

Article

Assessing ballast treatment standards for effect on rate of establishment using a stochastic model of the green crab

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Abstract

This paper describes a stochastic model used to characterize the probability/risk of NIS establishment from ships' ballast water discharges. Establishment is defined as the existence of a sufficient number of individuals of a species to provide for a sustained population of the organism. The inherent variability in population dynamics of organisms in their native or established environments is generally difficult to quantify. Much qualitative information is known about organism life cycles and biotic and abiotic environmental pressures on the population, but generally little quantitative data exist to develop a mechanistic model of populations in such complex environments. Moreover, there is little quantitative data to characterize the stochastic fluctuations of population size over time even without accounting for systematic responses to biotic and abiotic pressures. This research applies an approach using life-stage density and fecundity measures reported in research to determine a stochastic model of an organism's population dynamics. The model is illustrated with data from research studies on the green crab that span a range of habitats of the established organism and were collected over some years to represent a range of time-varying biotic and abiotic conditions that are expected to exist in many receiving environments. This model is applied to introductions of NIS at the IMO D-2 and the U.S. ballast water discharge standard levels designated as Phase Two in the United States Coast Guard's Notice of Proposed Rulemaking. Under a representative range of ballast volumes discharged at U.S. ports, the average rate of establishment of green crabs for ballast waters treated to the IMO-D2 concentration standard (<10 organisms/m³) is predicted to be reduced to about a third the average rate from untreated ballast water discharge. The longevity of populations from the untreated ballast water discharges is expected to be reduced by about 90% by treatment to the IMO-D2 concentration standard.

Keywords ballast water treatment; population dynamics; population viability analysis; environmental stochasticity; demographic stochasticity; *Carcinus maenas*.

1 Introduction

An unintended consequence of globalization in the last decades is a highly efficient dispersal process for marine organisms, bringing about dispersal distances far exceeding those provided by ordinary coastal circulation or species mobility. Shipping activities have been inadvertently transferring aquatic organisms to new continents in vast quantities as a side effect of global trade volume that has increased by orders of magnitude in the last half century. Hulme (2009) states that 'In 2006, more than 90% of global trade was carried by sea with a cargo-carrying fleet of over 50,000 ships transporting more than 1 million deadweight tonnes (IMO, 2008)', carrying an estimated 10,000 species in ballast water every day (Hulme (2009) citing Streftaris et al. (2005)).

The discharge of non indigenous species (NIS) in US coastal waters continues to pose a serious risk to estuarine and coastal ecosystems as well as the Great Lakes. For example, Grosholz et al. (2000) estimate that the invasive green crab has reduced native crab populations as much as 90% in some locations, and may have as much as a \$44M annual impact on commercial fishing industries (Grosholz (2002) citing Lafferty and Kuris (1996)). On the Great Lakes, the invasive zebra mussel filters up to 1 gallon of water per day per mussel, removing food vital to native fish (Johnson et al., 1996); and in 1989, Monroe, Michigan lost its water supply for three days due to blockages from zebra mussel infestations of the water supply infrastructure (USGS Great Lakes Science Center). The introduction of the comb jelly to the Black Sea is blamed for the damage to the anchovy fisheries (Carlton (1996) cites Harbison and Kapuscinski (1994)).

The United States Coast Guard (USCG), with participation from marine scientists affiliated with U.S. and international marine organizations, held various workshops to consider appropriate levels of standards to effectively reduce or eliminate risk of establishment of invasive species introduced via ballast water. Participants in a workshop held March 2003, the Study Group on Ballast Water and other Ship Vectors (SGBOSV), produced data to establish baseline levels of organisms in ballast and recommended standards at least three orders of magnitude below observed median concentrations of zooplankton and equivalent or higher for phytoplankton (USGS, 2009; SGBOSV, 2003). The current method used to help prevent/reduce introductions is oceanic exchange of ballast water – replacing coastal waters from the port of origin with mid-ocean water. Results from several studies have shown the effectiveness of ballast water exchange (BWE) varies considerably and is dependent upon vessel type (design), exchange method, ballasting system configuration, exchange location, and method of study. One group of studies suggests that the efficacy of ballast water exchange is 80 to 99 percent per event (Dickman and Zhang, 1999; Hines and Ruiz, 2000; Rigby and Hallegraef, 1993; Smith et al., 1996; Taylor and Bruce, 2000; Zhang and Dickman, 1999; Taylor et al., 2007). Other studies demonstrate that the volumetric efficiency of BWE ranges from 50 to 90 percent (Zhang and Dickman, 1999; USCG, 2001; Hunt et al., 2007).

Various physical and chemical technologies are now available or under development to treat ballast water on uptake, discharge, or both, removing or destroying organisms or rendering them unviable. Such technologies include filtering, ozonation, ultraviolet radiation treatment, chemical treatment, electrolysis or combinations thereof. The technologies are available for a range of ballast water pumping capacities. About two dozen commercially available systems have "Type" approval through IMO regulations as effectively reducing viable organisms to concentrations prescribed by the International Maritime Organization (IMO) D2 standards. These treatments provide concentration reductions of a few orders of magnitude from baseline concentrations, and are expected to be effective at reducing, but not eliminating risk of invasive species establishment. To reduce further or eliminate risk of establishment, the concentrations may need to be much lower. Even while the means of monitoring and verification of stricter standards are in development, there are

also initiatives to assess the impact of alternative ballast discharge standards on risk of establishment of introduced organisms.

The objective is no small order. The diversity of aquatic organism life cycles and survival strategies is large. The marine and freshwater ecologies in which these organisms would be introduced are highly complex. Moreover, available quantitative data are mostly inadequate to support model development involving multiple layers of processes to assess the impacts on organism population dynamics. Authors of various studies note the lack of sufficient quantitative data. In a study of disjunct habitats that support coastally connected populations of reef fish, Cowen et al. (2006) state that it is '...impossible to capture empirically the full range of spatial and temporal variability ...of oceanographic conditions and larval behavior'. Byers et al. (2001), who studied the impact of an invasive snail on a native marsh snail, note the '...paucity of ...information about interactions of ...native and non-native species ...is a major limitation'. In a development of plankton community models, Landis (2003) states that the '... lack of mechanistic information is ... a major source of uncertainty'. In a study examining locations for open-water ballast exchange which would have the least impact on coastal shores in the Pacific Northwest, Levings et al. (2004) discuss the difficulties in predicting viability of eggs/seeds/organisms in varying habitats due to lack of data. Ludwig (1996), demonstrating a Bayesian analysis of uncertainty of population extinction, states 'we seldom or never have enough information to determine the influential parameters ... with much precision'. This lack of data was most recently affirmed by the National Academy of Science (NAS, 2011) review of the relationship between NIS invasion risk and proposed discharge standards.

In principle, addressing the objective of the ballast water discharge standard policy analysis – what impact would reduced concentrations have on risk of establishment – requires only an assessment of the probability of success or failure of introduced organisms producing a sustained population. While the details of survival – such as finding adequate nourishment, avoiding predation, surviving environmental conditions, and successfully reproducing – underlie the success of the collected introduced organisms, policy analysts are not endeavoring to understand these factors per se. And, in general, quantitative information of these underlying processes is insufficient to provide a basis for modeling the specific mechanisms.

In previous work, Solow and members of the Volpe National Transportation Center (USCG, 2009) addressed the objective of determining the benefit of stricter ballast water discharge standards with a model that is general yet abstract. In their model the population dynamic is modeled as a Brownian process with linear growth trend, in which change in log of population size is assumed to be normally distributed conditional on the drift rate, instantaneous variance and time increment (USCG, 2009). The advantage of the Brownian diffusion model is its generality and simplicity, which makes it applicable to a wide variety of organisms, hence providing a general assessment and evaluation of discharge concentration standards alternatives. It is not used to predict which species are more likely to establish, their rates of spread after release, or how life-history stages might affect the outcome. The model uses only two parameters, does not require detailed data and lacks density dependence. Conversely, since it does not address specific organisms in ballast water, it provides no information about what parameters of the Brownian diffusion would be appropriate for various classes of fresh water or marine organisms.

The present research developed models for specific emblematic organisms common to ballast water, with specific vital rate characteristics, to address how ballast treatment standards might affect probabilities of establishment for various classes of organisms. The models represent organism stages as state variables and transitions and population dynamics with vital rates that incorporate demographic heterogeneity and environmental stochasticity. For example, Fig. 1 shows a schematic of the green crab model. The methods and results developed can be related to the Brownian model previously developed, and can be used to estimate

parameter values for the Brownian model in the absence of time series data (Cooper et al.; in submission). This paper describes the model development for the green crab (*Carcinus maenas*) and indications for the potential impact of regulatory standards on controlling organisms with similar characteristics.

The modeling activity provided quantitative characterization of emblematic aquatic invasive species, providing benchmarks that are indicative of appropriate choices of population dynamic parameters that the Brownian diffusion model did not prescribe. This model represents net processes that are at an appropriate level of detail for the essential objective of assessing risk of establishment, without complicating the model with insufficiently quantified mechanistic details that would represent factors such as predation, competition for resources, and environmental conditions. At the same time, these biotic and abiotic factors are incorporated into the dynamics as a result of the methods and data used to model the organisms' population trajectories. Finally, the receiving environment in this analysis is conceptually treated as an open system of coastally connected habitats, which kept the model simple and is well supported by research (Siegel et al., 2008; Cowen et al., 2006; Levings et al., 2004; Barth et al., 2002; Drake et al., 2005).

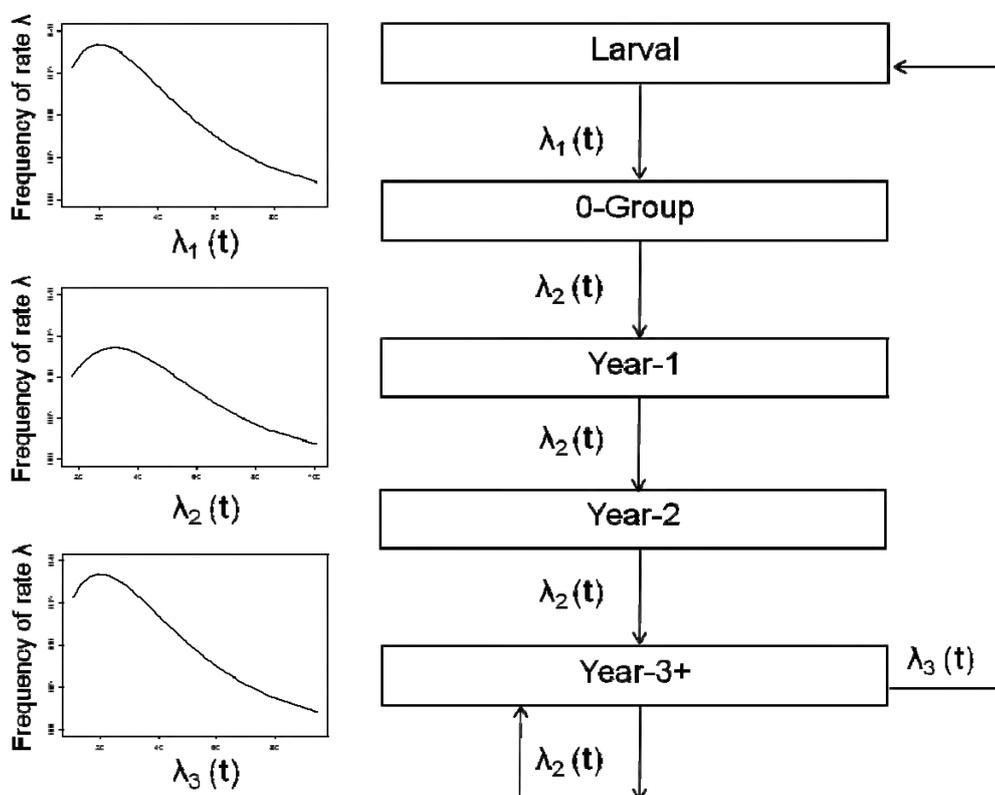


Fig. 1 Schematic diagram of population dynamic model. Boxes represent numbers of each age-class; distributions of vital rates are represented schematically by the probability density functions pictured on the left. Numbers change stochastically with each time increment as a result of randomly drawn vital rates and random outcomes conditional on these rates.

The paper is organized as follows. The first section describes some of the population dynamic models reviewed for consideration of frameworks to use. The next section describes the green crab model development. The results section describes what the model indicates for the discharge standards. Following the results section is a description of a sensitivity analysis performed to assess the model premises. The paper concludes with a discussion comparing approaches to modeling environmental and demographic stochasticity and summarizing factors that bear on risk of invasion.

Over 57 publications on population dynamics and invasive species dynamics were reviewed to support the model development. Among the 57 references reviewed, roughly one third were qualitative descriptions – e.g., discussions of when and where invasive organisms were first sighted, descriptions of the organisms' life cycles, consumption patterns and trophic level, predators, if any, and native organisms impacted by the invasive organisms. Another 15% of the references discussed theoretical models, including studies of plankton community dynamics and niche models. The remainder of the references reviewed were population dynamics models of particular organisms or ecological communities that incorporated quantitative data from other references or field studies. These latter references were primarily selected from studies of aquatic organisms and environments, and represent a great diversity of organisms, life cycles and ecological interactions.

Many papers involved some aspects of either community ecology or population dynamics. These included applications in fisheries, population viability analysis for threatened or endangered species, models for understanding invasion and the resistance or vulnerability of certain habitats to invasion, models of meta-populations used in strategies for establishing wildlife preserves and protected marine areas, and strategies for ballast exchange for reducing risk of invasion.

Methods presented in the references included state-space models that quantify dynamics of age- or size-class components of populations, or in some cases track interacting organisms in a community. Most of the models reviewed incorporated stochasticity in the population dynamics (Sharma and Raborn, 2011). Nakaoka (1996) compares growth rate determination over many realized simulations or by the average realization in five applications of population models characterized by stochastically selected fixed projection matrices, with organisms ranging from marine to terrestrial, including striped bass, desert tortoise, a marine mollusk, seaweed and gorgonian, and red deer. Higgens et al. (1997) fit a nonlinear age-class model with environmental perturbations to survival with 42 years of Dungeness crab data from the US Pacific coast. Morozov et al. (2005) show a non-intuitive result of top-down invasive predator impacts in an epipelagic community with nutrient, phytoplankton and zooplankton components. Mullon et al. (2004) describe predator-prey dynamics in a model of the Southern Benguela pelagic phytoplankton community. Hernández-García et al. (2006) model a theoretical open pelagic phytoplankton system, comparing impact of biological and flow temporal scales on patterns of extent.

Some of the methods reviewed incorporate both the demographic dynamics as well as coastal and tidal circulation dispersion processes. These types of models were common among plankton research. Anderson et al. (2005) developed a dynamic model of coastal circulation in the Gulf of Maine that indicates the importance of major cyst seedbeds north of Grand Manan Island in the Bay of Fundy and offshore of Penobscot Bay that replenish vegetative cells in Harmful Algal Bloom cycles. In a study of near-shore benthic fish off the coast of southern California, Siegel et al. (2008) model differences in coastal connectivity between patches of adult populations of benthic fish that result from dispersion of packets of larvae formed in eddy currents for varying dispersal durations. Cowen et al. (2006) model individual larval trajectories to determine rates of recruitment between sites along 9-50 km long segments of coral reef. Dunstan and Bax (2008) incorporate oceanic transport and estuarine exchange with larval settlement to assess management rules for controlling sea star spread along the Adelaide coast. These biophysical models were an influence on the decision to treat the ballast discharge receiving environment as an open system.

Some of the references reviewed described models of trajectories of total population size in time, using first- or higher-order temporal autocorrelation time series models, a special case being the Brownian diffusion model. These studies were appealing because, if modeled successfully, the population trajectory – specifically whether it crosses a threshold below which the population is effectively extinct – is ultimately the outcome of interest for the goal of evaluating risk of establishment. Ives et al. (2007) apply Bayesian methods to a delay-

difference (second-order autoregressive) model of biomass to understand recruitment influence on king prawn populations in Queensland, Australia. Ludwig (1996) applied a first-order difference equation on log growth (the Gompertz model) to calculate probability of early collapse indicated in Palila and Laysan finches and snow goose data. In the Draft Programmatic Environmental Impact Statement (DPEIS) (USCG, 2009) prepared by the USCG, preliminary assessment of the efficacy of alternative concentration standards is evaluated using the population dynamic parameter that characterizes Brownian diffusion used to represent a first-order temporal process of log population size. In these examples, the total population size is modeled with only the essential characteristic rate parameters, without layers of sub-processes requiring a suite of parameters associated with complex underlying mechanisms and dynamics.

Also of interest in invasive species research is niche theory. Trophic level, plasticity (e.g., in consumption behaviors) and biodiversity in the receiving environments have been studied to assess impact on the probability of invasion (Watts and Worner, 2011). Tilman (2004) simulates a hypothetical stochastic community resulting from competition for limited resources, which predicts that probability of successful invasion decreases as diversity in the infected environment increases. Romanuk et al. (2009) simulated a food web comprised of niche specialists, with changes in biomass controlled by metabolic efficiencies, in which trophic generality is identified from 17 food web metrics as key in predicting success or failure of invasion. These references tended to be more theoretical.

Common among the population dynamics research is a lack of sufficient quantitative data to develop models with many layers of mechanistic representations. The population dynamics models are characterized by the great diversity of organisms and of environments (although focus in this study was primarily on marine and freshwater habitats). This spectrum of organisms and communities and environments presents us with a problem in addressing the objective of evaluating the potential impact on ballast discharge standards on risk of establishment. To have a unifying answer, one would have to apply a very abstract model, as Solow and colleagues presented in the DPEIS (USCG, 2009). In the DPEIS, possible impacts were indicated by hypothetical ranges of the Brownian diffusion parameter without benchmarks for what the diffusion parameter values would be for specific organism types. Although the Brownian diffusion model approach provided a generic way to assess probabilities of establishment for reduced concentrations, it did not provide specific information about appropriate choices of the growth and variance parameters for specific types of aquatic organisms that would be transported in ballast waters. The present research developed benchmarks for several representative organism types, the details of which are described here for the green crab. Hunt et al. 2011 (in submission) provides a synopsis and comparison of the other benchmarks (zebra mussel, and dinoflagellate and diatom phytoplankton organisms).

2 Model Development

2.1 Overview

The present analysis is based on models that use general life-cycle data to characterize the dynamics of established populations to evaluate the risk that discharged organisms would produce sustained populations for varying inoculation concentrations. The model represents progression from initial inoculation (discharge event) to an organism's establishment or extinction. Establishment refers to the existence of the organism in sufficient numbers to provide for a sustained population. The transitions of organisms between key life stages are modeled as vital rates (denoted λ_i in Fig. 1). These rates characterize (1) probabilities that each individual will be selected to advance to the next stage; and (2) fecundity or asexual growth. Vital rates are determined using data from field research. Information about green crab densities of critical life stages was used to derive appropriate vital rates. The terms 'rate' and 'rate parameter' in the following paragraphs refer collectively to

the quantities characterizing (1) the probability that an individual larva settles, or that an individual settled organism survives to sexual maturity; or (2) fecundity rates.

Green crab survival and settlement rates were based on ranges in fecundity and densities of newly-settled ('0-group') young and adults observed in established populations of green crabs. Assuming the numbers of organisms that progress to the next life stage (i.e., net settlers out of the pool of larvae; or survivors from each cohort – indicated in the boxes in Fig. 1) are represented by a curve with an exponential decay, where rate of decay is a function of survival and settlement rates, the vital rates are determined by the ratios of settlers to larvae and adults to settlers (as elaborated below). The vital rate distributions are estimated numerically by Monte Carlo methods to obtain the full range of settlement and survival rates implied by the observed densities. In Monte Carlo methods, inputs to mathematical expressions are randomly drawn from specified probability distributions a large number of times and used in calculations to obtain an empirical distribution of the solution to the mathematical expressions. In this application, combinations of settler and adult densities are repeatedly drawn from the observed ranges, and the rates calculated from the exponential curve for each combination of drawn densities, to produce a distribution of settlement and survival rates.

The variation in observed settler and adult densities is a result of random success in transitions between life stages, and variable environmental conditions bearing on the rates of success in settlement, survival and fecundity of the individuals. Assuming the conditions at the locations at which scientists collected the demographic data represent the full range of biotic and abiotic conditions over the time period and geographic range that the studies were conducted, these rates are assumed to span the ranges of environmental conditions that would be encountered in habitats at which the organism can sustain populations. To assess risk of establishment, life-cycle dynamics of introduced organisms are simulated by first drawing settlement, survival and fecundity rates from the distributions determined based on these demographic data and then drawing the random outcome of successful settlers, survivors and eggs produced in each time increment. The model simulates environmental variability by drawing each vital rate for each time increment; and then demographic stochasticity is the result of the random outcome of settlement, survival and reproduction assuming the randomly drawn rates.

A decision rule to judge the outcomes of model runs relative to the success of the NIS introduction was required. This was addressed by setting a threshold (called the quasi-extinction number) that established whether the NIS population maintains numbers above the threshold for a simulated period of 100 years. The outcome is counted as a successful establishment if the population size is above the threshold at the end of the 100 year period. The period considered was arbitrary but long enough to provide an adequate trajectory to characterize the average population growth trend and fluctuations about the trend for comparison with the Brownian process model developed in the DPEIS (USCG, 2009). In addition to the establishment outcome at 100 years, the longevity (the number of years a population is sustained) of each simulated population trajectory was recorded. The population dynamics are characterized by the proportions of trajectories that are still sustained at any year prior to the full 100-year period.

2.2 Green crab model details

There are abundant data in the literature to support developing this population dynamic model of the green crab. Cohen et al. (1995) cite various researchers that provide ranges of densities (organisms per m^2) of 0-group (settler) and sexually mature green crabs in established populations. The data used in model development are presented in Table 1 with references. The key transitions identified for the green crab organism are the net settling rate, net rate of survival from the 0-group (recent settler) to sexual maturity, and the fecundity per molt. An exponential model, such as employed by Cowen et al. (2006), can be fit to these densities to determine a range of the net survival rates from recent settlement through 3 years (the minimum

age for green crab sexual maturity). In a similar application of density data, Largier (2003) discusses estimation of larval dispersal by examining settlement rates based on planktonic and adult survival rates.

Table 1 Green crab settlement and survival rate distributions were determined from density data, assuming exponential growth.

0-Group (Settlers)	10-2,000 /m ²	Cohen et. al. 1995 citing Hancock & Urquhart 1965; Crothers 1968; Klein Breteler 1976 (a,b); Schere & Reise 1981; Jensen & Jensen 1985; Janke 1990
Adult	0.1 – 20 /m ²	Cohen et. al. 1995 citing Hancock & Urquhart 1965; Crothers 1968; Klein Breteler 1976 (a,b); Schere & Reise 1981; Jensen & Jensen 1985; Janke 1990
Eggs/molt	185,000-200,000	Cohen et. al. 1995 citing Broekhuysen 1936

The exponential relationship, used frequently to model population decay, is expressed in Equation (1). In this equation the size of the population at time t (denoted N_t) is related to the size of the population at a previous time ($N_{t-\Delta t}$), assuming exponential decay due to mortality or removal at a rate, r , per unit time. This equation can be manipulated to solve for r given initial and subsequent population sizes and the time interval (Δt), as represented in Equation (2). In this form r is expressed as a function of the natural logarithm of the ratio of the initial and subsequent populations. Since the relationship involves the ratio, the densities of organisms can also be used, as indicated in Equation (2).

$$(1) \quad N_t = N_{t-\Delta t} e^{-r\Delta t}$$

$$(2) \quad r = -\ln(N_t/N_{t-\Delta t})/\Delta t = -\ln\left(\frac{N_t}{m^2} / \frac{N_{t-\Delta t}}{m^2}\right) / \Delta t$$

The Monte Carlo method was used to calculate a range of survival rates for the green crab by randomly drawing values for the 0-group and adult crab densities from the ranges reported in Cohen et al. (1995), computing the vital rate r using the relationship in Equation (2), and repeating the process enough times (for example, 1000 times) to reliably characterize the distribution of r (i.e., a sufficient number of computed values of r to produce a histogram that would not change significantly if additional Monte Carlo simulations were performed).

The exponential relationship is also used to establish the range of settlement rates. The settlement rate refers to the probability that an egg will survive through the larval stage and settle on suitable habitat. This is accomplished with an additional step of drawing from the observed ranges of fecundity (eggs/molt/m²) to provide an initial population concentration of eggs ($N_{t-\Delta t}/m^2$), and then drawing from the densities of 0-group settlers to provide the subsequent population density of settlers (N_t/m^2). Figure 2 shows histograms of settlement and survival rates produced by the Monte Carlo process.

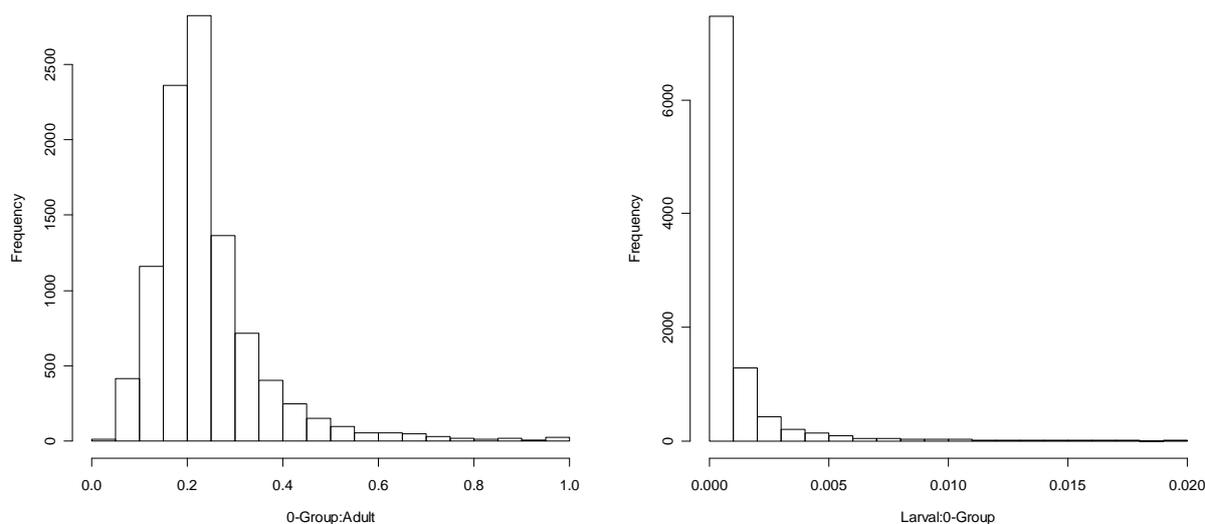


Fig. 2 Histograms of settlement and survival rates, based on field observations of densities and fecundity, produced from Monte Carlo methods assuming an exponential survival curve. Left – annual survival rates, right settlement rates.

These distributions of settlement and survival rates and the observed ranges in fecundity are applied in the model runs. The model uses Monte Carlo methods to simulate trajectories of fluctuating population sizes for a 100-year period. Monte Carlo methods are used to produce a large number of outcomes (1000 trials) to determine the proportion of times that a trajectory results in a population that was sustained. The steps of the Monte Carlo runs used to estimate risk of establishment follow:

(1) Monte Carlo Steps

1. Simulate number of NIS introduced
 - a. Initialize the concentration of crustaceans in ballast water, either based on concentrations of crustacean organisms in ballast water reported in Cohen et al. (1995) citing Wang (1990), for baseline conditions (~80-800 organisms per metric ton (MT)); or at one of the proposed standards for organisms >50 μm (10/MT (IMO D2); 1/100 MT (Phase Two)).
 - b. Draw volume of ballast (conditional on the port, for distributions based on National Ballast Information Clearinghouse (NBIC) records from 2005-2008 at 16 major U.S. ports).
2. Simulate number of settlers
 - a. Draw Larval: 0-group survival rate
3. Simulate number of settlers that survive to adults
 - a. Draw 0-group: adult survival rate
 - b. Calculate rate raised to 3rd power (to simulate a minimum of 3 years to adulthood)
4. Simulate “Year 3+” egg production
 - a. Randomly assign gender, with equal probability of male and female
 - b. Draw number of eggs for each female
5. Loop over steps 2-4 for 100 years
 - a. Adults persist from year-to-year with random reduction in numbers at randomly drawn annual survival rates. A new survival rate is drawn each year.
 - b. Combined Year-1, Year-2 and Year-3+ organisms below quasi-extinction threshold indicates failure to sustain population (*i.e.*, NIS establishment failure)

6. Record number of successfully sustained populations

(2) Assumptions

1. Net process rates, which are based on densities reported in Cohen *et al.* (1995), incorporate variability due to latent biotic and abiotic conditions. This provides a way of evaluating the population dynamic of NIS without explicitly modeling theoretical relationships of environmental conditions and their effects on rates such as settlement, survival, and reproduction.
2. Rates are based on steady state (established) populations and do not account for density-dependent variability that might result from such things as decreased resistance to predation pressures, decreased net fecundity or other non-linear effects of competition for food among native and introduced organisms. The simplification may result in over-estimating rate of successful establishments for very small initial concentrations of NIS.
3. The receiving environment is not a single bounded volume of water (such as a port or harbor). Risk of establishment implicitly involves ports, harbors and potentially 'circulation-connected' shores and waters around the ports. The ballast discharge NIS model does not represent the physical habitat of the ports and surrounding environments. Rather, settlement and growth rate parameters are assumed to incorporate variability due to coastal circulations and suitability of habitat within the receiving environment. However, the model does not account for invasive 'recruits' from nearby waters and only assesses the fate of organisms introduced by ballast discharge. Nor does it model range expansion.
4. No initial dilution is applied to the ballast NIS concentrations. According to some studies, ballast water behaves as an entrained parcel or parcels that maintain organism concentrations. Larson *et al.* (2003) report that NIS organisms are entrained in ballast water, and that mixing (dilution) is a secondary effect compared with dispersion due to tidal and buoyancy-driven currents, although the dilution may be on the order of 100 times at a 50-m depth. Barth *et al.* (2002) suggest that as ballast water spreads, it is stretched into streaks of high-concentration parcels rather than being diluted into a larger overall volume of water.
5. Rates that are based on densities of established populations are derived assuming exponential growth/decay. Cowen *et al.* (2006) also use an exponential growth relationship in some of their calculations.
6. For ballast discharge of organisms $> 50 \mu\text{m}$, 100% are larvae.

For each port, simulations were run 1000 times for baseline conditions and at each of the proposed standards (as explained in Step (1) above under Monte Carlo Steps).

3 Model Results

3.1 Rate of establishment

Table 2 reports the average rate of establishment, for the baseline and each standard. The average rate of establishment across ports for baseline inoculations (~80-800 organisms/MT) was 57.8%. At IMO D2 standards (10 organisms/MT), the average rate of established populations was 18.5%. At Phase Two standards (1 organism/100 MT, as designated in United States Coast Guard's Notice of Proposed Rulemaking), average rate of establishment across the ports was 1 in 1000 introductions. Based on the simulated population dynamics, limiting ballast concentrations to the IMO D2 standard achieves a three-fold reduction in the rate of establishment. Limiting ballast concentrations to Phase Two standards reduces rate of establishment by two orders of magnitude over both IMO D2 and baseline concentrations.

Table 2 Average rate of establishment across ports

	Concentrations (Organisms/MT)	Average rate of establishment
Baseline	~80-800	57.8%
IMO D2	10	18.5%
Phase Two	1/100	0.1%

3.2 Longevity

The longevity of each trajectory is the number of years that the population is sustained. Table 3 shows the percent of trajectories that had longevities of less than 5 years, 5-10 years, 10-20 years, 20-60 years, 60-99 years and 100 years. For inoculation concentrations at or below the baseline values, longevities of trajectories that were not sustained out to 100 years very rarely exceeded 60 years.

Table 3 Percent of trajectories in 6 ranges of longevity

	Concentrations (/MT)	Years					
		<5	5-10	10-20	20-60	60-99	100+
Baseline	~80-800	22%	10%	7%	3%	0%	58%
IMO D2	10	70%	6%	4%	1%	0%	19%
Phase Two	1/100	99.9%	0%	0%	0%	0%	0.1%

3.3 Model validation - age structure composition

The NAS report (NAS, 2011) discusses the lack of empirical values of rate of establishment of invasive species. The NAS authors note 'there are only loosely corresponding empirical estimates of risk and release'. They tabulated invasion records and ballast surveys of nine major coastal and freshwater water bodies, highlighting the gap between ballast records and when invasions were detected. They note that 'neither the dependent nor the independent variables is well resolved', stating that 'invasion risk is estimated from the outcome of a cumulative century-long historic process, whereas organism release is estimated over a [...] period of months to years' (NAS, 2011). For this reason, approaches to model validation are limited.

To validate the model, population characteristics were examined to verify that the population trajectories had expected properties. Darrigran et al. (2003) use the size class distributions of invasive mussels in Argentina to identify the year at which an introduced mussel population had become stable. Byers et al. (2001) also examine the size class composition to validate a model of interaction between a native and non-native marsh snail. The cohort composition of the green crab trajectories was examined to verify that the simulated population age class structure mimics observed structures in established populations. Among the trajectories that were sustained, 43-44% of the time the population was dominated by Year-3 crabs (60-80%) with the rest of the population diminishing to vanishing numbers of crabs from cohorts greater than 4 or 5 years of age. Similarly, the Year-4 crabs dominated in 43-44% of the outcomes, with older cohorts having orders of

magnitude fewer individuals. Year-5 crabs dominated in 12-13% of the trajectories (composing between 50-75% of the population), with older cohorts having diminishing contributions to the populations (decreasing in orders of magnitude as age increased). This is consistent with observations in Europe where green crabs survive only to about 5 years of age (Grosholz and Ruiz, 1996).

Comparing the green crab model with the DPEIS Brownian motion model provides additional validation. The DPEIS analysis tabulated predicted rates of establishment for three values of the growth-to-variability ratio parameter characterizing the Brownian process, and for initial concentrations across nine orders of magnitude, assuming 10,000 MT ballast volumes. The DPEIS analysis indicates a 75-80% chance of establishment for organisms with a ratio of growth to variability of 0.1 and initial concentrations on the order of $10^2 - 10^3$ organisms per MT. In 1000 runs of the green crab model with baseline concentrations (~80-800 /MT) and with ballast volumes fixed at 10000 MT, the median of empirical values of the ratio parameter was 0.13 and 77.7% of simulated trajectories were sustained. (See also Cooper et al., in submission).

3.4 Assessing model sensitivity

The premise of the model approach is that the data assembled in Cohen et al. (1995) is suitable to characterize appropriate ranges and frequencies of values for vital rates across a plausible range of environmental (biotic and abiotic) conditions. Cohen et al. (1995) report demographic data from a range of studies conducted at various locations around Europe over a time spanning over two decades, thus capturing a range of conditions in the established populations. To check the sensitivity of the results to the ranges in densities and fecundity reported, the vital rate distributions were reproduced after perturbing the density and fecundity data. The simulations were run with the resulting vital rate distributions. Each range reported in Table 1 was subjected to shifting the midpoint up or down by 20% or stretching or shrinking the range by 20% or both. For each perturbation, the simulations were repeated at the proposed standards concentrations for ballast volume fixed at either 5k MT or 50k MT (the 50th and 95th percentile of ballast volumes in the 2005-2008 NBIC port data, respectively). Results from the simulations were analyzed to estimate the effects of perturbing the input densities and fecundity on rate of establishment and on longevity.

Logistic regression was used to model the log-odds of establishment as a linear function of the mean and variance of the ranges of densities and fecundity to assess the sensitivity of outcomes to perturbations in the inputs. The model also included the discharge standard and ballast volume as covariates to adjust for initial inoculation. Table 4 below summarizes the average (and standard deviation) of the estimated rates of establishment grouped by standard and volume, where the estimated rates are the predicted rates from the logistic regression model.

Table 4 Average (and standard deviation) of the estimated rates of establishment of sensitivity runs grouped by standard and volume

	5,000 MT	50,000 MT
IMO D2	0.201±0.028	0.515±0.045
Phase Two	0.002±0.0004	0.007±0.001

Rates of establishment are not significantly associated with perturbations in the range of adult densities. There is a statistically significant influence on the response by variability in settler densities and in fecundity. For lower values of settler density, for any particular adult density, the survival rate is computed to be higher because fewer settlers net that same adult density (refer to Equation (2) above). The estimated rate of establishment varies as a function of settler density variability, from 16.9% to 24.3% for 5,000 MT volumes; and from 46.4% to 57.8% for 50,000 MT volumes.

The sensitivity to variability in fecundity may be due to an associated increase in the stochastic variability around the trajectory (the instantaneous variance of the Brownian process). That is, with a greater variability in reproductive capacity, the population would be subject to greater fluctuations in population size, which would increase vulnerability to extinction. While the association between the empirical stochastic variability and fecundity variability is not statistically significant, there may be a tendency for increasing variability in the trajectory associated with increasing variability in fecundity.

4 Discussion

4.1 Comparing approaches to modeling environmental and demographic stochasticity

Two components of stochasticity contribute to variable outcomes in population dynamics. Demographic variability is the result of variability between individual organisms in growth rate, reproduction and survival. Environmental variability is the result of varying biotic and abiotic conditions over the spatial domain of the population, as well as due to temporal variability in these conditions as a result of climatic oscillations and inter-annual variability. Biotic and abiotic conditions refer to everything that bears on an organism's chances of survival and reproduction, including competition for habitat and food resources, changes in predation pressures, environmental conditions that influence physiological processes such as metabolism, reproduction and aging, climatic influences on nutrient resources and distribution, catastrophic events that completely change the habitat, and any other varying conditions that bear on organism fitness (Lüi, 2011).

The models in references reviewed represented a variety of approaches to incorporating stochasticity. Nakaoka (1996) describes a few models in which multiple matrices characterizing changes in the population components may be applied with random selection to effect projections varying with environmental conditions. Lubow (1996) applies random shifts to mean growth rates for demographic and environmental variability for an analysis of a 2-patch strategy to preserving a population. Random effects are used in various applications for modeling inter-annual variation that may be interpreted as environmental perturbations to population dynamics. Higgins et al. (1997) incorporate random inter-annual effects in a nonlinear age-class model fit to Dungeness crab catch data. Jiao et al. (2008) develop a Bayesian model of dynamics of complexes of three species of sharks, comparing outcomes for growth rates that are homogeneous or species-specific or that vary with year. In their model of king prawn recruitment, Ives et al. (2007) compare models with and without year-to-year variability. In various models, demographic variation in outcome of mortality, growth and fecundity is modeled by the random outcome for organisms in a particular life stage, conditional on the rate parameters – for example, Dunstan and Bax (2008) in a model of sea stars; Byers and Goldwasser (2001) in an analysis of factors influencing the potential extinction of a native marsh snail as a result of introduction of a non-native snail.

Demographic and environmental stochasticity are also incorporated in the green crab model. Demographic stochasticity is achieved by simulating a random outcome for each time increment for the numbers of eggs produced, the numbers of larvae that settle and the numbers of individual crabs that survive, conditional on the settlement and survival rates and fecundity of that time increment. Fecundity and settlement and survival rates are drawn from the rate distributions in each time increment. This simulates environmental stochasticity as inter-annual variability. The distributions from which the rates are drawn are based on the full range of combinations of densities and fecundity that were observed in studies cited in Cohen *et al.* spanning over two decades and various locations around Europe. The degree to which the settlement and survival rates can vary, based on the derived distributions, indicates the amount of variation that would be possible for the observed densities and fecundity reported in those studies to have occurred. For a future extension of the analysis, it

would be interesting to assess how persistence of conditions for varying numbers of years (time increments) would affect population dynamics.

4.2 Factors that bear on risk of invasion

The proposed standards would be applicable and enforceable by vessel, although there is variation in invasion processes between coastal, estuarine and freshwater ports and between organism types. Generally organisms would not survive a complete change in environment, due to limitations in osmotic regulation and other limitations in physiological efficiencies associated with physical and chemical factors such as salinity and temperature.

In the analysis conducted here, the receiving environment is treated as arbitrary. No attempt was made to characterize habitat in the waters into which the organisms are discharged. The receiving environment, whatever port or open waters it may be, is not a closed system. As noted, Siegel et al. (2008) and Cowen et al. (2006) model patches of fish populations that exist across sections of coast or coral reef connected by coastal circulations. Levings et al. (2004) cite Lluch-Belda et al. (2003) as characterizing the entire Pacific coast from Alaska to Baja California as a homogeneous ecological unit. Barth et al. (2002) describe how dispersal of discharged ballast water stretches the ballast waters into streaks of high-concentration parcels. Drake et al. (2005) citing Imboden and Wüest (1995) note that horizontal diffusion due to circulation is orders of magnitude higher than vertical diffusion. Larson et al. (2003) also assume this. Taking into consideration the tidal and coastal circulation that could displace packets of entrained ballast water from the port of discharge, the importance of niche and habitat resistance to invasion may be diminished because the organisms would be shifted around over an extended range.

No attempt was made to characterize environmental conditions, nor food resources, nor predation pressures. Rationale for disregarding conditions in the receiving environment is that the findings needed to address a standard that would be applied to the entire vessel fleet, regardless of operations in various types of receiving environments. Assuming discharge into a suitable environment is a conservative approach to modeling risk of invasion. The simplification also facilitates being able to understand and document the model and its results, by limiting the layers of detail, keeping the modeling approach transparent. Omitting details of environmental suitability also bypasses the problem of not having sufficient quantitative data for developing appropriate parameters and relationships that would characterize how environmental conditions change the risk of establishment of each particular invasive organism.

Some research suggests that the rate and magnitude of invasive introductions is a primary factor in the outcome of establishment. Cassey et al. (2005) conducted a meta-analysis on 24 studies of invasive birds to identify factors that are consistently implicated in the outcome of establishment. The studies examined a variety of candidate covariates that considered characteristics of the introduced species, of the habitat and of the circumstances of the introduction. Species that are generalists in feeding habits, or that are very fecund, or adaptive to nesting or living in a variety of environments, or that are higher or lower on the trophic web have been hypothesized to have better chances of establishing in a new environment. Locations with greater diversity or greater abundance in nutritional resources or more or less disturbance are hypothesized to be more or less susceptible to invasion. Event-related circumstances, such as numbers introduced, frequency of and seasonal variations in introductions are also thought to bear on risk of invasion. In their meta-analysis, Cassey et al. categorized the studies' covariates as species-, event- or location-related and examined the Pearson correlation coefficients of effects (to standardize the effect sizes) to infer which categories consistently predict successful invasion. They report that propagule pressure (meaning, numbers and frequencies of organisms introduced), an event-related covariate, was consistently significant.

The Draft Programmatic EIS (USCG, 2009) reported on several workshops in which participants discussed whether standards should be stated in terms of percent reductions or concentrations of organisms. Many studies have suggested that, while not the only factor, the numbers and rates at which organisms are introduced has significant bearing on whether the organism becomes established in the non-native environment (Drake et al. (2005) cite Green (1997); Grevstad, 1999; Kolar and Lodge, 2001, and Lockwood et al., 2005). Similarly, results in Byers et al. (2001) suggest establishment is more likely as initial densities of the invading marsh snail increases. In the application of the Brownian diffusion model to characterize impact of proposed standards on risk of establishment, results in the DPEIS (Table 5-2, USCG 2009) are presented across nine orders of magnitude of organism concentrations.

Conclusions in this study also suggest that the numbers of organisms introduced is a dominating factor in the outcome of an invasion. Based on the assessment of the sensitivity of the results to ranges of green crab fecundity and densities, perturbing the ranges in fecundity or larval densities by 20% resulted in moderate changes in the probability of establishment. However, the odds of establishment increases more than 3-fold with each order of magnitude increase in organisms introduced.

4.3 Summary

The lack of data describing vital rates and life cycles across the range of potential invasive species was a major concern in our study. The population dynamic models developed here were based on published data that represent plausible ranges in the natural conditions in which these organisms exist. Therefore, the derived vital rates are indicative of rates of net processes of the life stages of these organisms. That is, these rates must at least overlap the true distribution of rates in order for the reported ranges in concentrations or densities of organisms to have been observed.

The model focuses on net processes at a level that is relevant for assessing the impact of the standards on risk of establishment. The receiving environment is treated as an open system of coastally-connected habitats. Building the model on net processes ensures that the model is transparent and is not compromised by insufficient data to quantify parameters and processes that underlie net rates of success of each life stage. The characterization of the net rates is based on data from studies cited in Cohen et al. (1995) that span over two decades and various locations across Europe. Variation in the cited study data is the result of and is representative of latent biotic and abiotic conditions that existed across the locations and dates that the studies were conducted. The simulated trajectories incorporate environmental stochasticity by randomly drawing vital rates from the derived distributions at each time increment; and demographic stochasticity is incorporated as random outcomes of each life-stage conditional on the drawn rates. Based on the model outcomes, the IMO D2 standard would reduce risk of establishment 3-fold; and the Phase Two standard would reduce risk by two orders of magnitude.

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