the other regions, suggesting the Gulf had fewer invaders than predicted given the volume of ballast discharge. The variance in PCIP among the regions indicates either regional differences in invasion probability or uncertainty in the input parameters among the regions. We believe the PCIP metric for the Pacific Coast is the most reliable because of the extensive effort in documenting invaders on the Pacific Coast and the less complicated invasion history compared to the North Atlantic (See Chapman et al. [2008] for example with *Littorina littorea*). However, the variance in PCIP values among the regions is one factor that could be considered when developing a biologically meaningful safety factor (Table 3).

The PCIP metric calculated for the U.S. Pacific coast was used to predict the number of invasions of organisms larger than 50 μm given various ballast discharge standards. Given a discharge standard of 1 organism/m^3 of ballast discharge, a PCIP value of 4.1×10^{-11}, an estimated annual discharge volume of 15 million cubic meters, and no safety factor (Fig. 3), the predicted invasion rate is 1 organism every 1000 years. This is approximately 10-fold lower than the proposed IMO standard. This value does not incorporate a safety factor, but it is calculated using the more conservative PCIP value based on the lower 0.025 quantile to estimate the total organisms discharged historically.

Uncertainty and assumptions

There are two sources of error associated with the PCIP metric: (1) the uncertainty generated from the model assumptions and (2) the uncertainty associated with the specific input values. Of these, the greatest source of uncertainty is the assumption of a linear dose–response between the number of organisms discharged and the number of successful invasions. Although we assume a linear relationship, when the PCIP metric was analyzed at the individual port scale, the data did not suggest a linear dose–response relationship (National Research Council 2011, Reusser et al. 2011). Even at the coastal scale, the data does not reflect a linear relationship between organisms discharged and invasion rates. So, while a linear dose–response model is unlikely to capture the full biological complexities associated with invasions, we contend that the more important question in terms of generating standards is whether it is protective. Given the low organism concentrations associated with the proposed standards, a linear model is likely to be protective regarding the establishment of sexual species due to Allee effects (Fig. 4). Allee effects occur in rarefied populations because population growth rates may be depressed by several, potentially interacting, mechanisms (i.e., mate limitation, increased predation, genetic inbreeding, and/or increased dispersal) (Drake 2004, Gascoigne and Lipcius 2004, Leung et al. 2004, Choi and Kimmerer 2008, Kramer et al. 2009). Allee effects have also been observed in parthenogenic species (e.g., Gertzen et al. 2011). However, because a single parthenogenic organism can become established (e.g., Gertzen et al. 2011), the linear dose–response may not be protective and standards derived from the PCIP model may underestimate the risk associated with parthenogenic and asexual species. The linear dose–response model may also be protective

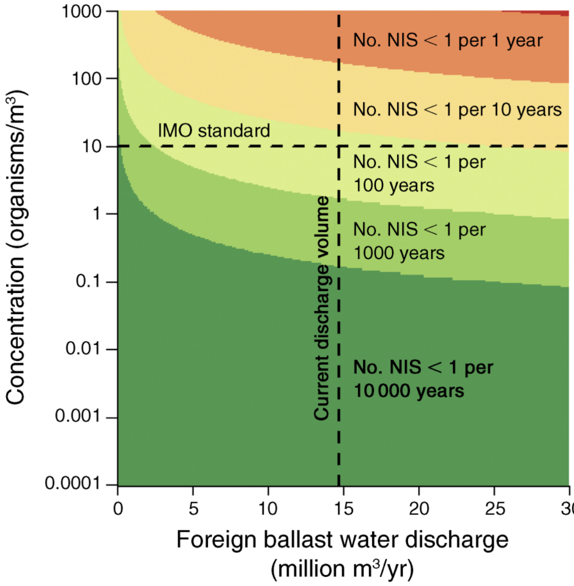

FIG. 3. Risk diagram for the predicted number of invaders per year for the U.S. Pacific Coast. Calculations are based on a PCIP of 4.08×10^{-11} and no safety factor. The current annual ballast water discharge volume for the Pacific Coast is approximately 15×10^6 m^3. Abbreviations are: IMO, International Maritime Organization; NIS, nonindigineous species.

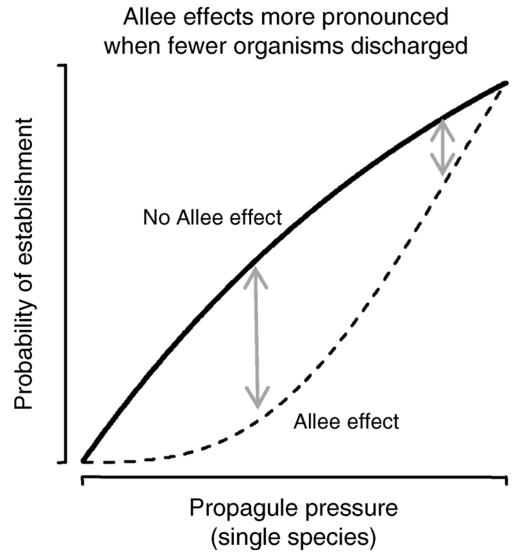

FIG. 4. For a single species, a reduction in the total number of organisms discharged in ballast water will result in a lower probability of establishment due to more pronounced Allee effects (based on equations from Leung et al. [2004]).

because rarefaction will reduce the number of nonindigenous species being discharged as the total number of organisms in the ballast water declines (Fig. 5), resulting in a reduction in colonization pressure (Lockwood et al. 2009). Such reductions in the total number of potential invaders reduce the risk of invasion by both sexual and asexual/parthenogenic species.

By using past invasion rates to predict future rates, fundamental assumptions of this approach are that neither the invasion potential of new invaders nor the invasibility of the environments on a given coast will change in the future. If the best colonizers tend to invade first, then the PCIPs derived from historical data would over predict the number of new invaders for a given number of total organisms discharged. However, the apparent increase in the rate of invasions in a number of aquatic ecosystems (e.g., Cohen and Carlton 1998, Holeck et al. 2004) contradicts the theory that new invaders are less virile. The exact cause of the increase in invasion rates is not known; however, the increasing volume of annual foreign ballast water discharge coupled with faster ships has been shown to be a factor (Carlton and Geller 1993, Ruiz et al. 1997). Changes in the invasibility of aquatic ecosystems are difficult to predict. In particular, the consequence of climate change on invasion is a "wild card" for any approach to setting discharge standards. Shifts in temperature can have a direct effect on reproduction and development as well as cascading indirect effects, including shifts in food quality and/or availability, increase/decrease in predator populations, and/or shifts in habitat suitability that could increase or decrease the probability of successful invasions. In addition, human activities such as land use changes in a watershed and/or port expansion could also change the invasibility of a particular system, but

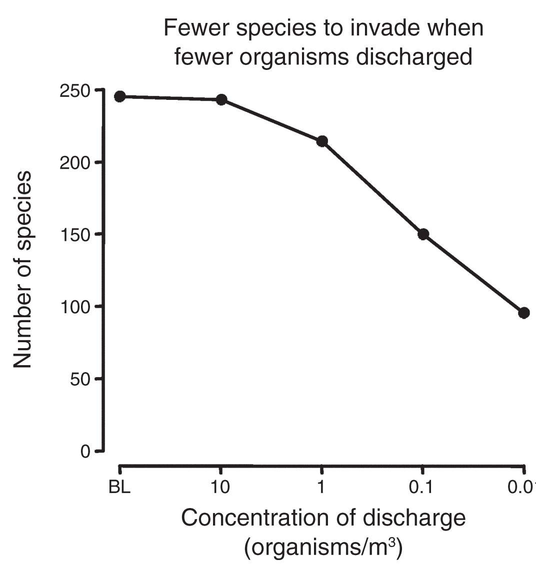

FIG. 5. This figure shows how the number of species in ballast discharge may decline from an observed baseline (BL) as the concentration of organisms is reduced by increasingly stringent ballast water management programs. These values are calculated by applying rarefaction methods (see Appendix) to data from Cordell et al. (2009), which describe the density of zooplankton taxa in the ballast tanks of 141 domestic ships arriving at ports in Puget Sound, Washington, USA. The BL is the actual number of taxa observed in the 141 tanks.

would have much less impact on invasion across an entire coast.

There is also some uncertainty in each of the three parameters used to calculate the PCIP metric. In terms of the historic number of invaders, Carlton (2009) identified 12 sources of error leading to invader underestimation including unknown, unreported, misclassified, and rare invaders. In some parts of the world, such as Denmark, South Africa, and Chile where no invasions prior to mid-19th century are recognized, the number of known invaders could be underestimated by as much as 5 to 10 times (Carlton 2009). For California, Cohen (in Falkner et al. 2006) suggested that unrecognized invaders could increase estimates of the invasion rate by 50–100%. A recent analysis of California invaders lists 457 cryptogenic species vs. 358 nonindigenous species (California Department of Fish and Game 2009); the California invasion rate would more than double if all these cryptogenic species were actually nonindigenous (data *available online*).[7] While some of these cryptogenic species are likely unrecognized native sibling species (e.g., Knowlton 1993), the high number of cryptogenic species suggests that the reported number of invaders may underestimate actual numbers by 50–100% within the United States.

Another source of uncertainty in the number of historic invaders is that many coastal nonindigenous species can potentially invade through multiple vectors, such as both ballast water and hull fouling (e.g., Fofonoff et al. 2003). Inclusion of these "polyvectic" invaders (Ruiz and Carlton 2003) potentially inflates the ballast-associated invasion rate, resulting in an artificially high PCIP metric. Thus, our inclusion of all potential ballast water invaders is a protective assumption.

Organism concentrations in untreated ballast water appear to vary about sixfold based on the available studies (Table 2). Several phenomena could be driving this broad range, including the source of the ballast water, type of vessel, and length of voyage (age of water; S. Gollasch, *personal communication*; G. M. Ruiz, *unpublished data*). Presumably this range would increase with additional studies, however by aggregating the data over all the ships discharging on a coast, the actual value should approach the Minton and MEPC values, which are based on the greatest total number of ships sampled. The final input parameter, the volume of foreign ballast water discharged, is well documented in the United States by the National Ballast Information Clearinghouse, and errors are likely to be minimal (see footnote 6).

Model limitations

One limitation of the current model is that while aggregating the data by regions allows the generation of national, or coastal, standards, it does not resolve the problem of ballast discharge standards for intracoastal shipping where secondary invasions have the potential to be a significant factor (Cordell et al. 2009, Lawrence and Cordell 2010). To understand the role of secondary invasions better, studies of individual invasion patterns along the coast among estuaries are needed as well as regular surveys for nonindigenous species in smaller ports and estuaries with no foreign ballast input. Additionally, further studies of the role of intracoastal shipping and ballast discharges are needed to help elucidate their role in spreading invaders into ports with and without minimal foreign ballast water discharges. Another limitation is that, while the approach can be applied to organisms smaller than 50 μm, there is more uncertainty about the historical invasion rates for smaller organisms and the total number of those organisms being discharged.

The PCIP value for macrofauna for the Great Lakes fell into the range observed for the three coastal regions (Table 1). However, less complete data were available for ballast discharge volumes and organism concentrations in the Great Lakes, and we consider these calculations a preliminary analysis.

The use of safety factors

Given the complexities and uncertainties plaguing all approaches to generating ballast water standards (National Research Council 2011, Lee et al. 2013), we encourage the incorporation of a safety factor in calculations of ballast discharge standards (Table 3). Safety factors have been utilized in other fields such as engineering to calculate the structural capacity of bridges beyond the expected load to compensate for uncertainties. Likewise, a safety factor used in calculating a ballast water discharge standard would help compensate for uncertainties in estimates of invasion probabilities. And, if we accept the premise of Ricciardi et al. 2011, that invasions are natural disasters to be avoided, the inclusion of a safety factor makes logical sense. Higher safety factors provide a greater margin of safety and will result in more stringent discharge standards. For example, using the same assumptions as above, a safety factor of 10 would result in a discharge standard of 0.016 organisms/m^3 and a safety factor of 20 would result in a discharge standard of 0.008 organisms/m^3.

We describe several issues to consider when deriving a safety factor (Table 3); however, we suggest using a single safety factor rather than multiplying a string of individual safety factors for each potential source of uncertainty, which quickly results in unrealistic values (see Chapman et al. 1998). Safety factors on the order of 5- to 20-fold have been proposed when calculating the potential risk to endangered and threatened species from exposure to pesticides (U.S. EPA 2004). A similar range appears appropriate for PCIP models based on the potential for underestimating the historical number of

[7] http://ceic.resources.ca.gov/catalog/FishAndGameBIOS/AquaticNonnativeOrganismDatabaseCANODds503.html

invaders by about 2- (U.S. Pacific Coast) to 10- (poorly studied areas) fold as well as the 6–10-fold range in PCIP values among regions. For cases where there is an environmental mismatch indicating the risk of invasion is lower (i.e., water from the South Pacific being discharged into the Arctic) a lower safety factor could be utilized.

Conclusions

The per capita invasion probability approach cuts through the "Gordian Knot" of uncertainties associated with predicting ballast water invasions (see National Research Council 2011, Lee et al. 2013) in order to arrive at environmentally based ballast discharge standards. Risk diagrams (Fig. 3) can be generated from this approach to illustrate how the likelihood of invasion relates to organism concentrations and ballast water discharge volumes, which allow risk managers to assess the risk with different discharge standards and safety factors. As with all approaches, a number of assumptions are made (Table 3). It was not our goal to develop or suggest specific discharge standards. Our strategy was to develop an approach that allows risk managers to develop discharge standards with different risk levels based on different sets of assumptions. Specifically, the following inputs can be set: (1) acceptable invasion risk as measured by an invasion rate; (2) ballast water discharge volume; (3) use of PCIPs based on median ballast water organism concentration or lower quantile values; and (4) magnitude of the safety factor. Fig. 3 shows how the predicted invasion rate changes with a broad spectrum of organism concentrations and ballast water discharge volumes based on the lower PCIP value for the Pacific coast. Risk managers can generate similar diagrams for the median PCIP value and/or different coasts to evaluate the differences in predicted invasion rates based on different PCIP values.

Overall, this method of generating ballast water discharge standards appears to resolve many of the limitations associated with other approaches. The uncertainty around the parameters going into the per capita invasion probability model is relatively small. Additionally, the PCIP model does not have to be parameterized for each species or type of species as with population modeling approaches. Finally, the data going into the per capita probability approach are readily understandable by managers and the public, which is beneficial in gaining acceptance for any ballast water discharge standard.

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Supplemental Material

Appendix

Detailed description of the method used to estimate species rarefaction in ballast water (*Ecological Archives* A023-016-A1).