Abstract

The ability to estimate dispersal and the subsequent spread of nonindigenous species is important because preventative methods most readily apply to these stages of the invasion sequence. This chapter addresses the development of models of spread for aquatic systems and implications for management decisions. We address several methods used to calculate dispersal kernels for nonindigenous species including natural movement, hydrological, aerial, and anthropogenic dispersal. In particular, we focus on gravity and random-utility models because they are suitable for modeling anthropogenic dispersal among aquatic systems. We then address mechanisms of population spread and link dispersal kernels to models forecasting spread. We compare the merits and data requirements for different models of dispersal and population spread and highlight the application of these models for bioeconomic and management decisions in terms of risk assessment and risk management.

Introduction

Invasions of aquatic ecosystems by nonindigenous species (NIS) are occurring at increasing rates in terms of the number of novel species entering a system (Ricciardi 2006) and the cumulative number of systems or geographic areas that have been invaded (e.g., Veit and Lewis 1996, MacIsaac et al. 2004, Gilbert et al. 2005). NIS are also becoming increasingly important agents in altering ecosystem processes and contributing to the global homogenization of biodiversity (Crooks 2002, Rahel 2002, Olden et al. 2004). Thus, the ability to accurately
forecast spread enables prediction of high risk areas and may lead to management strategies to contain or reduce spread.

NIS movement occurs during two stages of the invasion sequence: the initial transport of propagules from the native region and secondary spread once populations become established in novel habitats (Kolar and Lodge 2001). Management efforts focused on these stages of the invasion process is potentially easier and less costly than mitigation after the invasion has occurred as curbing species dispersal will likely have the greatest impact in determining establishment of the species (Leung et al. 2002, Jeschke and Strayer 2005). As an additional benefit, managers and decision makers will have the widest range of decision options available if their efforts are focused on the initial stage of the invasion sequence (Lodge et al. 2006). Through the identification of mechanisms, pathways and spatially-explicit invasion ‘hotspots’, management efforts become more feasible and cost effective. For example, by distinguishing high-risk sites, forecasts can guide prevention or rapid response efforts at the highest risk sites, while not wasting money on low risk sites. In addition, focusing on dispersal vectors allows for a management strategy applicable to multiple species transported by similar mechanisms as opposed to a strategy specific to each new NIS.

This chapter is divided into 3 sections: dispersal, spread, and risk management. Here, dispersal is defined as the process that describes the movement or redistribution of individuals from one place to another (e.g. Wiens 2001), and spread as the change in population density as a function of space and time. It is important to make this distinction between dispersal and population spread, as models of population spread implicitly address the additional invasion ‘filters’ of habitat suitability and biotic integration into the recipient community (Chapters 4 and 5). First, we address methods used to collect data and to calculate dispersal kernels for different
mechanisms such as animal movement, hydrological or anthropogenic dispersal. We define the dispersal kernel as the probability of an individual moving a specified distance from its last location per unit time, or proportion of the population dispersed within a time interval. In particular, we focus on two methods to describe the dispersal kernel for the anthropogenic transport of NIS: gravity and random-utility models because they are suitable for modeling dispersal among aquatic systems. Second, we address mechanisms of population spread and link dispersal kernels to models forecasting spread. For each section, we also compare the merits of different modeling approaches and data requirements for dispersal models and models of population spread. Finally, we highlight applications of these models for bioeconomic and management decisions in terms of risk assessment and risk management.

<1>Dispersal

Dispersal is an essential component in organismal biology, affecting individual survival and reproduction as well as population and ecosystem level dynamics (Turchin 1998). Dispersal continues to be one of the most studied aspects of ecology and has been fundamental to works on island biogeography, metapopulations and more recently metacommunities (e.g., MacArthur and Wilson 1963, Hanski 1999, Leibold et al. 2004). Depending on the transport mechanism, dispersal patterns are often characterized by two overlapping modes, local and long-distance dispersal. Patterns of local dispersal are frequently observed when the organism disperses under its own power (i.e. walking). Here, range expansion proceeds continuously from the periphery of the population (Shigesada and Kawasaki 2002). Long-term dispersal, on the other hand, is more of a passive process where the organism is transported by vectors such as water currents, wind or through interaction with human movement. In recent years, studies have recognized the importance of long-distance dispersal and have focused on the role of long-distance dispersal on
rates of spread and persistence of populations, dispersal and the genetic structure of populations and natural vs. human-mediated mechanisms (e.g. Okubo 1980, Avise 1994, Suarez et al. 2001, Trakhtenbrot et al. 2005). Understanding long-distance dispersal of nonindigenous species is important because in both theoretical and empirical examples, long-distance dispersal events result in a change from linear to exponential rates of population spread (Lewis 1997). As a consequence, the ability to characterize long-distance dispersal and predict the location of future ‘satellite’ colonies becomes increasingly difficult (Nathan et al. 2003).

Mechanisms involved in the introduction and subsequent dispersal of nonindigenous species can be divided into two major categories: natural and anthropogenic. An understanding of this distinction is necessary when addressing preventative measures of further spread or to apply appropriate educational or legislative management efforts. However, several dispersal mechanisms may be operating simultaneously and interactively for many NIS, thus increasing the number of vectors that need to be assessed and the level of uncertainty involved when forecasting spread. For example, as a byproduct of anthropogenic activity, the quality of habitat (Chapter 7) may also become stressed resulting in increased invasibility.

Natural dispersal

Without human intervention, species may spread under their own power and by the aid of abiotic factors. Life history characteristics of nonindigenous species, such as individual mobility, pelagic larval stages, or the production of resistant resting eggs, lend themselves to natural dispersal. Chance events from abiotic factors, like wind storms or floods, also contribute to the natural dispersal of species across distances far greater than would be possible under individual mobility. Finally, the loss of a restrictive barrier (e.g., glacial ice sheet, waterfall) may allow species to invade a new environment.
Hydrologic dispersal

Hydrologic pathways, such as rivers and streams (i.e. lotic systems), provide a natural mechanism for aquatic species to disperse into connected systems. For example, the planktonic veliger stage of zebra mussels (*Dreissena polymorpha*) has been widely recognized as a key factor in the invasion of entire river systems. After primary introductions, zebra mussel veligers drift through outflowing streams, colonizing downstream reaches and lakes (Horvath et al. 1996, Stoekel et al. 1997, Bobeldyk et al. 2005). Similar dispersal has been documented for *Daphnia lumholzi* drifting downstream from invaded reservoirs (Shurin and Havel 2002). Even species without planktonic stages, such as rusty crayfish (*Orconectes rusticus*), can spread naturally through lakes and stream corridors to invade other systems (Puth and Allen 2005).

In these systems, observations to collect dispersal data can be obtained through mark-recapture studies or radio-telemetry tracking of individuals (Table 1). Under the assumption that populations in lotic systems form along a one-dimensional strip of habitat, the dispersal kernel can then be fitted from the dispersal data of the tracked individuals (Lewis et al. 2006). Movements of the invasive signal crayfish (*Pacifastacus leniusculus*), for example, were tracked by radio-telemetry every 2 days (Bubb et al. 2004). The frequency distribution of movements upstream and downstream from the release location, as well as the total distance dispersed, was described by inverse power laws:

\[ m = cx^{-n} \]
where \( m \) is the probability of a movement, \( x \) is the displacement from the release point, and \( c \) and \( n \) are fitted constants.

However, if the underlying shape of the dispersal kernel is unknown, the moment generating function for the kernel is estimated from one-dimensional dispersal data:

\[
M^E(s) = \frac{1}{N} \sum_{i=1}^{N} \exp(sz_i)
\]

where \( s \) is the unknown slope, \( z_i \) is the observed individual dispersal, \( N \) is the number of individuals and the superscript \( E \) refers to the empirical estimate of the moment generating function (Lewis et al. 2006).

Alternatively, data on the movement of organisms may be collected such that the density of organisms (number per unit area) is recorded at distance intervals from the putative source. Horvath et al. (1996) recorded the density of zebra mussels in two streams in the St. Joseph River basin (Indiana and Michigan) and found that density within the streams decreased exponentially away from the lakes. In order to avoid bias due to the width of the stream or river when fitting the dispersal kernel, the density of organisms should be multiplied by the width of the stream and the dispersal kernel constrained so that the integrand is equal to 1 (Lewis et al. 2006).

Occasionally, data is in the form of frequency distributions, and the dispersal kernels are fit to histograms. Care should be taken with this approach as the width of the distance intervals
may bias the shape of the dispersal kernel. More formally, the associated moment generating function \( M^H(s) \) is represented as:

\[
M^H(s) = \frac{1}{s} \sum_{i=1}^{L} f_i \left[ \sinh(sb_i) - \sinh(sb_{i-1}) \right]
\]  

(3)

with \( f_i \) = the bin height of the histogram for bin \( i \), \( b_i \) and \( b_{i-1} \) are the endpoints of bin \( i \), \( L \) is the maximum number of bins in the histogram, and \( s \) as the unknown slope (Lewis et al. 2006).

Within a lake, diffusion of species through water currents will increase colonization rates of the entire lake. Hydrologic pathways can also assist in spreading aquatic plants, especially those with free-floating life forms, such as water hyacinth (\textit{Eichhornia crassipes}) and aquarium water moss (\textit{Salvinia molesta}). For submerged macrophytes such as water milfoil (\textit{Myriophyllum spicatum}), dispersal occurs via advective transport of vegetative fragments (Madsen et al. 1988).

Animal-mediated dispersal

Animal-mediated dispersal has been shown to spread several taxonomic groups over long distances. Plant seeds, for example, have the potential to be transported in the digestive tract of animals such as white-tailed deer and waterfowl (DeVlaming and Proctor 1968, Myers et al. 2004). Waterfowl have also been shown to carry species such as snails and zooplankton on their feathers and feet (Boag 1986, Green and Figuerola 2005). Fish may also act as dispersal agents after consuming species that can withstand gut passage and moving to a new environment. For example, the diapausing eggs of the invasive cladoceran, \textit{Bythotrephes longimanus}, have been shown to survive passage through fish guts (Jarnagin et al. 2000). As with hydrological dispersal,
models on animal-mediated dispersal may be parameterized by collecting data through mark-recapture or radio-telemetry (Table 1).

Aerial dispersal

Advective transport by air currents or gusts of wind is another dispersal mechanism for some nonindigenous species, even aquatic. Unlike dispersal via water currents, species that disperse aerially can move outside of closed systems and into new environments and are not limited to downstream movement. For example, small species such as zooplankton that have desiccation tolerant resting stages can be carried by the wind outside of isolated aquatic environments. Although ample anecdotal evidence exists for wind mediated species dispersal, manipulative studies necessary to calculate dispersal rates are rare (but see Cáceres and Soluk 2002, Skarpaas et al. 2005). Most studies have shown that zooplankton, especially rotifers, are capable of aerial transport, but that dispersal events are infrequent and limited to a few species, and that dispersal and colonization potential differ among different zooplankton species (Cáceres and Soluk 2002). As an example, in all samples of a one year-long study, only four species of rotifers were collected and were within 1 km of the source waterbody (Jenkins 1998). For aquatic species, one consequence of wind dispersal is that lower densities of species disperse and colonize new systems. Seeds from aquatic macrophytes carried by the wind, for example, have a lower chance of successfully colonizing founder populations than if dispersed through hydrologic pathways (Soons 2006).

Aerial dispersal of organisms is frequently estimated by collecting data on the density of individuals or on measured dispersal of propagules. For insects, mark-recapture methods based on pheromone traps provide an empirical measure of the mean number of recaptures as a function of distance from release (Table 1, Turchin and Thoeny 1993). Turchin and Thoeny
(1993) fit 2-parameter exponential decay functions to the recapture data, and relate the fitted parameters for the diffusion coefficient, recapture efficiency of the trap, number of beetles released from the source and survival rates.

Greene and Johnson (1989) were able to describe the dispersal of winged seeds based on a ballistic formulation. The resultant dispersal from a point source using the geometric mean and variance of wind speed in the downwind direction, $u_g$ and $\sigma_x$, release height $H$ and falling speed $W_s$ is described by:

$$K(x) = \frac{n}{\sqrt{2\pi x\sigma_x}} \exp\left[-\frac{(\ln(W_s x/Hu_g))^2}{2\sigma_x^2}\right]$$

(4)

where $n$ is total seed production. Jung and Croft (2001) used this model to parameterize mite dispersal with measurements of falling speeds in a greenhouse.

<2>Anthropogenic dispersal

Anthropogenic dispersal of nonindigenous species ecology can result in the transport of propagules at a faster rate and greater distance beyond their native range than they could naturally (Wonham et al. 2000, Mack and Lonsdale 2001, Hebert and Cristescu 2002). As a result of this rapid transport, propagules have a greater chance of surviving the trip. For example, both transoceanic vessels and vessels that remain in the Laurentian Great Lakes (“lakers”) make multiple stops for unloading and loading cargo at several ports within the Great Lakes. Many of these ships unload cargo in Lake Erie and Lake Ontario and take on ballast water at these locations for stability. These ships then proceed to Lake Superior ports where ballast water is then pumped out and cargo is picked up for the return trip. As a result, biotic
exchange of NIS among the Great Lakes occurs on the order of days, magnitudes faster than would be possible under the species intrinsic dispersal ability.

The spread of the pathogen *Phytophthora ramorum*, which causes Sudden Oak Death, is a well-documented example. This pathogen was first reported in central California in 1995 (Garbelotto et al. 2001) and has since been transported long-distances from infested nurseries via commercially-important hosts susceptible to disease (e.g., oak saplings, rhododendrons) in addition to local dispersal.

Two methods well-suited for modeling human-mediated dispersal of propagules are gravity models and random utility models. In both cases, the dispersal kernel is modeled on overland human-mediated transport, and describes the distribution of trip distances across a road-based network (Figure 1). Both methods are applicable for modeling dispersal of aquatic NIS, as lakes may be considered as discrete patches in a heterogeneous landscape. Like advective flow through rivers or streams, overland human-mediated dispersal is constrained to a network composed of one-dimensional segments.

Gravity Models

A common tool to model spatial interaction is a gravity model, which is used to describe how the influences of distances and the “mass” or attraction of origins and/or destinations affect the flow of people (Thomas and Hugget 1980, Roy and Thill 2004). The attractiveness of a location can be described as the property that creates an incentive for trips to be made to that location. The simplest formulation of a gravity model is:
\[ T_{ij} = kA_i B_j e^{-\alpha c_{ij}}, \]  

where \( T_{ij} \) is the interaction between locations \( i \) and \( j \), \( k \) is a constant, \( A_i \) and \( B_j \) define the propulsion from the origin and the attraction to the destination, respectively, \( c_{ij} \) is the distance between \( i \) and \( j \), and \( \alpha \) is a distance coefficient, or distance-decay parameter, which defines how much of a deterrent distance is to interaction. In a transportation context, \( A_i \) and \( B_j \) can be described as the number of individuals leaving and arriving at particular locations.

Gravity models can be used in heterogeneous landscapes, use various dispersal kernels, are based on a known mechanism, and do not solely simulate a resultant pattern. The cognitive process of humans in making decision about where they travel is incorporated into gravity models. These models are also spatially explicit as they model flow from specific origins to destinations, and enable the incorporation of large GIS databases as data sources for model parameterization. In addition, gravity models are created with an assumption that the specific perception of what is attractive to humans is correct and is the dominant driving force in destination choice.

Although gravity models were initially developed for use in economics (Reilly 1931, Linneman 1966) and other social sciences (Zipf 1946), they have more recently been used to predict the spread of diseases such as influenza (Viboud et al. 2006), plant pathogens (Ferrari et al. 2006), and nonindigenous species. The first published use of a gravity model successfully to assess the risk of human-mediated transport of an nonindigenous species was “A Transportation Model Assessment of the Risk to Native Mussel Communities from Zebra Mussel Spread” by Schneider et al. (1998). Schneider et al. (1998) used a doubly-constrained gravity model to predict the rank order in which inland lakes and reservoirs of Illinois are expected to become
invaded, resulting in a threat to the native mussel communities of these water bodies. A doubly-constrained gravity model is used when information is known about the number of individuals leaving and arriving at specific destinations. In general, Schneider et al. (1998) predicted that those water bodies with high boat use and close to sources of zebra mussels are the most likely to become invaded with zebra mussels. An assessment of the prediction of this study shows that only 2 of the 55 lakes that were assessed are now invaded by zebra mussels. These lakes were predicted to be the first and the 52nd lakes to become invaded, suggesting a re-evaluation of the risk to these lakes is necessary. Since this publication, several additional lakes have become infested in Illinois, but most are in the greater Chicago area, closest to Lake Michigan – a major source of zebra mussels.

Similarly, Bossenbroek et al. (2001) forecast the distribution of lakes invaded by zebra mussels in Michigan, Ohio, and northern Illinois and Indiana using a production-constrained gravity model. A production-constrained gravity model is used when only the number of individuals leaving an origin is known, but not the number of individuals arriving at a particular destination. Bossenbroek et al. (2001) showed that a gravity model could be used to mimic the existing pattern of the zebra mussel invasion. On a national scale, Bossenbroek et al. (2007) predicted the relative probability that zebra mussels would be transported to different watersheds throughout the United States. This analysis suggested that the watersheds most likely to experience new introduction events are those that already contain lakes invaded by zebra mussels. Bossenbroek et al. (2007) also identifies particular reservoirs not in currently invaded areas, such as the H.S Truman Reservoir in Missouri and Lake Mead, which have a higher probability of becoming invaded.
In addition to local dispersal, gravity models have also been successfully used to model some of the rare, long distance dispersal events. For example, the discovery of the zebra mussel congener, the quagga mussel (*Dreissena bugensis rostriformis*), in Lake Mead identifies the relevance of this type of modeling and the likelihood of such events since it is most likely that human-mediated transport was responsible for its introduction and not transport through connected waterways. In another example, MacIsaac et al. (2004) used a doubly-constrained gravity model to forecast the spread of the aquatic spiny waterflea (*Bythotrephes longimanus*) throughout Ontario Canada. The authors used recreational boater surveys to identify the strength of vector flows between different lakes and thus the risk of spread of *Bythotrephes* to noninvaded lakes.

Gravity models have been used successfully to assess human-mediated movement of terrestrial nonindigenous species such as the emerald ash borer (*Agrilus planipennis*) (Muirhead et al. 2006, Iverson et al. in press). The ash borer is an invasive beetle from China that rapidly kills the native ash tree species of North America. It was first discovered in North America in the summer of 2002 and since has spread from its point of introduction, Detroit, MI, to much of the lower peninsula of Michigan, southwestern Ontario and northern Ohio. The emerald ash borer can disperse by flight, but most movement is less than 1 km and only 1% travel farther than 4 km (Taylor et al. 2004). The rapid spread of the emerald ash borer suggests that human-mediated dispersal is a primary mechanism, such as the movement of firewood by campers, or ash products for use in landscaping (Figure 2). Both Muirhead et al. (2006) and Iverson et al. (in press) exhibit the importance of long-distance spread in predicting the overall dispersal rate of the emerald ash borer and Iverson et al. (in press) specifically predict the relative risk of campers.
moving wood from the core area of emerald ash borer infestation to campgrounds in Ohio (Figure 2).

[INSERT FIGURE 6.2 HERE]

The initial uses of gravity models were either untested in their predictions (e.g., Schneider et al. 1998) or parameterized based on their ability to recreate known patterns or distributions of an invasion (e.g., Bossenbroek et al. 2001). These analyses, however, did not assess if the model predictions were accurately simulating the mechanism behind the patterns. Leung et al. (2006) compared the results of a production-constrained gravity model to four different metrics of human movement behavior based on creel records and a mailed survey developed specifically for that project. Leung et al. (2006) found that gravity models were able to simulate the mechanism of long-distance transport, i.e. the movement of recreational boaters.

Gravity models used in invasion biology have mostly been used to assess the likelihood that a nonindigenous species will be transported to a particular location. These models have not included biological attributes of the NIS, such as colonization or reproduction potential. Leung et al. (2004), however, were able to use the gravity model framework to demonstrate that zebra mussels are subject to Allee effects within their invaded range in North America. Likewise, Leung and Delaney (2006) demonstrated that spread can be estimated with limited data sets particularly when propagule pressure is accounted for. Leung et al. (2004) and Leung and Delaney (2006) show the importance of accounting for population dynamics at early stages of an invasion when modeling patterns of dispersal.
The next steps in the development of gravity models for use in risk assessment require the inclusion of NIS population dynamics such as growth rate and mortality and more rigorous assessments of uncertainty (see Chapter 7). This would enable gravity models to serve as a bridge from describing dispersal of individual propagules to that describing population spread of NIS at a landscape level (Jerde and Lewis 2007). For example, models describing population growth can be coupled with gravity models describing immigration and emigration among systems, in a manner analogous to metapopulation models.

Random-Utility models

An alternative to the gravity model for estimating the human-mediated movement of organisms is the random utility maximization (RUM) model. The RUM model is the most widely used modeling framework for economist’s estimating the recreation demand of various sites. While gravity models are still used in other areas of economics and other disciplines, economists in recreation demand over the past thirty years have turned to RUM models, among others, that explain more fully the individual economic behavior driving their decisions of where to recreate. The primary reason for moving away from gravity models is the necessity to include travel costs so that a demand function can be estimated and utilized in the calculation of benefit values, for cost-benefit analysis. Travel costs in a RUM model (and all other models in recreation demand) incorporate road infrastructure, population centers, and varying attainable speeds. Included are out-of-pocket expenses from traveling to the site, such as the cost of gasoline and depreciation of your vehicle, and also the value of your time used-up during the transit (i.e., opportunity cost of time).

Once travel costs are estimated for each individual to each site in their choice set, a demand function for each site is recoverable, where the number of trips taken to the site and
travel costs is inversely related (i.e., individuals choose fewer trips to a site as it becomes more expensive per trip). Benefit values are easily recoverable from the demand functions (see Corrigan et al. 2007 for an overview). For example, if one wanted to estimate the benefits from the reduced spread of a nonindigenous species by human-mediated movement, a RUM model is suited to this task, whereas the gravity model is a “statistical allocation model” that does not include “the requisite economic behavior to estimate benefits” (Bockstael et al. 1989). Moreover, even if the interest is only the prediction of spread, the RUM model will most likely be superior, due to the more complete modeling of the individual’s decision making.

One particular advantage of RUMs is that they model individual level trips instead of aggregate zonal trips, such as done by gravity models. With the current state-of-the-art RUM, the repeated Mixed Logit model, the individual makes repeated choices of which sites to visit. In economics, “utility” is, “a measure of the relative satisfaction or desiredness from the consumption of goods”. Given this measure, one may speak meaningfully of increasing or decreasing utility, and thereby explain economic behavior in terms of attempts to increase one’s utility. The assumption is individuals visit the sites that give them the most utility, constrained by their income and time to recreate. The RUM model assumes the utility of individual $i$ choosing site $j$ on choice occasion $t$ is of the form:

$$U_{ijt} = V(X_{ij}; \beta) + \epsilon_{ijt}, \quad i = 1...N; \quad j = 0...J; \quad t = 1...T \quad (6)$$

where $V$ represents the observed portion of utility, and from the perspective of the researcher, $\epsilon_{ijt}$ represents the random, unobserved portion of utility (hence the name Random Utility Model). The observed portion of utility is a function of explanatory variables, $X_{ij}$, such as
travel costs, site characteristics (e.g., lake size), and household characteristics; and $\beta_i$ is the estimated parameters on the explanatory variables, where these parameters are routinely allowed to vary across the population of individuals, allowing for substantial heterogeneous trip taking behavior (hence the random effect leading to the mixed model).

Conditional on knowing $\beta_i$, the probability that individual $i$ chooses alternative $j$ on choice occasion $t$ is defined as:

$$
\Pr_{ijt}(\beta_i) = \frac{\exp(V_{ijt}(\beta_i))}{\sum_{k=0}^{J} \exp(V_{ikt}(\beta_i))},
$$

and the unconditional probability can be obtained by integrating the conditional probability over all possible values of $\beta_i$ and then using maximum simulated likelihood to estimate the parameters (Train, 2003). For the modeling of the human-mediated movement of organisms, it is convenient that RUM models estimate a trip probability (i.e. dispersal kernel) for each individual to each site (e.g., lakes). These estimated trip probabilities can easily be augmented with additional data on the biological attributes of the destination site concerning their candidacy for the accidentally transported nonindigenous species (Macpherson et al. 2005), as well as including biological attributes of NIS that may facilitate dispersal such as the production of resistant resting stages in zooplankton or vegetative reproduction in plants.

While Macpherson et al. 2005 discuss a simulation exercise with a dynamic RUM model, no papers to date have applied the RUM model to the spread of invasive species with actual data; not even a simpler static model. The downside of utilizing RUM models is the more intensive
data requirements, as individuals must be surveyed about which sites they visit and how often, along with other information such as their income. However, in the case of zebra mussels, Leung et al.’s (2002) high estimates of the partial economic costs from the spread of zebra mussels indicates the extra data collection costs would be worth undertaking to better predict NIS spread based on a more accurate modeling of boaters’ recreation activity.

Population spread

The development of spatial models for the spread of nonindigenous species has a long history starting with diffusion theory and gas kinetics in physics and chemistry. In the biological literature, dispersal models have been developed for a wide range of applications including gene flow (Fisher 1937), spread and susceptibility of infectious diseases (Kendall 1957, Noble 1974), predator-prey dynamics (Okubo 1980), and aerial dispersal of fungal spores (Aylor 2003) (see reviews in Higgins and Richardson 1996, Hastings et al. 2005).

The application of these modeling approaches to forecasting nonindigenous species spread is a logical extension, and the choice of a particular model depends on the type of information available (Shigesada and Kawasaki 1997). For many invasions, species presence/absence data may be the only information available from historical records. With this scenario, pattern-based, or spatial-phenomenological models (using the terminology of Higgins and Richardson 1996), can be used to forecast range expansion, or expanding the extensive margin in economic terms. These types of models assume that the location of the invasion wavefront corresponds to the location of first recording, and forecast rates of spread are equivalent to past spread rates. These models are more applicable to terrestrial systems at regional spatial scales than aquatic systems, and do not incorporate the ecology of the species or recipient habitat in predictions. As with many dispersal models, there is also the assumption that
sampling effort is sufficient to detect the species if present beyond the invasion wavefront – otherwise rates of spread would be underestimated. An example of a phenomenological invasion model is the spread of *Mimosa pigra* in Australia (Lonsdale 1993). *M. pigra* is an invasive shrub that has been identified as one of the 100 worst invaders in the world by the Global Invasive Species Programme. The area invaded by *M. pigra* was strongly related to the time of occurrence extracted from historical records and aerial photographs. Invaded areas were then predicted for subsequent years assuming this relationship remains constant and expansion occurs similarly in all directions.

In contrast to the spatial-phenomenological class of models, forecasting patterns of spread from process-based or mechanistic models can be done using information on the ecology of the nonindigenous species or properties of the transport mechanism. One of the first forms of a process-based approach is a reaction-diffusion model (RD) that predicts population density as a function of space and time. RD models describe exponential or logistic population growth that diffuses randomly across homogenous space (Okubo 1980). Population spread assuming exponential growth in a 2-D environment is represented as:

\[
\frac{\partial n}{\partial t} = D \left( \frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) + rn
\]  

(8)

where \(n\) is the population size, \(r\) is the intrinsic per capita population growth rate, and \(D\) is the diffusion coefficient (distance\(^2\)/time) for propagules dispersing in \(x\) and \(y\) directions. Here, distances that individuals disperse from a source are assumed normally distributed, with corresponding directions uniformly distributed from 0 to 360° (i.e. isotropic). The resulting pattern of population spread forms a series of concentric circles spreading away from the source.
through time. The diffusion coefficient $D$ is often measured using mark recapture data, for example, and can be estimated by:

$$D = \frac{\left( \sum_{n=1}^{m} \frac{x}{m} \right)^2}{\pi t}$$

(9)

where $x$ is the distance from the marking site, $m$ is the number of marked individuals released, and $t$ is the time since marking (Lockwood et al. 2007).

For marine or aerial dispersers, the basic diffusion model may be modified to include advective flow. Two-dimensional spread in these systems is described by:

$$\frac{\partial n}{\partial t} = D \left( \frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) + rn - w_x \frac{\partial n}{\partial x} - w_y \frac{\partial n}{\partial y}$$

(10)

where $w_x$ and $w_y$ describes velocity down x-axis and y axis, and other terms in the model are as previously defined from eqn. 8 (Holmes et al. 1994). Here, dispersal distances are also assumed to follow a normal distribution, but spread is not isotropic.

In one-dimensional RD models, the location of the invasion wavefront is expected to travel away from the epicenter at a constant rate of $\sqrt{4rD}$, where $r$ is the intrinsic rate of population increase and $D$ is the diffusivity coefficient providing population density is sufficient for detection. This, however holds true only when the dispersal kernels reach an asymptote at large distances (e.g. exponential decay). For fat-tailed dispersal kernels, the velocity of the wavefront increases through time.
In addition to assumptions about the homogeneity of space and random dispersal, this class of models assumes continuous reproduction and dispersal through time, and that there is no finite border limiting geographic spread.

Reaction-diffusion models have been successfully applied in describing secondary spread for a number of species. Skellam’s (1951) assertion that the European range expansion of muskrats followed a linear rate of increase as predicted from the model is generally supported. Predicted rates of range expansion of the small cabbage white butterfly, *Pieris rapae*, based on estimates of intrinsic rates of increase and survivorship fit with observed expansion rates in North America (Andow et al. 1990). However, in the same study, predicted rates of spread of *Oulema melanopus* (the cereal leaf beetle) from diffusion models were underestimated by at least 2 orders of magnitude. The authors suggested that other mechanisms such as human-mediated dispersal or advection in air currents were responsible for long-range transport. Current patterns *O. melanopus* spread in the U.S are consistent with “stratified diffusion” (Hengeveld 1989), in which spread proceeds by a combination of local and long-distance dispersal events (Shigesada et al. 1995). These long-distance dispersal events appear to be important in determining both the speed of the invasion as well as variability in population density at the invasion wavefront.

Although RD models that assume a continuous landscape have been successful for predicting geographic range extensions (e.g. Hengeveld 1989), they are limited in their applicability to heterogeneous systems. Consequently, spatially-discrete RD models have been developed that convert a continuous landscape into a lattice of grid cells representing suitable and unsuitable habitat (e.g. Flather and Bevers 2002). In their model, individuals of a hypothetical species dispersed from one habitat cell to another with distances according to a Weibull distribution and with uniformly distributed directions. Habitat amount relative to habitat
arrangement was key to the overall regional population size. No studies to date, however, have applied this method to predict NIS spread although it seems like a promising approach for terrestrial species.

The limitations of RD models for predicting the spread of aquatic invasive species was first highlighted with zebra mussels. Buchan and Padilla (1999) attempted to fit a RD model to the spread of zebra mussels in the state of Wisconsin. They determined that due to the heterogeneous nature of the landscape and the need to understand the mechanism of dispersal (in this case, recreational boaters) that RD models were not sufficient for this system. Due to the limitations of RD models, researchers have developed more sophisticated statistical methods for dealing with long-distance dispersal (see below) and have adapted techniques from other disciplines, namely geography and economics, to model different mechanisms of dispersal (see Dispersal section).

Several modeling approaches have been developed to forecast range expansion without the restrictive assumptions underlying reaction-diffusion models. Integrodifference models (ID) (e.g. Kot et al. 1996, Veit and Lewis 1996, Krkošek et al. 2007) have two primary advantages over reaction-diffusion models: 1) They estimate dispersal of individuals according to their life-stage at discrete time intervals, and 2) they are flexible due to their use of non-Gaussian dispersal kernels. The shape of the dispersal kernel can be fitted to data from mark-recapture experiments, and include rare, long-distance dispersal events observed with invasive spread (i.e. leptokurtic, or "fat-tailed" dispersal kernels (Kot et al. 1996). With flowering plants, for example, seeds are the primary dispersing stage transported by vectors such as wind, water and animals. Sensitivity analysis on the contribution of each life-stage to the overall rate of spread allows may then guide management efforts (Neubert and Caswell 2000). Like their reaction-diffusion counterparts,
basic integrodifference models assume a homogenous landscape and that population growth and dispersal are the same at each point in space. Consequently, they are better suited to aerial or terrestrial invasions. In ID models, population density at time $t+1$ and location $x$ is represented as:

$$n_{t+1}(x) = \int k(x - y) f(n_t(y)) dy$$  \hspace{1cm} (11)$$

where $n$ is population size, $t$ is time interval, $k$ is the dispersal kernel for displacement from $y$ to $x$, and $f(n_t)$ describes population growth as a function of population size in the previous time step at location $y$.

Population-based models such as the reaction-diffusion or Integrodifference equations have been adapted for the scenario when propagules of the nonindigenous species are first introduced into novel habitat and finding a mate becomes much more difficult due to the low population size. As a result, the population experiences reduced or negative growth rates at low density, called “Allee effects”, which then translates to fewer individuals who are able to undergo secondary spread. In theory, Allee effects may serve as an alternate mechanism to explain increasing rates of spread as a contrast to long-distance dispersal events, as Allee effects may cause a lag in the initial stages of secondary dispersal (Kot et al. 1996). Allee effects have shown to be present in the spread of the invasive weed, *Spartina alterniflora* (Davis et al. 2004), and modeled for several organisms including the plant pathogen, *Tilletia indica* (Garrett and Bowden 2002), the house finch, *Carpodacus mexicanus* (Veit and Lewis 1996) and the gypsy moth, *Lymantria dispar* (Liebhold and Bascompte 2003). In the last study, the authors suggest
that 100% eradication of the species may not be necessary as long as the population density is reduced to a threshold below which Allee effects will cause the population to crash.

<1>Management Guidance

Historically, dispersal models have been used to describe the patterns and processes by which organisms colonize novel habitat (Shigesada and Kawasaki 1997). However, these models are increasingly being used to predict locations likely to become invaded (e.g. Leung et al. 2004, Bossenbroek et al. 2007) so that monitoring and control actions can be implemented. However, success in predicting biological invasions has been limited, and Gilpin (1990) advocates a probabilistic approach for predicting biological invasions. The “probability of a prescribed undesired effect,” in this particular case the probability of invasion, is by definition risk (Suter 1993). Risk analysis involves estimating probabilities of invasion, while management activities involve deciding how to respond to each risk. Together, risk analysis and management form a risk assessment approach to biological invasions (Suter 1993). The development of spread and dispersal models is critical in estimating the risk of invasion and evaluating management decisions (Leung et al. 2002).

Risk analysis has a variety of modeling approaches (Suter 1993). Each of the models discussed in this chapter represent a different approach that may be more appropriately suited for predicting the dispersal of the NIS depending on the mechanism of dispersal, the environment the organism is being introduced into, the life history of the organism, the risk assessor’s understanding of these processes, and the data available to parameterize the models (Stohlgren and Schnase 2006). In general, the goal of risk analysis for a single species is to predict when and where the species is likely to invade (MacIsaac et al. 2004, Bossenbroek et al. 2007) and report the probability associated with an invasion event (Jerde and Lewis 2007).
Management efforts may change significantly whether the goal is to stop the initial dispersal of propagules into novel habitat or to contain a spreading population. In the first scenario, risk management involves a preventative approach and relies on some knowledge of the dispersal mechanisms. Here, we try to assess the risk of one destination being invaded relative to another. In the latter case, putative transport mechanisms also should be considered, but management efforts are focused on restricting the outbound flow of propagules through quarantine or other methods. Patterns of population spread also may give an indication of the optimal management decision. Sharov and Liebhold’s (1998) model for spread reduction of the gypsy moth, Latin name, for example suggest that the optimal method to reduce the rate of spread is to eliminate satellite colonies outside the expanding population front.

Leung et al. (2002) provide a general risk management framework that links risk analysis to an economic model, which evaluates the costs and benefits of management actions through stochastic dynamic programming (Chapter 10). This framework requires estimating the probability of invasion, valuating the costs of an invasion and management actions, and measuring the reduction in the probability of invasion from the different management actions (Stohlgren and Schnase 2006). An overview of the process of valuing market and non-market costs of invasion is discussed in Chapter 7. From the management framework, connecting models of dispersal and spread to risk management rests on the risk analysis and the potential changes in the probability of invasion due to management actions (Leung et al. 2002).

Although predicting invasions through modeling is gaining popularity, more attention is needed in communicating and connecting risk analyses to management (Bossenbroek et al. 2005). The main problem is the lack of reporting probabilities or the type of model used to estimate the probabilities (Nelson et al. 2007). One common approach to communicating risk is
to rank order locations from greatest risk to least risk for invasion (e.g. Schneider et al. 1998; location A is more likely to be invaded than location B under the assumption that they are independent). Alternatively, it may be possible to estimate the relative risk of invasion, where the relative risk is a ratio of invasion probabilities for two locations (e.g. Herborg et al. 2007; location A is 10 times more likely to be invaded than location B). While both rank orders and relative risk measures are formulated from probabilities and represent a risk analysis, they do not directly communicate the probability of invasion needed to apply risk management as proposed by Leung et al. (2002). Therefore, it is unclear if ranked and relative risk measurements provide sufficient information to make risk management decisions (Nelson et al. 2007). For some systems, it may be necessary, due to data limitations, and reasonable, given simplifying assumptions, to apply relative risk estimators to perform a risk analysis (Jerde and Lewis 2007), and the use of ranks and relative measures may be useful for sampling design and monitoring, but needs further development.

Risk management includes evaluating the potential influence of management actions on reducing the invasion probability (Suter 1993, Leung et al. 2002). Experiments that estimate this influence are undoubtedly useful but may be costly. Alternatively, models of dispersal and spread can be analyzed using sensitivity analysis. Sensitivity analysis evaluates how perturbations of model parameters influence the probability of invasion (Suter 1993). Small changes in model parameters may substantially change the probability of invasion. Identifying which parameters are sensitive may provide insights into the effectiveness of management actions on reducing invasion risk.
Conclusions

When forecasting the dispersal of NIS a number of issues need to be considered, including multiple dispersal mechanisms and the spatial heterogeneity of suitable habitat. The development of flexible modeling frameworks such as gravity models of NIS dispersal or integrodifference spread models addresses some of these considerations. By combining model output that identifies at risk regions with expert knowledge about invasive species allows for more refined predictions, and thus more accurate and efficient use of targeted management efforts.

References


Environmental Protection Agency under cooperative agreement CR-811043-01-0, Washington, D.C.


Ferrari, M. J., O. N. Bjornstad, J. L. Partain, and J. Antonovics. 2006. A gravity model for the spread of


Figure captions and legends

Figure 6.1. Exponential dispersal kernel fitted to distances recreationalists traveled in Ontario (z) after visiting a lake invaded by the spiny waterflea (*Bythotrephes longimanus*). The histogram and fitted dispersal kernel, $k(z) = 0.005 \exp(-0.005z)$, have been scaled so that $\int k(z)dz = 1$.

Figure 6.2 Relative risk of an introduction of emerald ash borer to Ohio campgrounds due to higher attractiveness and/or travel from the EAB infested core area in southern Michigan based on a gravity model.

Table 6.1. Examples of natural and human-mediated dispersal, methods to collect data and estimate dispersal kernels.
Figure 6.1
Figure 6.2
<table>
<thead>
<tr>
<th>Dispersal mechanism</th>
<th>Types of organisms</th>
<th>Method of data collection</th>
<th>Method to estimate dispersal kernel</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aerial</td>
<td>Insects, plant spores, seeds</td>
<td>Pheromone, seed traps</td>
<td>Moment generating functions fit to density data</td>
<td>Turchin and Thoeny (1993)</td>
</tr>
<tr>
<td>Hydrologic</td>
<td>Plankton, fish, macroinvertebrates</td>
<td>Mark-recapture, radio-telemetry</td>
<td>Moment generating functions fit to density or dispersal distances</td>
<td>Bubb et al. (2004)</td>
</tr>
<tr>
<td>Terrestrial (Animal movement)</td>
<td>Reptiles, mammals</td>
<td>Mark-recapture, radio-telemetry</td>
<td>Moment generating functions fit to dispersal distances</td>
<td>Murray et al. (1986)</td>
</tr>
<tr>
<td>Anthropogenic</td>
<td>Gravity and Random utility models: Surveys, government databases of recreationalist/commercial movement</td>
<td></td>
<td></td>
<td>Bossenbroek et al. (2001)</td>
</tr>
</tbody>
</table>