

Chapter 4

Modeling Marine Invasions: Current and Future Approaches

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4.1 Introduction

This chapter focuses on how dynamical mathematical modeling has been and could be useful in understanding marine biological invasions. Mathematical models have long been central to the development of general ecological and invasion theory (e.g., Case 1990; Hastings et al. 2005; Lewis and Kareiva 1993; Neubert and Parker 2004; Shigesada and Kawasaki 1997). Although the dynamics of marine systems can be challenging to observe and model (e.g., deYoung et al. 2004; Kinlan et al. 2005), mathematical models are nonetheless beginning to provide insights into invasion dynamics in marine systems.

4.1.1 Why Marine Invasion Modeling?

Mathematical modeling is a tool, like natural history observations, field and laboratory experiments, and genetic analysis, that can provide insight into biological processes in general, and invasion dynamics in particular. The mathematical tools associated with ecological, epidemiological, evolutionary, and even economic theory can all be brought to bear one way or another on problems of invasions. While models can provide new insights and perspectives into invasions, invasions can also motivate new ways to combine modeling approaches.

Before delving into this material, it is perhaps useful to consider two questions. First, is invasion modeling different from any other ecological modeling? Second, is marine invasion modeling different from any other invasion modeling?

Does invasion modeling differ from other ecological modeling? Current human-mediated invasions offer a dramatically sped up version of natural processes of colonization and extinction. At the community scale, the rapid accumulation of invaders requires us to consider in ecological time the global-scale dispersal and homogenization that traditionally have been the domain of paleontology and biogeography (e.g., Drake and Lodge 2004; Olden and Poff 2004). At the population scale, invasions prompt us to focus on the dynamics of small populations, and have

spurred mathematical innovation in modeling spatial population dynamics in general, and Allee effects in particular (e.g. Hastings 1996). Invasions also encourage us to adopt and develop traditional conservation-oriented modeling tools, such as population viability analysis or fisheries harvest models, and turn them around to ask how best to eradicate, rather than to protect, a species. The striking impacts of selected invaders also provide a compelling incentive to combine ecological and economic modeling to help prevent and control invasions (e.g., Leung et al. 2002; Sharov 2004; Sharov and Liebhold 1998).

Does marine modeling differ from other invasion modeling? Marine systems differ in a multitude of ways from terrestrial ones, and can demand different modeling approaches. With respect to invasions, a conspicuous difference is the mobile nature of the habitat: water moves faster than continents. Ocean circulation operates in three dimensions, which can prove challenging to model. Depending on the question, marine invasion models may be nonspatial or may incorporate one or more spatial dimensions. One dimension may suffice for characterizing spread along a coastline, and two dimensions may adequately capture the movement of certain surface or benthic organisms. Three-dimensional models may be required to capture large-scale pelagic systems, or local settlement processes influenced by turbulent flow, eddies, and tidal exchange. As the number of spatial dimensions increases, so does the complexity of the model. Perhaps as a consequence of the habitat differences, models that effectively predict invasion-spread rates in terrestrial systems largely fail in marine systems (Grosholz 1996; Kinlan et al. 2005). This disparity highlights the need to focus on additional environmental processes when modeling the marine invasions.

4.1.2 Scope of this Review

To contain this review, we have chosen to focus on dynamical mathematical models, which means we largely omit statistical models. We have also chosen to highlight how models have been applied to non-native species, which means we skip over many mathematically similar models that treat native species dynamics. We have organized the resulting collection of models in terms of biological invasion processes, mathematical model types, and the goals of the model.

Biologists and mathematicians may look at invasion modeling in somewhat different ways. A biologist may conceptualize invasions as a series of qualitatively distinct stages. A given invasion begins with a species being transported. The species will then establish and spread, interact with the resident community, have some degree of impact, and may or may not be subject to control or enhancement efforts. At a community scale, where multiple invasions occur, questions of invasibility, and the roles of disturbance, resource availability, and resident species diversity may arise.

A mathematician, in contrast, might categorize invasion processes according to the type of model that could be applied. For example, single-species population

models can be used to ask questions about establishment and control, and multispecies models may provide insight into establishment, impacts, and biological control. These models must be extended to a spatial context to address questions of invasion spread (Shigesada and Kawasaki 1997). A quite different category of bioeconomic cost-benefit analysis may be used to optimize invasion control efforts.

The goals of a model will determine its approach and structure. In any modeling enterprise, there is a tension between a model's tractability and its realism. Where a biologist may find a given model unrealistically simplified, a mathematician may find it excessively complex. The goal of a model can run the gamut from being highly strategic, intended to provide general insight into a certain kind of process, to highly tactical, intended to simulate and forecast the detailed operations of a particular system (Levins 1968). Where a model falls along this continuum likely dictates where it falls along a series of related spectra (Table 4.1). The success of a model can only be evaluated in the context of its goals: a highly strategic model is not intended to be very realistic, and a highly tactical model is not intended to be broadly applicable. A more detailed discussion of modeling philosophy and practice is beyond the scope of this chapter, but we refer in the Appendix to sources that we find helpful on these topics.

To review current marine invasion modeling, we mix and match freely between biological and mathematical perspectives of invasion biology, and also highlight differences in modeling goals. First, we look at models of human-mediated species transport, as this process sets the stage for the invasion dynamics that follow. Next, we turn to models that focus on the invader. In invasion biology terms, these models treat species establishment, impacts, and control. In modeling terms, they are population dynamics models that may be extended to include interspecific interactions, or integrated with bioeconomic cost-benefit analyses. Third, we delve into the very rich literature on invasion-spread modeling, which extends population dynamic models over one, two, or three spatial dimensions. Finally, we look at models that focus on the invaded community to explore questions of invasion resistance over space and time.

In each section, we briefly highlight relevant modeling approaches in general invasion biology and marine ecology. We then provide examples of marine invasion models that represent current and future directions in this area, and illustrate some of the contrasting goals of different models (Table 4.2). We end this review by identifying some promising areas for future mathematical modeling in the study of marine bioinvasions.

4.2 Invasion Pathway Models

Modeling an invasion pathway allows us to address questions of invader source and propagule pressure, the associated risk of species establishment, and invasion prevention (Jerde and Lewis 2007). In marine systems, the dominant invasion pathway is commercial shipping, with its associated ballast water, sediment, and hull fouling

Table 4.1 Modeling tradeoffs. Depending on its goals, a mathematical model may be more strategic, focusing on general insight into a certain kind of process, or more tactical, focusing on specific forecasting of a particular system. Broadly speaking, a model will tend to fall towards the left or the right side of these continua simultaneously, although there is room for mixing and matching approaches. The goal of a model is important to consider when evaluating its effectiveness

Tradeoffs	Continua	
Goal	Insight.....	Forecasting
Approach	Strategic.....	Tactical
Biology	Abstract.....	Realistic
Detail	Less.....	More
Uncertainty	Deterministic.....	Stochastic
Analysis	Analytical.....	Numerical
Applicability	General.....	Specific

communities. Two primary kinds of dynamic models have developed in this area: those that focus on a particular invasion vector, and those that model spatial patterns in regional or global species transport pathways.

Ballast-transport dynamics have been investigated using population models to compare the invasion potential of different species, and to evaluate prevention methods (e.g., MacIsaac et al. 2002; Wonham et al. 2005a, b). For marine and estuarine species, for example, Wonham et al. (2005b) used a simple population growth model to illustrate how the timing and level of open-ocean exchange can be optimized to reduce invasion risk for species with different salinity tolerances (Fig. 4.1). A more detailed population model applied to freshwater zooplankton resting stages in ballast sediments (Wonham et al. 2005a) could be extended to marine species as well.

A single invasion pathway rarely operates in isolation, and is typically connected to a larger spatial network of species transportation. Such networks can be modeled in a spatially implicit way using gravity models that represent the connections between pairs of points linked by a given transport pathway. This approach has been used regionally to model boat traffic and zebra mussel invasions, and globally to characterize shipping routes with high ballast water discharge (Bossenbroek et al. 2001; Drake and Lodge 2004; Leung et al. 2006).

In principle, invasion pathway models that predict propagule pressure over space and time could provide the initial conditions required for the population establishment and spread models treated in the following sections.

4.3 Population Models: Invasion Dynamics

In this section, we treat models that focus on a particular invader and its establishment, impacts, and control. These are all nonspatial models; spatial models, which use an additional set of mathematical tools, are considered in the next section. We begin with models of the invader dynamics alone, followed by models of invaders interacting with other species.

Table 4.2 Dynamical mathematical models of marine invasions reviewed here. Models classified by invasion stage and model focus. Some models are specifically developed for particular marine invaders; others are motivated by or applied to marine species, but are more general in their application

Invasion aspects	Physical and biological processes	Invader	Taxon	References
<i>Pathways</i>				
Delivery, prevention	Population growth	Multiple ^a	Invertebrates	Wonham et al. (2005b)
Delivery, establishment, prevention	-	Generic	Generic	Drake and Lodge (2004)
Population: invasion dynamics				
<i>Single species</i>				
Establishment	Chromosomal reversion, population growth	<i>Crassostrea ariakensis</i>	Bivalve (oyster)	Dew et al. (2003)
Establishment	Population and metapopulation growth	<i>Pseudodiaptomus marinus</i>	Crustacean (copepod)	Barry and Levings (2002)
Establishment, control	Population growth, removal	<i>Caulerpa taxifolia</i>	Macroalga	Ruesink and Collado-Vides (2006)
Control	Population growth, removal	<i>Ocenebrellus inornatus</i>	Gastropod (oyster drill)	Buhle et al. (2005)
<i>Multiple species</i>				
Establishment	Foodweb	<i>Mnemiopsis leidyi</i>	Ctenophore	Gucu (2002)
Establishment	Genetic fixation	Transgenes; <i>Oncorhynchus kisutch</i>	Transgene	Hedrick (2001)
Establishment, impact	Population growth, infection dynamics	Phocine distemper	Virus	Grenfell et al. (1992); Heide-Jørgensen and Härkönen (1992); De Koeijer et al. (1998); Harding et al. (2002, 2003); Loneragan and Harwood (2003)
Impact	Primary production, herbivory, predation	Generic; <i>Mnemiopsis leidyi</i>	Ctenophore	Morozov et al. (2005)

(continued)

Table 4.2 (continued)

Invasion aspects	Physical and biological processes	Invader	Taxon	References
Impact	Population growth (fish) + bioenergetic (jelly)	<i>Mnemiopsis leidyi</i>	Ctenophore	Knowler (2005)
Impact	Interspecific competition, parasitism	<i>Batillaria attramentaria</i>	Gastropod (mud snail)	Byers and Goldwasser (2001)
Impact	Foodweb	<i>Tapes philippinarum</i>	Bivalve (clam)	Pranovi et al. (2003)
Impact, control	Bioeconomic	<i>Crepidula fornicata</i>	Gastropod (slipper shell)	Frésard and Boncoeur (2006)
<i>Population: invasion spread</i>				
<i>Single species</i>				
Establishment, prevention	Hydrodynamics, population growth, dispersal	Multiple ^b	Invertebrates	Drake et al. (2005)
Spread	Hydrodynamics, population growth, dispersal	Multiple ^c	Invertebrates	Grosholz (1996)
Spread	Hydrodynamics, dispersal	Multiple ^d	Invertebrates, macroalgae, fish	Kinlan et al. (2005)
Spread	Hydrodynamics, dispersal	<i>Phyllorhiza punctata</i>	Cnidarian (jellyfish)	Johnson et al. (2005)
Spread	Hydrodynamics, dispersal	<i>Asterias amurensis</i>	Echinoderm (sea star)	Parry et al. (2001)
Spread	Hydrodynamics, dispersal	<i>Crepidula fornicata</i>	Gastropod (slipper shell)	Viard et al. (2006)
Spread	Hydrodynamics, dispersal	<i>Theora lubrica</i> , <i>Musculista senhousia</i>	Bivalves (clam, mussel)	Inglis et al. (2006)
Spread	Population growth, dispersal	<i>Spartina alterniflora</i>	Plant (cordgrass)	Taylor et al. (2004)
Spread	Population growth, dispersal, control	<i>Spartina alterniflora</i>	Plant (cordgrass)	Taylor and Hastings (2004)

Spread, impact	Population growth, dispersal, habitat modification	<i>Spartina alterniflora</i>	Plant (cordgrass)	Cuddington and Hastings (2004)
<i>Multiple species</i>				
Spread, impact	Dispersal, infection dynamics	Phocine distemper virus	Virus	Swinton et al. (1998)
Spread	Population growth, dispersal	<i>Caulerpa taxifolia</i>	Macroalga	Hill et al. (1998); Aussem and Hill (1999, 2000)
Spread, impact	Hydrodynamics, dispersal, bioenergetics	<i>Mnemiopsis leidyi</i>	Ctenophore	Volovik et al. (1995)
Spread, impact	Hydrodynamics, dispersal, bioenergetics	<i>Mnemiopsis leidyi</i>	Ctenophore	Berdnikov et al. (1999)
Spread, impact	Hydrodynamics, dispersal, bioenergetics	<i>Mnemiopsis leidyi</i>	Ctenophore	Oguz et al. (2001)
Spread, impact	Hydrodynamics, dispersal, bioenergetics	<i>Mnemiopsis leidyi</i>	Ctenophore	Lebedeva and Shushkina (1994)
Spread, impact	Hybridization	Generic, <i>Spartina alterniflora</i>	Plant (cordgrass)	Hall et al. (2006)
Impact	Hydrodynamics, host-parasite dynamics	<i>Salmo salar</i>	Fish (salmon)	Krkošek et al. (2005, 2006)
Spread, impact, control	Population growth, dispersal, herbivory	<i>Elysia subornata</i> , <i>Caulerpa taxifolia</i>	Mollusc (sea slug) macroalga	Coquillard et al. (2000)
Impact	Hydrodynamics, foodweb	<i>Sabella spallanzani</i>	Annelid	Murray and Parslow (1999)
<i>Community invasibility</i>				
-	Growth, spread, competition	Multiple ^e	Invertebrates	Dunstan and Johnson (2005, 2006)
-	Foodweb	Multiple ^f	Invertebrates	Castillo et al. (2000)

(continued)

Table 4.2 (continued)

Invasion aspects	Physical and biological processes	Invader	Taxon	References
-	Species persistence	Multiple ^a	Invertebrates	Costello and Solow (2003); Solow and Costello (2004)
-	Species persistence	Multiple ^b	Invertebrates, macroalgae, fish, plants	Wonham and Pachevsky (2006)
^a Wonham et al. (2005b). Model is applied to the marine invertebrates <i>Crassostrea gigas</i> , <i>Crassostrea virginica</i> , <i>Pinctada imbricata</i> , <i>Mytilus galloprovincialis</i> , <i>Ruditapes philippinarum</i> , <i>Rapana venosa</i> , <i>Pacifastacus leniusculus</i> , <i>Carcinus maenas</i> , <i>Eriocheir sinensis</i> , <i>Dikerogammarus villosus</i> , <i>Eurytemora affinis</i> , and <i>Asterias amurensis</i>				
^b Drake et al. (2005). Model is applied generally to ctenophores, copepods, amphipods, decapods, and fish				
^c Grosholz (1996). Model is applied to the marine invertebrates <i>Botrylloides leachi</i> , <i>Carcinus maenas</i> , <i>Elminius modestus</i> , <i>Hemigrapsus sanguineus</i> , <i>Littorina littorea</i> , <i>Membranipora membranacea</i> , <i>Mytilus galloprovincialis</i> , <i>Perna perna</i> , <i>Platyleptus auriformis</i> , and <i>Tritonia plebeia</i>				
^d Kinlan et al. (2005). Model is applied to a number of marine algae and invertebrates, and one fish species				
^e Dunstan and Johnson (2005, 2006). Model represents an epibenthic community in Tasmania, where at least two of the invertebrates (<i>Botrylloides leachi</i> and <i>Watersipora subtorquata</i>) are non-native (Hewitt et al. 2004) but are not singled out for analysis				
^f Castillo et al. (2000). Model represents a soft sediment community in Oregon, USA, which includes the introduced and cryptogenic invertebrates <i>Mya arenaria</i> , <i>Nippoleucon hinumensis</i> , <i>Heteromastus filiformis</i> , <i>Hobsonia florida</i> , <i>Pseudopolydora kempii</i> , and <i>Sireblosipio benedicti</i>				
^g Costello and Solow (2003); Solow & Costello (2004). Model is applied to marine invaders of San Francisco Bay				
^h Wonham & Pachevsky (2006). Model is applied to the marine invaders of the Baltic, Black, Caspian, Mediterranean, and North Seas; the Northeast Atlantic and Northeast Pacific Oceans; Hawai'i and Australia				

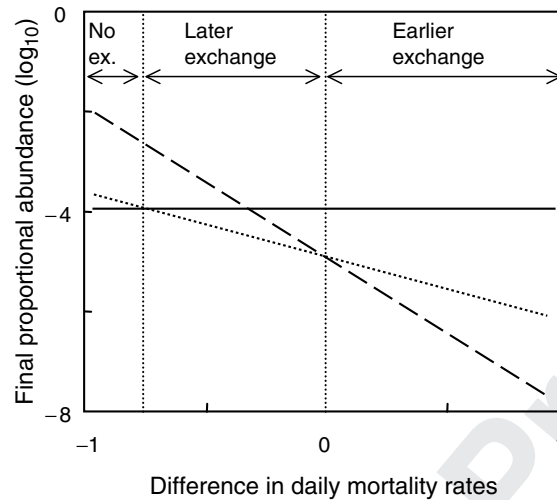


Fig. 4.1 Predicted effectiveness of three ballast-water exchange strategies. The *vertical axis* indicates the final abundance of organisms at the end of a ballast-water voyage, as a proportion of their initial abundance. The *horizontal axis* indicates the difference in a species' daily mortality rates in a ballast tank before and after exchange. Species with broader salinity tolerances would be near 0; those with narrower tolerances would be towards either end. Three scenarios are plotted, showing final abundance given later exchange (*dotted line*), earlier exchange (*dashed line*), and no exchange (*solid horizontal line*). *Vertical lines* separate the three regions in which each exchange strategy minimizes the final organism abundance. Redrawn from Wonham et al. (2005b)

4.3.1 Single-species Models

A dynamic model of a single invading population is generally the central element of an invasion modeling enterprise. Depending on the goal, such models can increase in complexity from simple exponential growth to include negative (intraspecific competition) and positive density dependence (Allee effects). Likewise, they can increase in detail from representing a homogeneous, to an age- or stage-structured, to an individual-based population.

In ecology and conservation, single-species models have been applied particularly effectively to population viability analysis (PVA) of threatened and endangered species (Holmes 2004; Morris and Doak 2003), and more recently to PVA of invasive species (Andersen 2005; Bartell and Nair 2003; McEvoy and Coombs 1999; Parker 2000; Shea and Kelly 1998; Shea and Possingham 2000). Most PVA work has been done with terrestrial species, but notable marine examples include cetaceans and turtles (e.g., Burkhart and Slooten 2003; Crowder et al. 1994). In these instances, single-species models can usefully identify key life stages for management actions. However, lessons learned from fisheries modeling illustrate the

limitations of this isolated approach for modeling and managing complex systems of interacting species, and have led to more detailed multispecies and ecosystem scale modeling of marine systems (e.g., Butterworth and Plaganyi 2004; Fulton et al. 2003; Hollowed et al. 2000).

Only a small handful of marine invasion models use nonspatial single-species approaches alone. Most of these focus on the biological questions of population establishment and its inverse, invasion control. To investigate establishment at the genetic scale, Dew et al. (2003) developed an age-structured algorithm to model the risk of chromosomal reversion and establishment of outplanted triploid Suminoe oysters *Crassostrea ariakensis* in the northwest Atlantic. Barry and Levings (2002) implemented a stage-structured model of the copepod *Pseudodiaptomus marinus* in the northeast Pacific, to evaluate the establishment risk of a single population and of a spatially implicit metapopulation. The life history and component data presented by Rudnick et al. (2005) for the Chinese mitten crab (*Eriocheir sinensis*) could readily be formalized in a similar mathematical model. These models fall at the tactical end of the spectrum, in that they are focused on detailed predictions in a particular system.

Invasion control introduces additional elements into single species models. Ruesink and Collado-Vides (2006) used growth and recruitment data to parameterize a tactical model of the area occupied by the green alga *Caulerpa taxifolia* in the Mediterranean. They then numerically evaluated how the timing of control altered the total occupied area. In a more strategic approach Buhle et al. (2005) constructed and analyzed a matrix population model of the oyster drill *Ocenebrellus inornatus* in the northeast Pacific (Fig. 4.2). They then incorporated the predicted population growth rate into an economic cost-benefit analysis to determine which life stages offered more cost-effective control opportunities (Fig. 4.2). An intriguing spatial extension to these bioeconomic models involves long-term cost-benefit analysis of managing barrier zones adjacent to the population front (Leung et al. 2002; Sharov 2004; Sharov and Liebhold 1998) – an approach that could be applied to marine invasions as well.

There are many methods available for attempting invasion control, including physical, chemical, and biological means. In a single-species model, the control element can be formulated to represent the removal of a certain number or proportion of individuals. As such, it is analogous to the harvest element in simple fisheries models, and it best represents the effects of physical or chemical control. To model biological control, with feedback between the invader and the control species, takes us into the realm of multispecies models.

4.3.2 Multi-species Models

A number of classical modeling frameworks for species interactions, which have proved useful in developing ecological theory in general, have also been applied to understanding invasions. These include Lotka-Volterra competition models,

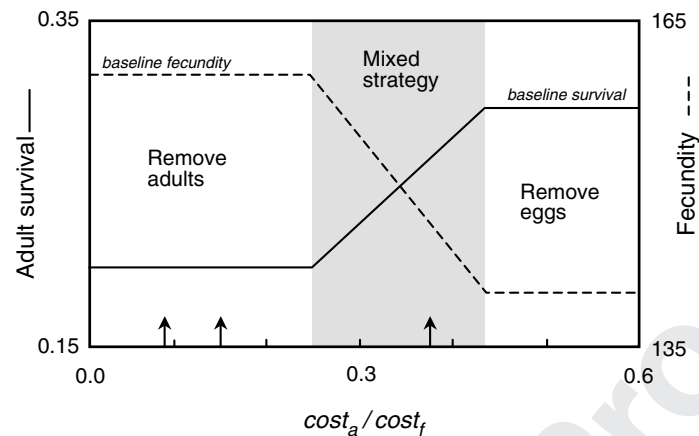


Fig. 4.2 Optimal control strategy determined from a bioeconomic model of invasive oyster drills, *Ocenebrellus inornatus*. The x -axis shows the ratio of costs of the same proportional reduction in adult survival and fecundity. The y -axes show the optimal target values for adult per capita survival (left axis) and fecundity (right axis) for controlling the invader. In this instance, the baseline adult survival probability is 0.3, and the baseline fecundity is 160 surviving offspring per adult. When removing adults is much cheaper than removing egg capsules ($\text{cost}_a \ll \text{cost}_f$), the optimal control strategy is to remove adults only, reducing survival to ~ 0.20 . When the cost of removing adults begins to approach that of removing eggs, the optimal strategy becomes removing eggs only, reducing fecundity to ~ 140 . At intermediate $\text{cost}_a/\text{cost}_f$ values, the optimal control strategy is a mixed one of removing both adults and eggs. Arrows indicate empirically estimated values of $\text{cost}_a/\text{cost}_f$ from different sites. Redrawn based on Buhle et al. (2005), and E. Buhle, personal communication to MJW

Volterra predation models, Nicholson-Bailey host-parasitoid models, Kermack-McKendrick epidemiological models, and their extensions and generalizations. (For an introduction to these models and their application to invasions, see Shigesada and Kawasaki 1997.)

In their simplest and most strategic formulations, these models remain theoretically tractable, and stability analysis can provide general insights into ecological invasion processes. Two particular biological questions can readily be addressed with these models: the ability of a species to invade an equilibrium population of one or more other species, and the impacts of its invasion on that equilibrium.

Generally, however, this strategic approach does not suffice to represent detailed processes of species interactions, or the combined interactions of a group of species at a community or ecosystem scale. As a result, many multispecies models of specific invasion systems move away from these classical strategic approaches to more detailed tactical formulations. Two marine invasion examples illustrate the interplay between these approaches.

Pathogen invasions are increasingly being reported from marine systems (e.g., Harvell et al. 1999), but classical epidemiological modeling (Anderson and May 1991; Kermack and McKendrick 1927) has rarely been applied to these diseases. However, certain long-established epidemiological models, known generally as *S-I* or Susceptible-Infectious models, have an impressive history of contributing to the understanding of infectious disease dynamics and control (Anderson and May 1991; Kermack and McKendrick 1927).

A series of three *S-I* models of phocine distemper virus (PDV) outbreaks in the northeast Atlantic illustrate a generally strategic approach (De Koeijer et al. 1998; Grenfell et al. 1992; Harding et al. 2002, 2003; Heide-Jørgensen and Härkönen 1992; Loneragan and Harwood 2003). Admittedly, PDV can perhaps only tangentially be considered a marine invasion, as its transmission is airborne. We mention it here since it can play a significant role in marine mammal population dynamics, and it illustrates an important class of models that can be applied to invasive infectious diseases.

These three PDV models illustrate how the same epidemic may be modeled using very different infection dynamics (mass action vs frequency dependent incidence functions), different treatments of time (continuous vs discrete), and different treatments of uncertainty (deterministic vs stochastic). One prediction from the first of these models was that another outbreak would not occur until the seal population had recovered for at least ten years after the 1988 outbreak (Grenfell et al. 1992). Indeed, a second outbreak occurred in 2002, prompting further modeling to explore the potential impact of recurring outbreaks on the population (Harding et al. 2002, 2003; Loneragan and Harwood 2003).

The second example is the invasion of the Black Sea by the comb jelly *Mnemiopsis leidyi*, which has been investigated with models that range from the strategic to the tactical. At the strategic end is a generic nutrient-phytoplankton-zooplankton (N-P-Z) model developed by Morozov et al. (2005) to investigate the impacts of adding a top predator to a marine plankton community. Although this exercise was motivated by the example of *Mnemiopsis*, its strategic generality makes it applicable, at least conceptually, to any such invasion.

Knowler (2005) took a somewhat more complex and detailed approach to developing a bioeconomic model of the impacts of *Mnemiopsis* on the Black Sea anchovy fishery. This study combined a Ricker stock-recruitment model of the anchovy population with a balance model of *Mnemiopsis* biomass and an economic cost-benefit model. It then used analytical methods to determine the optimal anchovy harvest policy in the post-invasion system.

At the tactical end of the spectrum is the mass balance model developed by Gucu (2002) to investigate factors contributing to the establishment of *Mnemiopsis*. This approach used the software package ECOPATH to develop a steady state model of the Black Sea marine ecosystem before and after the *Mnemiopsis* invasion. This detailed model helped visualize the differences in food web structure correlated with overfishing, eutrophication, and the subsequent comb jelly invasion (Gucu 2002).

An additional five case studies further highlight the difference in approach between simpler strategic and more complex tactical approaches to multispecies models of marine invasions. Hedrick (2001) used a very general algebraic framework to determine the invasion criteria and fitness impacts of transgenes. The model was developed nominally to consider competition between wild type and transgenes in coho salmon, for which reason we include it in our treatment of marine multispecies (or in this case, multigene) invasions, but it could apply broadly to transgene invasions from genetically modified organisms in any system (Hedrick 2001).

Also at the genetic level, Hall et al. (2006) developed a model of the population dynamics and genetics of hybridization between the Atlantic cordgrass *Spartina alterniflora* and its native congener, *S. foliosa*, in the northeast Pacific. Interestingly, they found that even without a selective advantage, the hybrid increased at the expense of the native and introduced genotypes (Hall et al. 2006).

To study a competitive interaction in detail, Byers and Goldwasser (2001) modeled the impact of the introduced mudsnail *Batillaria attramentaria* on a similar native species in the northeast Pacific (Fig. 4.3). They constructed an individual-based simulation model of the two snails and their respective resource conversion, parasitism, and mortality rates. The model was parameterized and validated with extensive field data, and then used to rank *Batillaria*'s competitive advantages and to predict the native snail's time to extinction (Fig. 4.3).

At an ecosystem scale, Pranovi et al. (2003) developed a complex, numerical mass balance model of the Manila clam *Venerupis (=Tapes) philippinarum* in the Venice lagoon. The clam has become an important commercial species, and is harvested with mechanical dredges that disturb the bottom sediments and associated community. In the so-called *Tapes* paradox, the clam is more abundant inside than outside fished areas. The model suggested that these positive feedback effects were somewhat limited, and predicted the degree to which eliminating the commercial clam harvest would increase the trophic level, total catch, and market value of the lagoon's other artisanal fisheries (Pranovi et al. 2003).

Finally, Frésard and Boncoeur (2006) conducted a cost-benefit analysis of controlling the slipper shell *Crepidula fornicata* on stocked commercial scallop beds in the northeast Atlantic. The costs of *Crepidula* to the fishery are direct, in that it must be removed from the shells of harvested scallops, and indirect, that it preemptively outcompetes settling scallops. The direct costs were estimated from the time devoted to scallop removal. In the absence of a *Crepidula* population dynamics model, and of competition coefficients between *Crepidula* and the scallops, the indirect costs were represented simply as a fixed reduction in harvestable area (Frésard and Boncoeur 2006). Thus, this model explores the impact of an invader on another species without explicitly having to model the population dynamics of either.

All the single and multispecies models considered thus far have been nonspatial, or have treated space implicitly. In the next section, we consider invasion models that incorporate space explicitly in one, two, or three dimensions.

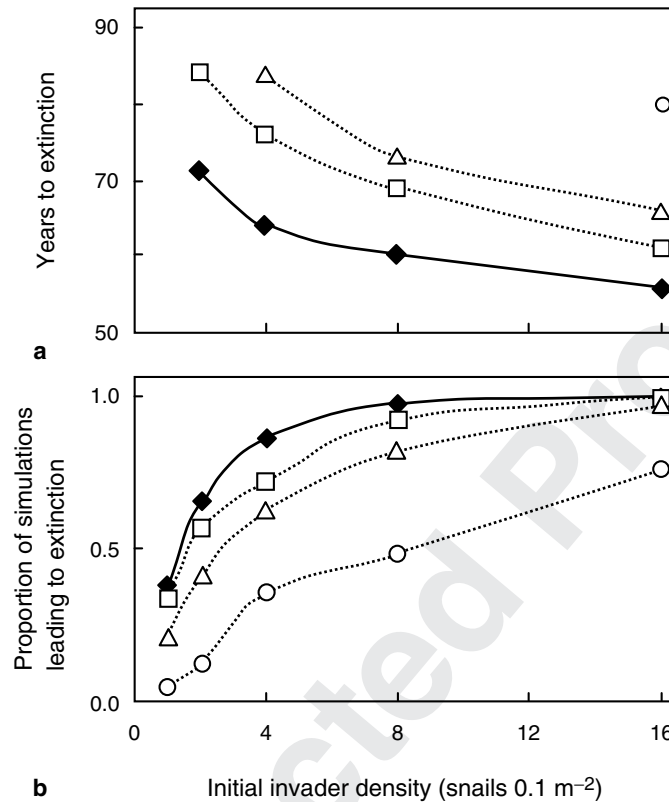


Fig. 4.3 Predicted impacts of the non-native mud snail *Batillaria attramentaria* on the native mud snail *Cerithidea californica*, based on a simulation model. **a** Median predicted years to extinction of the native snail after initial introduction of the invader at different densities. **b** Proportion of simulations that resulted in extinction of the native snail within 90 years. Outcomes shown for four scenarios: interspecific differences in parasitism and competition as observed in the field (*diamonds*), parasitism rates set equal for the two species (*squares*), competition parameters set equal (*triangles*), and both set equal (*circles*). In the last case, no median values are shown for lower invader densities in A because <50% of simulations led to extinction. Redrawn from Byers and Goldwasser (2001)

4.4 Population Models: Invasion Spread

A substantial proportion of the modeling work on invasions to date has focused on the rate at which the invader spreads. Marine environments, where the habitat itself is in motion, provide additional challenges for modeling spatial spread. We will first present models of a single invader spreading alone, followed by spatial models that incorporate multispecies interactions.

4.4.1 *Single-species Models*

The now-classic Fisher equation for modeling spread was originally developed to represent the spread of advantageous alleles through a population, and assumed logistic growth and random movement via diffusion (Fisher 1937). It was later adapted by Skellam (1951) to model the spread of invasive species, assuming exponential growth and diffusion. Both models lead to the same compact formula for the rate of spread, expressed in terms of the population's intrinsic growth rate and its so-called diffusion coefficient, which can be interpreted as measure of spatial movement (for details and extensions, see Shigesada and Kawasaki 1997).

The appeal of Fisher's formula lies not only in its simplicity, but also in the possibility of validation. Intrinsic growth rates and diffusion coefficients can be estimated from life history tables and mark-recapture studies, allowing spread rate predictions to be tested against historical data. This validation approach was pioneered by Andow et al. (1990) for terrestrial species. Here, Fisher's diffusion formula generally holds up well, although it tends to underestimate spread for invaders that exhibit long-distance non-diffusive jumps in space. For model extensions that incorporate such jumps using integrodifference equations (Kot et al. 1996; Neubert and Parker 2004; Lewis et al. 2005).

Marine and aquatic habitats differ notably from terrestrial ones in that they move on a relatively short timescale. Indeed, several recent reviews have highlighted the particular challenges of studying and modeling dispersal, particularly of larvae, in these systems (Kinlan et al. 2005; Kinlan and Hastings 2005; Levin 2006; Lutscher et al. 2005; Shanks et al. 2003; Siegel et al. 2003). These studies have emphasized the importance of local and regional hydrology and geomorphology, as well as larval physiology and behaviour, in influencing organism dispersal and spread.

Given the mobile nature of the habitat, we might expect simple diffusion models to perform poorly for most marine species. Specifically, we would expect them to underestimate downcurrent and overestimate upcurrent spread rates. Advection-diffusion models, which incorporate unidirectional current flow as well as diffusive spread, might be expected to work better. Advection rates would be expected, intuitively, to conspire with larval planktonic duration to influence a species spread rate: the longer an organism is in its planktonic stage, the farther it can spread, so the faster its invasion can progress.

However, the empirical relationship between larval duration and invasion rate has proved stubbornly elusive (Fig. 4.4) (Grosholz 1996; Kinlan et al. 2005). Nevertheless, both reaction-diffusion and advection-diffusion models have been developed based on larval duration (Grosholz 1996, Kinlan et al. 2005). Given the empirical observations, it is perhaps not surprising that these models have had negligible predictive power – curiously, though, they have an interesting tendency to overpredict spread rates for marine invertebrates and underpredict those for marine algae (Grosholz 1996, Kinlan et al. 2005).

This result leads us to ask what other factors could be at work to influence marine invasion spread rates. Likely candidates for slowing invasion rates are Allee

effects and negative interspecific interactions, which are discussed in Sects. 4.4.2 and 4.4.3. Candidates for speeding up invasion rates are human-mediated transport, models which we discussed in Sect. 4.2, and positive interspecific interactions, which we mention briefly in Sect. 4.5. It is also important to consider that a species' spread rate may differ in different directions, and that models may have to be parameterized carefully to capture and predict this variation (e.g., Krkošek et al. 2007; Lubina and Levin 1988).

Although advection-diffusion models may not predict marine invasion rates very successfully, they may still provide insight into possible routes of organism transport. In this way, Johnson et al. (2005) used a modified surface advection component of the three-dimensional Princeton Ocean Model to hindcast possible sources of a jellyfish *Phyllorhiza punctata* bloom in the Mississippi Bight.

Similarly, Parry et al. (2001) modeled the dispersal of the sea star *Asterias amurensis* larvae, using an existing three-dimensional advection-diffusion model of Port Phillip Bay, Tasmania. The model predicted an overall *Asterias* distribution consistent with observed records, and local-scale incongruities were attributed to possible differences in predation pressure.

Viard et al. (2006) used a two-dimensional advection-diffusion model of the English Channel to predict the degree of larval slipper shell (*Crepidula fornicata*) exchange between populations. They found no correlation between predicted larval exchange and the observed genetic distance between populations, indicating high gene flow among populations.

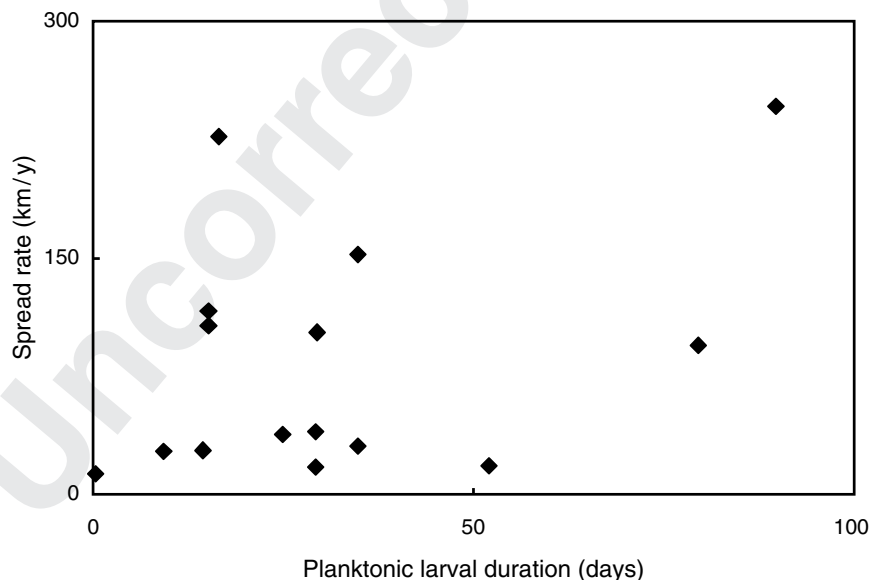


Fig. 4.4 Observed spread rates of marine invertebrate invaders as a function of observed planktonic larval duration. Redrawn from Kinlan et al. (2005)

Using a novel modeling approach, Inglis et al. (2006) combined a particle diffusion model with two different statistical habitat models to predict the distribution of bivalves *Theora lubrica* and *Musculista senhousia* in a New Zealand harbour. The diffusion component significantly improved the fit and accuracy of the habitat suitability index model, but only marginally improved the environmental regression model, and the improvement was more pronounced for *Theora* than for *Musculista* (Inglis et al. 2006).

4.4.2 Allee Effects

One mechanism that is well known to slow observed spread rates in terrestrial systems is an Allee effect (Hastings 1996). The hallmark of Allee dynamics is positive density dependence at low population levels. In other words, very small populations have lower per capita growth rates than slightly larger ones (Allee 1931; Gascoigne and Lipcius 2004). Demographic Allee effects – known in the fisheries literature as depensatory mortality – are likely to be particularly relevant at the establishment stage of a biological invasion.

In marine populations, Allee effects could arise from a wide range of mechanisms, and could be exacerbated or mitigated by the role of currents and eddies in dispersing or aggregating individuals. Although the empirical evidence for Allee effects in marine populations remains mostly indirect (Gascoigne and Lipcius 2004; Hutchings and Reynolds 2004), the potential interaction between harvesting and Allee effects (Gascoigne and Lipcius 2004; Hutchings and Reynolds 2004; Lundquist and Botsford 2004) suggests that invasion management actions could exploit Allee thresholds in controlling unwanted invaders.

An Allee effect is considered strong if the per capita growth rate becomes negative at a small population size, and weak if the growth rate decreases but remains positive. Mathematical extensions of Fisher's equation, in which logistic growth is replaced with Allee dynamics, make two predictions. First, both weak and strong Allee dynamics give rise to a slower invasion speed than the original model. Second, when Allee dynamics are strong, the initial colonization of invaders must exceed a threshold in both density and spatial extent if the invasion is to succeed (Kot et al. 1996; Lewis and Kareiva 1993; Wang and Kot 2001).

Allee effects have been shown empirically to play a role in the *Spartina alterniflora* invasion of the North American Pacific coast. This Atlantic cordgrass spreads rapidly across intertidal mudflats, filling in behind the invasion front to create dense meadows. The fecundity of individual *Spartina* is orders of magnitude higher for plants in established meadows than for isolated plants, which are limited by pollen availability and have reduced seed production. This leads to weak Allee dynamics. Taylor et al. (2004) developed and parameterized a spatially-explicit stochastic simulation model and a spatially-implicit deterministic model of this invasion in Willapa Bay, USA. By running the models with and without the Allee dynamics, they showed that even though the Allee effect is defined as weak, its effects are

dramatic, almost halving the predicted spread rates (Fig. 4.5). From simulations, the Allee dynamics were deduced to confer heightened sensitivity of spread rates to the level of self-fertilization (Taylor et al. 2004).

Taylor and Hastings (2004) investigated the effectiveness of barrier zones for controlling the *Spartina alterniflora* invasion in the same location. They asked whether it was more efficient to prioritize removal of young, low-density outlier areas at the edge of an invasion, or older core population meadows. Their results indicated that *S. alterniflora* eradication was only possible if control of the faster growing low-density plants was prioritized. The most effective strategy, however, which would also require more resources, was to target the older core population areas as well. This was because, under the Allee dynamics seen in *Spartina*, eliminating high-density meadows lowered the risk of new propagule production far more than eliminating the lower-density outlying plants (Fig. 4.5).

Working in the same invasion system, Cuddington and Hastings (2004) developed a *Spartina alterniflora* spread model that included positive feedback dynam-

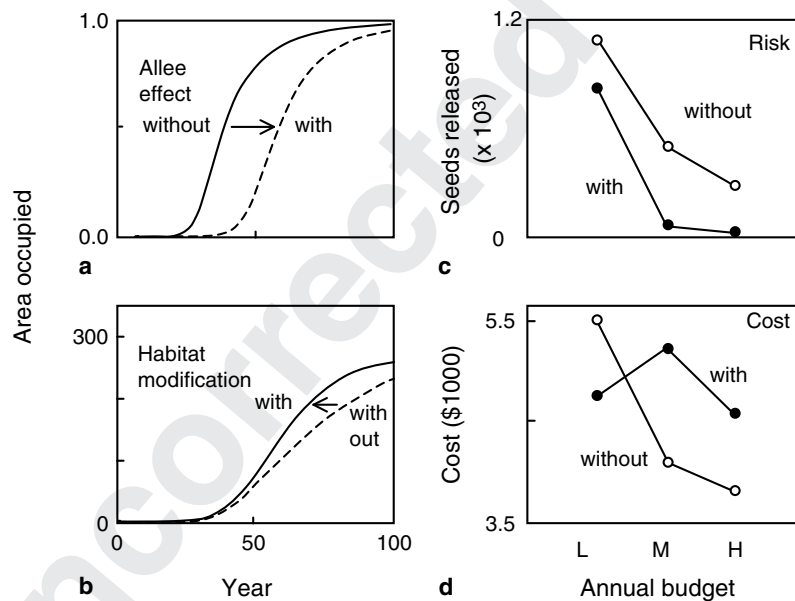


Fig. 4.5 Modeling analyses of the cordgrass *Spartina alterniflora* invasion. **a** Results of a simulation model showing that the empirically-observed Allee effect slows the rate of *Spartina* spread. Redrawn from Taylor et al. (2004). **b** Model results illustrating that habitat modification by spreading *Spartina* speeds up its invasion. Redrawn from Cuddington and Hastings (2004). **c** Predicted risk (thousands of potentially escaping seeds) associated with optimal *Spartina* control strategies, given low, medium, and high annual budgets, for a model with and without an Allee effect. Risk decreased with increasing budget, and when the Allee effect was incorporated. **d** Predicted cost (thousands of USD) for the same model. Allee effects led to cheaper eradication at a low budget, but more expensive eradication at higher budgets. Redrawn from Taylor and Hastings (2004)

ics driven by habitat engineering. As *Spartina* stands develop, they reduce water flow, trapping sediments and elevating the substratum into and eventually above the intertidal zone. In this way, the plant increases its available habitat. The model linked the area occupied by the invader and the distribution of habitat quality in a spatially implicit system of ordinary differential equations. The results illustrated that an engineer may enhance or reduce its own growth and spread rates, depending on the initial habitat quality distribution and the rate of habitat modification (Cuddington and Hastings 2004). Although this model is not explicitly spatial, we introduce it here because the positive feedback process shows intriguing similarities to Allee effects, in both its density dependence and its qualitative impacts on population spread (Fig. 4.5).

In a more general approach, Drake et al. (2005) developed a reaction-diffusion model with Allee dynamics to explore the chance of establishment for a range of planktonic marine organisms released from ballast water. Using this model, they found that for a given level of invasion risk, the acceptable release volume was far more sensitive to variation in the intrinsic rate of population growth than to variation in the strength of the Allee effect.

All the spread models treated so far are process oriented, in that specific terms represent movement, growth, reproduction, mortality, dispersal, and so forth. This makes it possible to evaluate the importance of each process in the invasion outcome. By way of contrast, if one is simply interested in forecasting a particular invasion, a less mechanistic approach can be used. For example, the goal of one series of papers was to predict the expansion of the invasive green alga *Caulerpa taxifolia* in the Mediterranean Sea (Aussem and Hill 1999, 2000; Hill et al. 1998).

Initially, a stochastic discrete event simulation model of the algal spread was developed and integrated with GIS habitat data (Hill et al. 1998). However, this model proved too computationally intensive to investigate the effects of various environmental variables, such as bathymetry, substrata and resident species, on the invader's spread. Accordingly, the authors developed a neural network metamodel designed to approximate the original simulation model but be more computationally efficient (Aussem and Hill 1999, 2000).

The neural network was trained by having it form rules connecting input (environmental variables) with output patterns (algal spread). The model was then tested by having it predict a sequence of historical spread independent of the data used to train the network, and was found to forecast accurately (Aussem and Hill 1999, 2000). Unlike the first and more mechanistic model, the *Caulerpa* metamodel is more phenomenological, in that the network rules do not necessarily have a biological interpretation. Both *Caulerpa* models are more tactical than strategic, in that accurate prediction rather than general insight is the goal.

Single-species spread models can incorporate aspects of the physical environment, such as advection, and intraspecific dynamics, such as Allee effects. However, no invader establishes in a vacuum: all interact to a greater or lesser extent with resident species, and some are targeted for biological control. This brings us to the next section, in which we consider multispecies models of marine invasion spread.

4.4.3 Multi-species Models

Spatial multispecies models allow interspecific interaction dynamics to play out while species are dispersing across a domain via diffusion and advection. Many of the invasion systems studied with these models are extensions of nonspatial dynamics, derived by simply including diffusion and/or advection terms in the equations.

Lotka-Volterra competition dynamics have been extended to include random motion via diffusion, and used to model the spatial spread of one competitor into another's territory. The result is a system of nonlinear coupled reaction-diffusion equations. An early application of this model was to the spread of larger, introduced grey squirrels into areas occupied by native red squirrels in the United Kingdom (Okubo et al. 1989). Here a simple and compact formula, similar to that for Fisher's equation, was constructed. This formula described the predicted speed at which grey squirrels spread into, and displaced, the red squirrels, and could be calculated in terms of relative growth rates, competition coefficients and diffusion coefficients. Okubo et al. (1989) then measured the rates and coefficients and compared the predicted and observed spread rates, showing that they correlated closely. With both advection (unidirectional flow) and diffusion (random motion) included, competition models have been extended to aquatic systems, where they have been used to study mechanisms for species coexistence in river ecosystems (Lutscher et al. 2007).

Multispecies predator-prey models that include diffusion can be used to predict the rate of spread of an invasive predator into a native prey population, or, alternatively, the rate at which an invasive prey species can facilitate the spread of a predator that consumes it (Owen and Lewis 2001). This latter scenario has been analyzed in the context of biocontrol. If an invasive pest (prey) is spreading into a new environment, will a biocontrol agent (predator) be able to catch up to it and control its spread? Fagan et al. (2002) showed how to use coupled reaction-diffusion models to predict the biocontrol species attributes needed to catch up to the prey and control it effectively. Behind an invasion front, spatial predator-prey dynamics can become extremely complex and patchy. This phenomenon has been researched widely (Sherratt et al. 1997), and includes the patchy distribution of phytoplankton and fish in marine systems (Medvinsky et al. 2002) or virally infected phytoplankton (Malchow et al. 2004).

As with the models considered above, most of the marine invasion systems studied with spatial models are extensions of nonspatial models we have already considered, including those for phocine distemper virus (PDV), *Mnemiopsis leidyi*, and *Caulerpa taxifolia*. Additional models treat the effects of increased filter feeding by the introduced annelid *Sabella spallanzani*, and the indirect effects of non-native farmed Atlantic salmon, *Salmo salar*.

The spatial spread of the 1998 PDV outbreak was modeled by Swinton et al. (1998), using an *S-I* type model distributed across a patchy network of seal subpopulations. The authors found that the persistence of the epidemic depended on the number of patches when the patches were weakly coupled, and on the size of the patches when they were tightly coupled. They concluded that the 1988 outbreak

died out because smaller, tightly coupled seal subpopulations could not sustain the infection (Swinton et al. 1998).

Three multispecies extensions of *Mnemiopsis* population modeling take a very different approach, coupling complex bioenergetic and hydrodynamic models to study the comb jelly invasion dynamics (Berdnikov et al. 1999; Oguz et al. 2001; Volovik et al. 1995). The goal of these models was to capture the observed pelagic foodweb dynamics before, during, and after the *Mnemiopsis* invasion. These tactical models, implemented as complex algorithms, are amenable to numerical but not analytical study. The models were assessed by qualitatively comparing their predictions to empirical data.

In a multispecies extension of *Caulerpa* spread models, Coquillard et al. (2000) focused on the potential reduction of the alga by the grazing ascoglossan *Elysia subornata*. In general, when biocontrol agents are introduced, a first objective is to optimize the release strategy to maximize the establishment of the agent (Shea and Possingham 2000). Another is to reduce the target species significantly by affecting vulnerable life-history stages (Shea and Kelly 1998). For a spreading invader, a third objective is to choose a control agent that will spread as quickly as the invader itself (Fagan et al. 2002). In the *Caulerpa-Elysia* model, all three objectives were analyzed by combining laboratory data and a spatially-explicit age-structured algorithmic model of the mollusc's growth to determine the optimal size, time, and age, and number of releases for effective algal control (Coquillard et al. 2000).

Murray and Parslow (1999) developed a detailed bioenergetic and hydrodynamic model of Port Philip Bay, Australia. The model was used to consider the impacts of a number of environmental changes including nutrient loading and species invasions. As an example, the authors evaluated the potential impacts of the introduced annelid *Sabella spallenzani* by simulating an increase in filter-feeder biomass in the bay.

Finally, even without establishing in the wild, a non-native species can affect the community into which it is placed. For example, non-native farmed salmon, *Salmo salar*, serve as resident year-round hosts of parasitic sea lice in British Columbia estuaries (Krkošek et al. 2005). A spatially explicit model of sea lice population growth on migrating juvenile salmon migrating past fish farms showed that farm hosts greatly amplified the natural infection levels and therefore juvenile salmon mortality (Fig. 4.6) (Krkošek et al. 2005, 2006).

In the previous two sections, we have looked at models that focus on an invading species and its establishment, spread, impacts, and control. The next section treats invasions from the community perspective, and examines models that focus on the dynamics of invasion success in different communities over space and time.

4.5 Community Invasibility Models

Spatial and temporal questions of community invasibility can be read, generally,

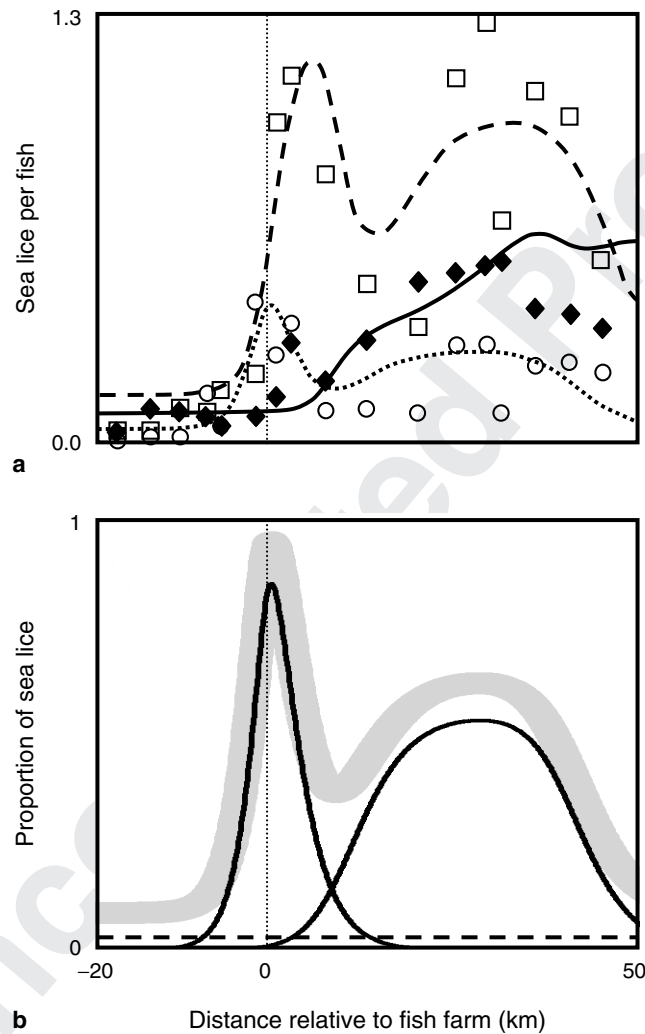


Fig. 4.6 Impacts of non-native farmed salmon, *Salmo salar*, on native host-parasite dynamics. **a** Observed (points) and predicted (lines) number of sea lice per native juvenile pink salmon along a coastal British Columbia migration route. Sea lice life stages are early juveniles (circles, dotted line), late juveniles (squares, dashed line), and adults (diamonds, solid line). **b** Planktonic distribution of sea lice early juveniles inferred from model. Horizontal dashed line is natural background lice level. Solid black lines are first generation (left) and second generation (right) lice originating from farm. Thick gray line is total early juvenile abundance in the plankton. Vertical dotted lines indicate farm location. Redrawn from Krkošek et al. (2005)

under the longer-running ecological discussion of the connection between species diversity and community stability – both variously defined (e.g., Drake 1990; Post and Pimm 1983). In the invasion literature, this area has developed primarily as a discussion of community diversity and resistance to invasion – which can also be framed as a community's ability to repel or accommodate an invader, or as the likely success of an invader). The question of resilience in the face of invasion – which can also be framed as the scale of an invader's impact – has generally been treated separately in empirical work, but often simultaneously in modeling work.

Empirical studies, primarily in terrestrial plant communities, have led to a number of related conceptual models of the relationships among species richness, resource availability, disturbance, and invasibility (for recent reviews, see Davies et al. 2005; Richardson and Pysek 2006; Shea and Chesson 2002; Stachowicz and Byrnes 2006). Most of the abstract mathematical models exploring these relationships have focused on single-trophic level competitive interactions (Byers and Noonburg 2003; Case 1990, 1991; Hewitt and Huxel 2002; Melbourne et al. 2007; Mitchell et al. 2006; Rouget and Richardson 2003; Tilman 2004) and neutral dynamics (Fridley et al. 2004; Herben et al. 2004).

In marine systems, these questions have been investigated in a combined empirical and modeling study focused on competitive interactions in a marine fouling community (Dunstan and Johnson 2005, 2006). A spatially explicit individual-based model was parameterized with field data on growth, recruitment, and competitive interactions among 13 species in Tasmania, of which at least 3 were non-native (Hewitt et al. 2004). Community invasibility was defined in terms of species recruitment, whether native or non-native. The authors found that the relationship between species richness and invasibility was strongly mediated by the size of the patch being invaded. Larger patches had a more stable community composition over time, leading to less free space, and therefore lower recruitment and higher invasion resistance (Dunstan and Johnson 2006).

Compared to invasion resistance, comparatively few models have addressed the question of resilience, i.e., a community's response to invasion. Analytical exceptions are the patterns of resident species extinction reported for some community assembly models (Case 1990, 1991), and the biotic homogenization models developed in the context of freshwater fish invasions (Olden and Poff 2004).

In a marine case study, Castillo et al. (2000) constructed and analyzed a series of guild models of a soft-bottom invertebrate assemblage in the northeast Pacific. They found that for most of the models, the net feedback strength of the intertaxon interaction matrix was low, indicating that these systems would be expected neither to move away from nor return to an equilibrium following a perturbation. The authors therefore suggested that this community was particularly able to accommodate the addition of invaders without experiencing species losses (Castillo et al. 2000).

One result that has emerged from both empirical and modeling approaches is the importance of spatial scale and invasion scenario in detecting and interpreting patterns of invasion resistance (Byers and Noonburg 2003; Hewitt and Huxel 2002). Since these empirical and theoretical approaches have so far primarily addressed single trophic level and competitive interactions, it would be interesting to evaluate

them, along with the related question of resilience, in the more complete context of a multi-trophic system.

Temporal patterns in the accumulation of invaders were initially highlighted by the striking marine example of San Francisco Bay (Cohen and Carlton 1998). Subsequent empirical and conceptual work connected this trend to the ideas of biotic resistance resulting from negative interactions, and invasional meltdown resulting from positive interactions (Ricciardi 2001; Simberloff and Von Holle 1999). Recent modeling has shown, however, that the observed pattern of acceleration in invasion numbers can be accounted for without any necessary increase in invasion rate or invasibility (Fig. 4.7) (Costello and Solow 2003; Solow and Costello 2004; Wonham and Pachevsky 2006). When null models reproduce observed patterns, it does not mean that other processes are not occurring. Rather, null models illustrate the patterns that would be expected in the absence of those processes, giving us a benchmark against which to compare empirical data.

4.6 Summary and Future Directions

The incorporation of modeling into the study of marine biological invasions is relatively recent, and holds exciting promise. In the sections above, we have touched on the range of existing marine invasion models. In this section, we briefly consider three areas that seem especially rich for future development.

4.6.1 Formalizing Conceptual Models Mathematically

The study of invasions has been characterized by an independent development of concepts and mechanisms that can, in many cases, be aligned with more general ecological concepts (e.g., Shea and Chesson 2002; Tilman 2004). On a broad scale, key invasion concepts of propagule pressure, species invasiveness, and community invasibility have largely been treated separately from each other in invasion biology. (For recent broad reviews, see Davies et al. 2005; Hails and Morley 2005; Melbourne et al. 2007; Mitchell et al. 2006; Richardson and Pysek 2006; Rouget and Richardson 2003; Shea and Chesson 2002; Stachowicz and Byrnes 2006; Tilman 2004.)

Recent invasion models, focused primarily on terrestrial plant systems, have offered general mathematical frameworks that begin to unite these concepts: Rouget and Richardson (2003) combined propagule pressure with environmental factors, Tilman (2004) connected success to resource competition, Mitchell et al. (2006) combined the effects of both abiotic and biotic factors, and Melbourne et al. (2007) examined the effects of a heterogeneous environment on the outcome of competition. More generally, ecological modeling that couples species dispersal

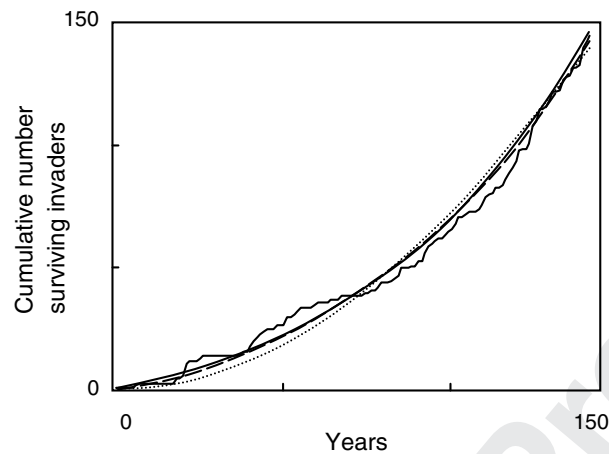


Fig. 4.7 Three different models capture the shape of the cumulative number of surviving invaders introduced into San Francisco Bay since the mid-1800s (*solid jagged line*). Predictions from a model incorporating introduction rate and discovery probability, for an increasing (*dashed curve*) and constant (*dotted curve*) introduction rate redrawn from Solow and Costello (2004). Predictions from a model incorporating introduction rate and survival probability, given constant introduction rate and constant survival probability (*solid curve*) redrawn from Wonham and Pachepsky (2006)

and species coexistence may be brought to bear on the problem of invasions (e.g., Fox and Srivastava 2006; He et al. 2005; MacArthur and Wilson 1967).

Mechanistic hypotheses toward explaining these general concepts include the influence on species establishment of propagule abundance, frequency, and quality, the influence on invasiveness of inherent traits, minimum residence time, enemy release, evolution of increased competitive ability, long distance dispersal, phenotypic plasticity, genetic drift, inbreeding, and hybridization for species invasiveness, and the influence on community invasibility of resource availability, disturbance, diversity, mutualisms, competition, predation, indirect interactions, spatial and temporal heterogeneity, and niche opportunities for community invasibility.

As invasion concepts are synthesized with each other and with classical ecology, they become increasingly amenable to formalization and testing through mathematical modeling. General ecological modeling that connects dispersal to species coexistence could also be brought to bear on the specific problem of invasions. For example, the nature and significance of propagule pressure (Colautti et al. 2006) has parallels in recruitment limitation and source-sink dynamics (e.g., Connolly et al. 2001; Levins 1969, 1970) which recent conceptual and mathematical syntheses can help explore (e.g., Amarasekare and Nisbet 2001; Hanski and Gaggiotti 2004; Holyoak et al. 2005). Patterns of invasion resistance and invasional meltdown (Elton 1958; Simberloff and Von Holle 1999) may be driven in part by the underlying processes of facilitation and inhibition first synthesized in classical

succession dynamics (Connell and Slatyer 1977); recent modeling has scratched at the surface of these concepts and provides a framework that could be developed to explore these connections more explicitly (Costello and Solow 2003; Solow and Costello 2004; Wonham and Pachepsky 2006). It would be very interesting to explore the parallels between the notion of fluctuating resource availability (Davis et al. 2000), and the conceptual and mathematical formulations of the intermediate disturbance hypothesis (Connell 1978; Roxburgh et al. 2004).

A growing area of mathematical modeling in marine systems treats the design and impacts of marine protected areas (e.g., Gerber et al. 2003; Guichard et al. 2004). In so doing, it considers the problems of species dispersal and persistence, and connects to more general ecological and mathematical theories of minimum viable populations, habitat fragmentation, minimum available suitable habitat, and critical domain size (e.g., Pachepsky et al. 2005; With 2004), all of which apply also to invasion establishment and control. Other models that have provided insight into predicting marine population and community dynamics (e.g., Crowder et al. 1994; Wootton 2004) would be similarly informative in studying marine invasions. The considerable modeling tools developed in fisheries biology concerning harvest management (e.g., Kritzer and Sale 2004; Rose and Cowan 2003) could provide further insight into marine invasion control strategies.

4.6.2 *Coupling Dynamical and Statistical Models*

We have focused here on dynamical mathematical models, but there is a further wealth of statistical modeling of invasion patterns and processes. A number of examples concerning invasion transport and establishment illustrate ways in which these two modeling approaches could be coupled.

Statistical invasion risk analysis is extensively developed in the terrestrial realm, where it informs the International Plant Protection Convention, the international agreement on Sanitary and Phytosanitary measures, and numerous other international, national and regional policies regarding intentional and inadvertent imports and releases (Drake and Lodge 2006; Hayes 2003; Holt et al. 2006; Powell 2004; Wilson and Anton 2006). In marine systems (see also Chap. 20, Campbell), statistical risk analysis has been applied to organism transport in and on commercial and recreational vessels (Floerl et al. 2005, Hayes 2002a, b), and more generally to the accumulation of molluscan invaders, both terrestrial and marine, in the US (Levine and D'Antonio 2003). Any of these statistical frameworks could incorporate the kind of dynamic population modeling described in Sect. 2. Hayes (1998) outlines how this dual approach might be developed and the conceptual framework developed by Landis (2003) for green crab *Carcinus maenas* risk assessment would be amenable to this kind of mathematical formalization.

Statistical models of morphological and genetic population data (e.g., Bolton and Graham 2004; Daguin and Borsa 2000; Geller et al. 1997) and invader traits (e.g., Kolar and Lodge 2002; Reichard and Hamilton 1997; Rejmánek and

Richardson 1996) could also be coupled to dispersal models e.g., (Bossenbroek et al. 2001) to identify invasion sources. Recent developments in modeling invasion dynamics as stochastic processes (e.g. Drake and Lodge 2006; Jerde and Lewis 2007; Perrings 2005; Tilman 2004) also hold considerable promise for connecting to statistical analyses and their explicit treatment of uncertainty and variance.

A widely used statistical tool in species range predictions is environmental niche modeling. This approach has developed primarily in the context of predicting climate change impacts in terrestrial systems; there are a few examples of its use in forecasting invasions or describing their impacts (Herborg et al. 2007; Inglis et al. 2006; Peterson 2003; Peterson and Vieglais 2001; Vincent et al. 2006). The coupling of environmental niche modeling to population dynamics models (e.g., Akçakaya 2001; Akçakaya et al. 1995, 2004; Gutierrez et al. 2005), and hydrodynamic dispersal models (Inglis et al. 2006) holds promise for incorporating spatial variation in population dynamics and invasion speeds (e.g., Tobin et al. 2007).

4.6.3 *Integrating Modeling and Empirical Work*

Empirical and mathematical tools provide different kinds of insights into biological invasions. To a certain extent, their independent development can be profitable, but an interactive approach that incorporates both may generate the most understanding and predictive power.

Empirical and mathematical analysis complement and prompt each other in a number of ways. A model may generate a prediction that can be tested in the field, or a field study may generate a result that can be explored mathematically. Extensive empirical data – both observational and experimental – are required to parameterize and validate a model; models can help to synthesize empirical results across systems and scales. In some cases, modeling and empirical work can be combined in a single study, providing greater insight into local dynamics (e.g., Dunstan and Johnson 2005, 2006; Krkošek et al. 2005, 2006). In other cases, modeling may evolve in light of growing field data (e.g. Harding et al. 2002, 2003; Loneragan and Harwood 2003), or the synthesis of data may evolve with continued modeling (e.g., Byers and Noonburg 2003; Davies et al. 2005; Fridley et al. 2004). Neither the data nor the equations are an endpoint: it is the iteration between them that leads to evolution in understanding.

Many of the invasion hypotheses mentioned in Sect. 5.2 have arisen primarily from empirical observation, experimentation, and statistical analysis. Their current and future mathematical analysis holds exciting promise, and will in turn generate new ideas that can be examined again empirically. Marine systems provide additional challenges for both empirical and modeling work, and incorporating their unique elements is essential to a general understanding of marine invasions in particular, and invasion biology in general.

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Appendix

For an introduction to the philosophy and practice of mathematical modeling in ecological systems, we find the texts by Case (1999), Haefner (1996), and Kot (2001) particularly helpful. Morris and Doak (2003) give a very accessible entree into population modeling, and the edited volume of Ferson and Burgman (2003) illustrates statistical and dynamical modeling case studies in conservation biology. For specific focus on likelihood methods applied to model selection, we recommend Burnham and Anderson (1998) and Hilborn and Mangel (1997). For a the mechanics of practical model building and analysis, including thoroughly worked computer exercises, Donovan and Weldon (2001a, b) provide ecology and conservation spreadsheet exercises in Microsoft Excel®, Roughgarden (1998) provides ecological examples and code in Matlab®, and Ruth and Lindholm (2002) investigate marine conservation problems using Stella®.

Uncorrected Proof