Chapter 10

The Use of Quantitative Models in Sea Otter Conservation

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INTRODUCTION

The use of quantitative or mathematical models as tools in wildlife conservation has a rich history, dating back to the birth of conservation biology as a distinct branch of science (Gilpin and Soulé, 1986; Soule, 1985). Researchers working within sub-disciplines of conservation science—population biology, genetics, community ecology, landscape ecology—make extensive use of

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mathematical models for bridging ecological theory and empirical data sets (Alvarez-Buylla et al., 1996; Brook et al., 2000; Lamberson et al., 1992; Mac Nally, 2000; Morris and Doak, 2002; Wennergren et al., 1995). This has certainly been the case for research focused on the conservation of sea otters where mathematical models have played a central role in many advances of our understanding of sea otters and their ecosystems. However, before delving into examples of the use of models in sea otter conservation, it may be helpful to take a step back to explain what I mean by the term "model," since this term may convey different things to different people, and indeed there are many different kinds of models that are used in many different ways.

Within the scientific disciplines of ecology and conservation biology, a model is first and foremost an analytical tool used to achieve a specific aim (Hilborn and Mangel, 1997). According to the Merriam-Webster's dictionary, a model is defined as "a description or analogy used to help visualize something (such as an atom) that cannot be directly observed" or "a system of postulates, data, and inferences presented as a mathematical description of an entity or state of affairs." Together these two definitions encompass the key features of most mathematical models used by conservation biologists. Fundamentally, models are conceptual or mathematical abstractions, stylized representations, or simplifications of reality that are meant to capture the most important elements or dynamics of a phenomenon of interest, while stripping away extraneous details. The distinction between models and "hypotheses" is worth noting here, as they are closely related but not synonymous (Levins, 1966). A scientific hypothesis is a proposition or unproved theory about some phenomenon of interest, tentatively accepted to explain certain facts or observations, or to provide a basis for further investigation. A good hypothesis can be verified or falsified by experiments, while a model cannot really be verified because *all* models are false by definition (since models are intentional simplifications or characterizations of reality). However, a hypothesis may be represented or described by one or more mathematical models, which may be used as part of the hypothesis testing process, or for generating new hypotheses (Hilborn and Mangel, 1997).

But that still doesn't answer the question of why models are necessary at all. In practice, scientists use models as tools to achieve a number of different objectives, including (1) to formulate a simplified statistical or quantitative description of a phenomenon; (2) to gain or improve a mechanistic understanding of a phenomenon; (3) to act as conceptual tools for generating new hypotheses; (4) to evaluate the feasibility of alternate explanations or hypotheses about the cause of an observed event (e.g., a population decline); (5) to make predictions about the future, by synthesizing the data in hand about a situation, or (6) to provide a systematic framework for the decision-making process (Maynard-Smith, 1978). In this last case, a model can provide a means for evaluating the potential effects or implications of various kinds of decisions, as well as evaluating which data sets are adequate and

which need to be improved for better decision making. So long as their limitations are clearly recognized, models can provide a scientist with powerful mathematical tools to help guide intuition about how various processes interact, evaluate testable hypotheses, generate key predictions, suggest appropriate experiments, and provide novel insights or new ways of thinking about a problem (Caswell, 1988).

The effective conservation of sea otters, and most other species, requires that scientists solve problems across a wide range of topics, from behavior and physiology to complex population dynamics, genetics, disease ecology, food-web interactions and physical/biological oceanography. These are complicated subjects, and the data sets collected by researchers in each subject area are vast and complex in their own right. Models provide one of the key tools for simplifying and integrating all these data, allowing scientists to test hypotheses, elucidate the underlying mechanisms of a particular problem, and make sound decisions. As computing power increases and new analytical techniques such as Bayesian approaches become more readily available, it is inevitable that models will become even more valuable for solving conservation challenges (Clark and Gelfand, 2006). In the following sections, I will discuss several branches of conservation science in which sea otter researchers have used mathematical models to aid in their research. For each subject area, I will explain some of the key research questions, provide a few examples of how models have been used to help answer those questions, and then highlight promising areas for future and ongoing work in sea otter conservation. I will end by exploring some of the general lessons that can be drawn from these examples, focusing on points that may be useful for wildlife conservation more broadly.

MODELS OF BEHAVIOR

Animal behavior may seem at first blush to be a rather esoteric subject in the context of wildlife conservation, as the term "behavioral science" often conjures up images of lab-coated scientists watching rats running through mazes. However, applied studies of animal behavior have actually played a vital role in animal conservation, mainly because knowledge of how animals behave in different environments is often necessary to inform management decisions. To provide just a few examples relevant to sea otters: (1) studies of foraging behavior and diet choices can provide important insights as to the role of food resources in regulating population abundance at a particular location; (2) information on individual movement behavior is vital for determining the habitat needs for a threatened population, and may also provide clues about exposure to human-caused threats such as harvests, oil spills, or pollution; and (3) an understanding of social behavior and reproductive strategies can be informative for interpreting why and how populations grow and expand the way they do, and can shed light on the factors contributing to declining or threatened

FIGURE 10.1 Sea otters are unique among marine mammals in that they bring all captured prey to the surface to handle and consume, and they do this while lying on their backs. This behavior, in combination with their nearshore distribution, makes them ideal subjects for studies of feeding behavior. Equipped with powerful telescopes, biologists are able to record each item of prey that sea otters capture and consume (such as this kelp crab, captured by a female sea otter near Monterey, CA), as well as the time it takes to locate and process those prey, and then use these data to estimate diet composition and energy consumption rates. *(Used by Permission of Nicole LaRoche.)*

populations. Quantitative models have been—and will continue to be—useful tools for exploring and understanding all these themes.

Sea otters are uniquely amenable to studies of foraging behavior and diet, due to a number of aspects of their behavior and biology. Because they feed exclusively on benthic invertebrates in shallow nearshore coastal waters (most feeding dives are made to depths of less than 40 m) and because they bring all their food to the surface to consume while lying on their backs (Figure 10.1), they are unique among all marine mammals (and perhaps among all large carnivores) in that it is possible for an observer equipped with a high-powered telescope to directly observe, identify, and record all prey items as they are consumed. There is a rich tradition of biologists capitalizing on this unusual behavior, with the result that there is now more known about the foraging behavior and diet of sea otters than almost any other carnivore (see, e.g., Estes et al., 1982; Garshelis et al., 1986; Laidre and Jameson, 2006; Ostfeld, 1982; Watt et al., 2000). This wealth of information has been used to test hypotheses associated with some of the central theories of ecology, such as optimal diet choice, and the effect of competition for food on the range of different prey types consumed by predators (often referred to by ecologists as "niche diversity"). The intersection of theoretical models with empirical data on sea otter diets and feeding behavior

has revealed some unexpected but fascinating patterns, and it has become clear that sea otter foraging behavior holds clues to solving many challenges of sea otter conservation.

Models of optimal diet choice (see Box 10.1) have been applied to sea otter populations, resulting in a number of specific predictions, as described by Estes et al. (1981). When sea otters first begin to colonize a new habitat,

Box 10.1 Primer on Models of Foraging Behavior and Diet Choice

Some of the most fundamental questions of ecology concern predator–prey interactions, and in particular (1) why predators choose to prey on some species but not others, (2) how predators affect the abundance of their prey populations, (3) whether there are predictable ways in which predators adjust their behavior and diet diversity in response to reductions in abundance of their preferred prey (which may be caused in part by their own predation), and (4) whether the dynamics described in questions 1–3 may set into motion a broader suite of changes in the larger food web. Questions 1–3 have been explored by ecologists within a set of mathematical models together referred to as "foraging theory." In brief, these models adopt a cost-benefit approach to predicting the foraging decisions of predators, similar to the models of human consumer behavior used by economists (and indeed, fundamental economic models and foraging theory models utilize the same mathematical and conceptual framework). Unlike economic models, where consumers are predicted to make decisions so as to minimize monetary costs while maximizing their material benefits, the currency of many foraging models is food energy, or calories. This makes sense because energy represents a scarce but critically important resource for wild animals: they require energy to grow, keep warm, move through their environment, hunt for food, and reproduce and raise their young. Energy-based models are premised on the idea that, all else being equal, predators will select prey species and utilize prey "patches" in the environment in such a way so as to minimize the energetic "expenditures" of feeding while maximizing their energy intake (Schoener, 1971).

One of the building blocks of foraging theory is the diet choice model (Charnov, 1976; Emlen, 1966). This model, while fairly simplistic, provides the basis for more elaborate models and illustrates many of the basic principles of foraging theory, so it is worth taking the time to examine and understand the model mathematically. In Eq. (10.1), E represents total consumed food energy and T represents time, so that E/T is the rate of energy intake (e.g., the number of kcal the predator consumes per minute), calculated as

$$E/T = \frac{\lambda_1 e_1 P_1 + \lambda_2 e_2 P_2 + \ldots \lambda_n e_n P_n}{1 +_1 \lambda_1 h_1 P_1 + \lambda_2 h_2 P_2 + \ldots \lambda_n h_n P_n} \tag{10.1}$$

Other symbols in Eq. (10.1) include λ_i, representing the relative abundance of a particular type of prey and thus the rate with which it is encountered by the predator (note that the subscript numbers in Eq. (10.1) are used to keep track of

(*Continued*)

Box 10.1 (Continued)

the parameter values for different types of prey, $i = 1, 2, \ldots, n$, where n is the number of potential prey types); e_i, representing the net energy content of each prey type; h_i, representing the time it takes to acquire, handle, and consume each prey type; and P_i, the probability that a predator will attack and consume items of each type of prey when encountered. If we assume that prey 1 is the most profitable and thus highest ranked prey (its ratio of net energy content to handling time, e_i/h_i, is higher than for all other prey types), it makes intuitive sense that a predator should always attack it when encountered ($P_1 = 1$). But what about the other prey types: should the predator include them in its diet, or ignore them when encountered and continue searching? We assume that predators will tend to make decisions so as to maximize their overall rate of energy gain, all else being equal (since this will allow them to maximize their lifetime reproductive output). Mathematically, this is achieved by adjusting the attack probability values (P_i) for each prey type until we find the maximum value of E/T. It turns out that the overall rate of energy intake (E/T) is maximized if the predator makes its decision to attack or ignore each prey type based on the relative abundance of all higher-ranked prey types. Specifically, if we assume that prey 2 is ranked just below prey 1 in terms of profitability, the predator should include prey 2 in its diet ($P_2 = 1$) if the following inequality holds:

$$e_2/h_2 \geq \frac{\lambda_1 e_1}{1 +_1 \lambda_1 h_1} \tag{10.2}$$

Otherwise, the predator should ignore items of prey 2 when encountered ($P_2 = 0$). A similar equation can be used to predict whether or not prey 3 will be included, and so on. Some algebra reveals that Eq. (10.2) will be satisfied—and prey 2 included in the diet—if the abundance of prey 1 (λ_1) is sufficiently low. Likewise Eq. (10.2) will not hold—and prey 2 will be excluded from the diet—if the abundance of prey 1 (λ_1) is sufficiently high. However, you might notice that the abundance of prey 2 (λ_2) does not appear in Eq. (10.2): this means that the abundance of prey 2 is itself predicted to be irrelevant to the predator's decision to include it in the diet! This prediction may seem surprising, and indeed it was quite controversial when first proposed; however, years of data from experiments and wild predator populations have largely supported these predictions. When highly preferred prey is abundant in the environment, predators tend to rely primarily on these profitable prey types and ignore less profitable prey, resulting in low diet diversity. As the relative abundance of the preferred prey decreases, predators add additional lower-ranked prey types to their diet, resulting in more diverse diets. What would cause the relative abundance of preferred prey to decline? This can occur when the predator population is capable of depleting its own prey populations, thereby reducing prey density. But even if the absolute prey density remains the same, a decrease in relative *per capita* abundance of prey (i.e., number of items per individual predator) can occur if there is an increase in the predator population density: this is because the same number of prey items per unit area are now competed for by a larger number of predators (there are more diners at the table). And of course prey populations can vary over time in response to factors independent of predation.

they are expected to limit their diet primarily to highly profitable prey types (e.g., abalone and large red sea urchins in kelp habitats, or large Dungeness crabs and butter clams in soft sediment habitats) that allow a high rate of energy intake. As the sea otter population grows, and per capita availability of these preferred prey types goes down, it is expected that the rate of energy intake will decline and diet diversity will go up (as less profitable prey are sequentially added to the diet). Ostfield (1982) tested these predictions by studying the diets of sea otters as they first recolonized pristine habitat near Santa Cruz, CA. He found that, consistent with model predictions, sea otters initially preyed mostly on large red sea urchins, the prey species with the highest energy content to handling time ratio. These highly profitable prey were quickly depleted, after which sea otters increased their usage of the next most profitable prey (abalone and cancer crabs) and eventually began to add lower-ranked prey (kelp crabs and smaller clams) to their diet. The resulting pattern was an increase in diet diversity and a decrease in energy intake rates over time. A similar pattern was found by Estes et al. (1981) near Monterey, CA. Moreover, going back to the same area of California three decades later, Tinker et al. (2012) found that diet diversity is even greater, with a high frequency of low profitability prey types in the average sea otter diet. In soft sediment habitats, similar but more subtle patterns have been reported: in southeast Alaska, Kvitek and Oliver (1992) and Weitzman (2013), found that sea otters preyed mostly on large butter clams, mussels, and urchins when those energy-rich prey were sufficiently abundant; however, as otters became more abundant and depleted these profitable prey, their energy intake rates declined and they began to add less profitable prey to their diets (diet switching was less dramatic than in kelp habitats, possibly because soft sediment clam communities, in some cases, provide a more sustainable prey base over the long term). Thus the predictions of the basic diet model appear to hold up well for sea otters, at least when examined at the population level—but more on this below.

At this point we should pause and note that in the above discussion of changes in sea otter diets and energy intake rates over time, we have assumed that it is possible to obtain unbiased estimates of sea otter diet composition and intake rates. For most free-ranging carnivores, such a requirement represents a very tall order; in fact, there are few systems for which this is even remotely possible. Sea otters are, fortunately, an exception, although there are still some substantial challenges involved in obtaining unbiased estimates of diet composition, and even greater challenges to overcome in estimating energy intake rates. The reason that estimating these statistics is so challenging is not due to paucity of data—indeed, with a little practice and effort it is possible to amass vast quantities of observational data on sea otter feeding behavior and prey capture rates. Rather, it is because the data records collected are quite often incomplete, and there tends to be a non-random pattern to the bits of data that are missing—for example,

prey that are very small, or consumed quickly, are more frequently unidentified by the observer, as are prey that are captured and consumed far from shore—and this non-random nature of missing data introduces the potential for biased estimates of diet. Overcoming this potential bias has been made possible by a very different type of model, something called (intriguingly) a "Monte Carlo simulation model."

The term "Monte Carlo simulation" is derived, as the name suggests, from the Monte Carlo Casino, and like the games of chance played at the casino, Monte Carlo simulations take advantage of the aggregate statistical properties of many random events. Monte Carlo models are especially useful for simulating complex systems, where there is substantial uncertainty and interactions between model inputs, making more traditional "deterministic" models inappropriate (a deterministic model is illustrated by Eq. (10.1) in Box 10.1). The general approach of the Monte Carlo method involves defining the range and "probability distribution" of possible values for a series of input statistics, generating large numbers of random samples from these probability distributions, performing a series of computations on each set of random input values (the computations correspond to the presumed dynamics of the system being modeled), and then aggregating and describing the results of these computations. Now, unless you are very comfortable with probability and statistics, the above explanation may not make that much sense to you, so let's consider a simplified model of sea otter foraging to better illustrate the Monte Carlo method. Imagine we are observing sea otters feeding at an island in the Aleutian Archipelago where sea urchins make up almost all the prey. Let's say that we decide to record the number of urchins captured by sea otters during each of 1000 feeding dives. We also record the size of the urchins captured on each dive (it is possible to estimate the size of sea otter prey by comparing each item to the width of the feeding sea otter's paw, which is approximately 45 mm). However, we notice that the size of the urchins depends on the number of items captured: sea otters tend to either capture a few large urchins or many small urchins on each dive (this is because prey patches on the bottom tend to be made up of many urchins of a similar size). Luckily, because we kept track of both number of urchins AND size of urchins on each dive, we can account for the interaction between prey number and prey size in our model, as we'll see shortly. Finally, we record the duration (in seconds) of each dive cycle, which includes the time underwater finding prey plus the subsequent time at the surface handling and consuming the prey. Tallying up the results of our recorded feeding dives, we can plot histograms of the three types of data (Figure 10.2). If we have recorded enough data, these histograms can be easily translated into "probability distributions," which are useful mathematical formulas that tell us the likelihood of observing a particular value of a given statistic in the future. For example, if we find that the size of the urchins captured on feeding dives with three prey items is well

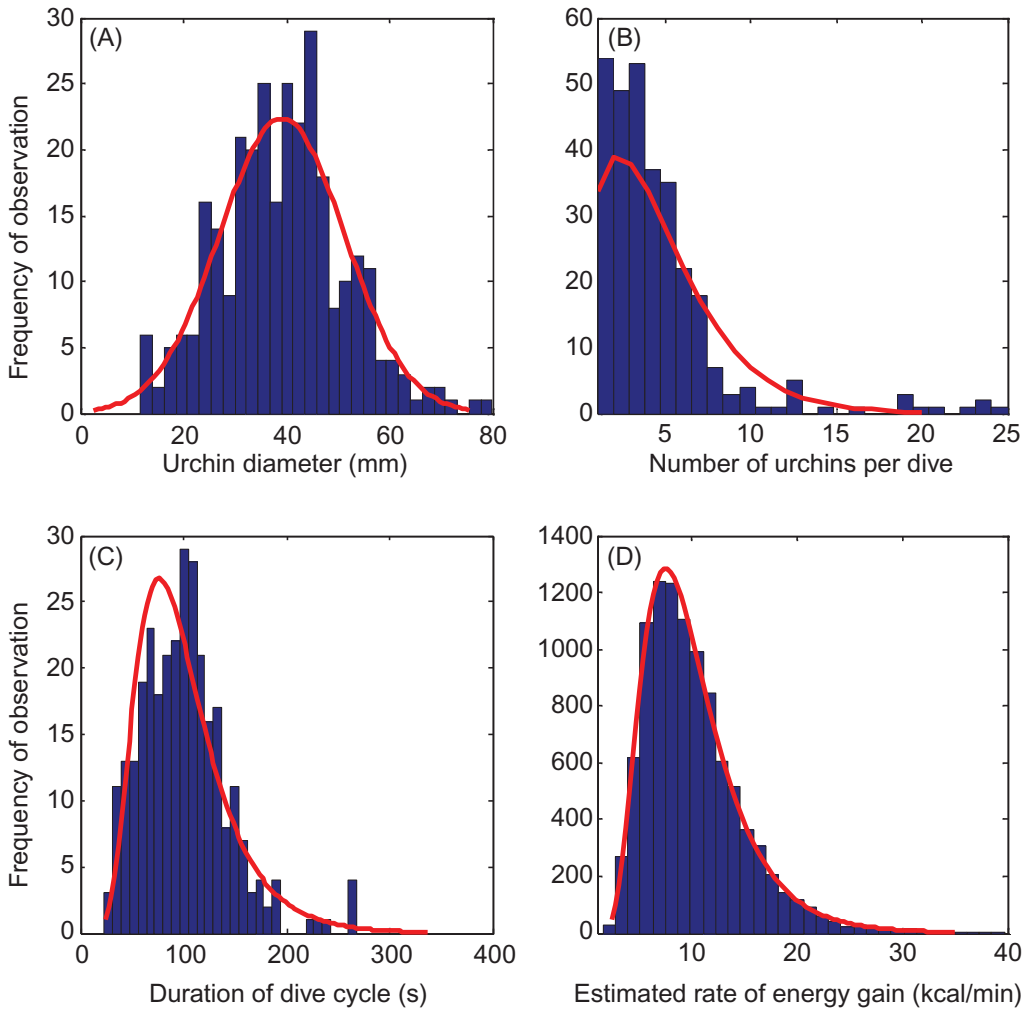


FIGURE 10.2 Frequency distributions and fitted probability density functions for several variables (and one estimated parameter) recorded during observations of sea otter foraging in the Aleutian Islands, AK. (A) Blue bars show a frequency histogram of the size (test diameter) of sea urchins captured on feeding dives, and the red line shows a normal probability density function that was fit to these data using maximum likelihood methods. (B) Blue bars show a frequency histogram of the number of sea urchins captured per feeding dive, and the red line shows a negative-binomial probability density function that was fit to these data using maximum likelihood methods. (C) Blue bars show a frequency histogram of dive cycle durations (i.e., the time spent under water finding prey plus the subsequent time at surface spent handling and consuming that prey), and the red line shows a log-normal probability density function that was fit to these data using maximum likelihood methods. (D) Blue bars show a frequency histogram of estimates of the rate of energy gain, calculated from the variables shown in panels A–C using Eq. (10.3) in the text. The red line shows a log-normal probability density function that was fit to these estimated values using maximum likelihood methods.

described by a normal probability distribution having mean of 38 mm and standard deviation of 13 mm, then we know that the probability that the urchins captured on the next three-urchin dive will have a size of 50–55 mm is 8.2% (Figure 10.2A). The normal distribution is just one

type of probability distribution (although the one that is familiar to most people), but there are other distributions as well, and it turns out that the number of prey items per dive is better described by the "negative binomial distribution" (Figure 10.2B) while the duration of the dive cycle is better described by the "log-normal" distribution (Figure 10.2C). Next we use a random number generator to create a sample of new values drawn at random from each of the above-described probability distributions, and we repeat this until we have 10,000 sets of random values for our three statistics (number of urchins/dive, size of urchins per dive *given* the number of items captured, and the duration of the dive cycle). For each set of randomly generated values, we perform the following calculations to calculate the rate of energy intake (E/T), or the number of kcal consumed per minute in this "simulated future dive":

$$E/T = \frac{n \times 0.396 \times 0.0005(s|n)^{2.9035}}{d} \tag{10.3}$$

In Eq. (10.3), the symbols used are n for the number of items captured, s for urchin size (the expression $s|n$ simply indicates that the value of s is dependent on n because there is a different probability distribution of s for each value of n) and d for the duration of the dive cycle (in minutes). Note that the calculations performed in Eq. (10.3) allow urchin energy content to be estimated from urchin diameter: this is possible because we have previously measured the relationship between urchin diameter and urchin biomass (in grams), as well as the number of kilocalories per gram of urchin biomass. Equation (10.3) is solved for each of the 10,000 sets of random values, and the results are tabulated in a histogram (Figure 10.2D). Thus by using this basic Monte Carlo model, we are able to estimate that sea otters consume, on average, approximately 10.4 kcal/min of time spent feeding at our Aleutian Island. Just as importantly, we also have an idea of how *precise* our estimate is (or how much uncertainty there is associated with this mean value, as represented by how "spread out" the Monte Carlo estimates are in Figure 10.2D).

The above example is of course highly simplified, but illustrates the key concepts of how the Monte Carlo method has been applied to sea otter foraging data sets. In reality there are many more characteristics of feeding behaviors and prey that are recorded, and many more interactions among these statistics that have to be accounted for in the calculations. The power of the Monte Carlo method in these cases is that (a) all the interactions between recorded variables can be accounted for in the calculations, no matter how complex, and (b) the algorithm can properly incorporate the additional uncertainty and biases caused by missing data points. For example, prey species is less likely to be recorded for small items that are handled very fast: we can account for this by incorporating the *context-specific* probability that prey species is unidentified within our Monte Carlo simulation. On a given iteration

of the simulation, if prey species is drawn as "unidentified," we then randomly assign a value by drawing from the list all recorded prey species for that area (or individual otter) having the *appropriate dive attributes* (e.g., if our randomly generated dive has a short surface interval and small prey size, then we draw randomly from all recorded prey that were captured on dives with short surface intervals and small prey size). In this way, the more data points that are missing the more uncertainty there is in our resulting estimates of diet composition and energy gain, and we can remove the biases that are inherent in the raw data sets due to non-randomness of missing data.

Dean et al. (2002) used a Monte Carlo model to estimate diet and prey consumption rates at two sites within Prince William Sound: Knight Island, which had been heavily impacted by the *Exxon Valdez* oil spill (EVOS), and Montague Island, which had escaped oiling (Chapter 4). They found that prey consumption rates were significantly higher at Knight Island, and thus were able to reject the hypothesis that food limitation was preventing further population recovery of otters at Knight Island. A similar comparison was made by Tinker et al. (2008a, 2012) in California: comparing long-established, high-density sea otter populations in central California to a recently established, low-density population at San Nicolas Island, they found that diet diversity was high and rate of energy intake was very low in the high-density central California sites, in contrast to the low-density San Nicolas site where diet diversity was low (and diets were dominated by energy-rich red urchins) and the rate of energy intake was high. The examples mentioned above demonstrate that using Monte Carlo models to analyze foraging data can provide valuable insights into the role of food resources in limiting growth of sea otter populations. In fact, if we apply this Monte Carlo model to the combined database of foraging data collected by many researchers at sites across the sea otter's range, from California to Alaska to the Commander Islands in Russia, we find a consistent pattern in terms of how foraging success (energy intake per minute) varies as a function of sea otter population density and population growth rate (Figure 10.3). This is important for two reasons: first, it tells us that in most cases, the relative per-capita abundance of energy-rich prey is ultimately the factor that determines sea otter population growth and equilibrium abundance. Second, it means that it is important to understand the status of a population with respect to foraging success because it can highlight situations where something other than food abundance is limiting a population. In Figure 10.3, for example, we notice that two populations fall outside of the expected relationship between foraging success and population density and growth rate: sea otters in the central Aleutian Islands and Alaska Peninsula are currently at low density (having declined by more than 80% in the last two decades), and yet have a high rate of energy intake. If food abundance were the only important factor then we would expect them to have a very high rate of growth, but instead we find populations that are stable or declining. We can therefore surmise that some factor other than

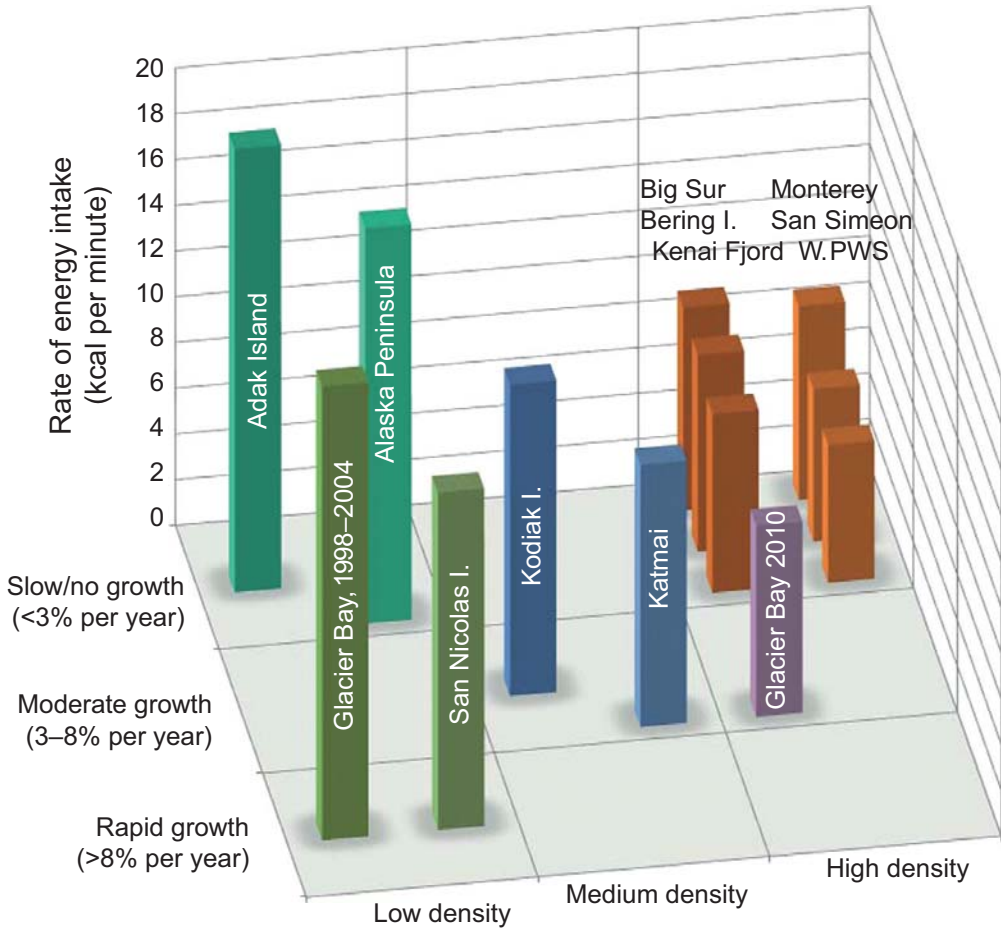


FIGURE 10.3 Estimated rate of energy intake while feeding for 13 sea otter populations, ranging from the Russian Commander Islands to southern California (see Figure 10.2 and text for description of Monte Carlo model used to estimate energy gain from observational feeding data). Each population has been classified into one of three categories organized along two independent axes: (1) rate of population growth (slow, moderate, rapid) and (2) population density (low, medium, high). In general, rate of energy gain tends to decrease as populations vary from low-density, rapidly growing populations to high-density, slowly growing (or stable) populations. Two sites that deviate from this axis are Adak Island and the Alaska Peninsula during the mid-2000s, where populations had been reduced to low density by factors other than resource abundance.

food abundance is limiting abundance in the Aleutians and Alaska Peninsula. At this time, the preponderance of evidence points toward elevated mortality due to predation by killer whales (Estes et al., 1998; Chapters 4 and 6). Similar logic can be applied to other situations as well, for example to determine places in California where land-based pollution may be affecting sea otter health and reducing population growth even though food resources may be relatively abundant (Jessup et al., 2007).

The models and patterns discussed above are useful for understanding the factors that affect sea otters at the population level—that is, they focus on an "average" individual within the population. However, a study by Estes et al.

(2003) demonstrated that the population average diet was not necessarily reflective of individual diets: to the contrary, individual sea otters tended to specialize on just a few prey types, and it was the differences between these specialized individual diets that gave rise to diverse diets at the population level. While this finding at first appeared to contradict the predictions of optimal diet theory, further investigations have shown that this is not the case. Specifically, theoretical predictions that individual prey choices should tend to converge upon an "optimal diet" are based on the assumption that individuals within a population are more or less similar with respect to foraging ability, or are "phenotypically similar." From a distance, one sea otter may look much like another, but in fact if one carefully measures the behavior and prey-specific capture and handling efficiency of tagged sea otters, it turns out that individuals differ considerably. A sea otter that specializes on feeding on turban snails, for example, can handle 42% more snails per hour than can a sea otter that specializes on some other prey type (Tinker et al., 2012). This variability in foraging skills appears to represent the effect of learned traits in sea otters, rather than genetic variation (Estes et al., 2003). Tinker et al. (2009) developed a stochastic dynamic model (a type of behavioral model that can incorporate learning: Mangel and Clark, 1988) that showed that the ability to learn foraging skills through extensive practice, or to lose those skills through lack of practice, would lead to the maintenance of diet specialization within a population, and moreover that the ability of females to pass on some of these skills to their offspring (a form of cultural transmission, also observed in sea otters) would further increase the degree of diet specialization observed. Another analysis of these data used network theory (the developing science of analytical approaches for studying networks, or graphical representations of the pattern of relationships between discreet objects) to examine how resource abundance affected the degree of specialization (Tinker et al., 2012). In this analysis, individual resource use was modeled as a bipartite network in which two sets of nodes, one representing individual consumers and the other representing their prey resources, were connected by links representing utilization of each prey by each individual. It was found that network modularity (the diversification of individual sea otters into specialized "dietary modules") increased greatly as preferred food resources became less abundant. This finding has important implications for sea otter conservation, because many of the pollutants and disease-causing parasites that affect sea otter health and survival are acquired by sea otters through their diet. Indeed, in an analysis of the factors that potentially increased the risk of infection in sea otters from two protozoan parasites that can cause lethal brain infections, it was found that a sea otter's diet specialization was one of the most important predictive factors (Johnson et al., 2009). Thus understanding and measuring individual diet specialization in sea otters provided a useful tool for elucidating the mechanisms and pathways of disease exposure.

Models of foraging behavior are perhaps the best examples of behavioral models for sea otters in the published literature; however, other types of behavior can also be investigated using models, such as time-activity budgets, habitat selection patterns, and movement behavior. Describing and quantifying the movement of animals in marine environments can be challenging, but technological advances in bio-logging instruments have greatly improved our ability to regularly and reliably geo-locate individuals and investigate how they move within their environment. As these types of data have become more common, a number of different models have been brought to bear to understand the factors that underlie the observed patterns and answer questions such as "what habitats are critical for this population?" or "how far will a typical individual move within a specified period of time?" The former question has been investigated with models of individual home range and habitat use (an individual's home range is the spatial extent or outside boundary comprising all or most of that animal's movements over some standardized period of time, such as a year). Home range models frequently make use of probabilistic utilization distributions, calculated from repeated observations of an animal's locations over time (see Borger et al., 2008). The utilization distribution is a probability density surface representing the likelihood of finding the individual at any particular point in space. Non-parametric kernel density models have been used to calculate home range utilization distributions and home range boundaries (corresponding to the area encompassing 95% of the kernel probability density function) for sea otters in California (Tinker et al., 2008a) and in Washington (Laidre et al., 2009). In the latter example, individual home ranges were estimated as kernel probability distributions along the one-dimensional axis represented by the coast. Future work will need to focus on estimating two-dimensional utilization distributions that account for the particular habitat restrictions of this coastal marine species.

Related to the concept of home range and habitat use are questions about individual movements and dispersal behavior: that is, given an animal's location right now, how far away is it likely to have moved by some future time (e.g., by next year)? The answer to this question is critical for developing models of population growth and range expansions (see "Population Dynamics," below), and can be represented by probability distributions of "net linear displacement," also called "dispersal kernels." Empirically derived dispersal kernels have been calculated by fitting exponential probability distributions to data on the movements of radio-tagged sea otters in California (Ralls et al., 1996; Tinker et al., 2008b). Expected dispersal distances can also be predicted using "random walk" models, which are a family of Lagrangian, individual-based models of animal movements (Turchin, 1998). These models simulate animal movements as a series of steps whose direction and distance are either random (random walk model), random but correlated (correlated random walk model), or random and

correlated and biased in some way (biased correlated random walk model), such as toward the center of a home range (Borger et al., 2008). A correlated random walk model fit to data on the movements of radio-tagged sea otters in California demonstrated a strong bias in the observed versus expected net linear displacement over time, suggesting that individuals exhibited a strong site fidelity and were less likely than expected to move very far from the center of their home range (Kage, 2004; Tinker et al., 2006b). Future models will build on this approach to develop biased correlated random walk models that incorporate multiple centers of use (i.e., more than one home range center) and the unique bathymetric habitat restrictions of sea otters.

MODELS OF POPULATION DYNAMICS

There is perhaps no other subject in wildlife conservation to which the use of models is more central than the analysis of wildlife populations, or population biology. The reasons for this are fairly straightforward: although the concept of a population is simple enough (the assemblage of a specific type of organism living within a defined area at a given time), it is very difficult to say useful things about how that population is currently behaving, or will behave in the future. Actually measuring the characteristics of a population—its abundance, its spatial extent, and how individuals of the population are distributed over the landscape—is challenging enough for wide-ranging animals such as sea otters, but actually being able to interpret how those characteristics are changing over time, and why, is far more challenging. To accomplish the latter, we need to understand all the processes that cause a population to change in abundance and distribution: taken to the extreme, this would entail being able to predict the movements, reproduction, and survival (and time of death) for each member of the population! Obviously that is not practical or even possible for any wildlife population; however, it is possible to do the next best thing: to use mathematical equations that correspond to simplified cartoons of how typical individuals within the population will move, produce offspring, live, and die. In other words, we can describe aggregate properties of the population using a model. Of course we obviously have to sacrifice an awful lot of detail in so doing, but it turns out that even simple models can be quite useful both for understanding how a population came to have the abundance and distribution that we currently observe, and (more importantly for conservation) for forecasting how those characteristics might change in the future, under different management scenarios.

Relatively simple, unstructured population models can provide a useful way of interpreting the patterns of growth seen in many recovering sea otter populations. Exponential models (see Box 10.2) form the basic tool for interpreting short-term rates of change—for example, estimates of r derived from trend data collected by wildlife surveys can be used to assess current

Box 10.2 Primer on Models of Population Dynamics

The simplest type of model for a population can be summarized by a single number, N, the number of individuals in the population. Or to be more precise, N_t, where the subscript "t" indicates that we are interested in the number of organisms in the population at a particular point in time. The simplest type of model that is used to describe the dynamics of N_t is something called a differential equation, which describes how N_t changes over time (as represented by the expression "dN/dt"). Specifically, the change in population size that can be expected over a small increment of time is calculated as

$$\frac{dN}{dt} = rN_t \tag{10.4}$$

Equation (10.4) is pretty easy to interpret: the rate of change in population size is equal to the product of the current population size and r, which is known variously as the instantaneous growth rate or the *intrinsic rate of population growth*. Biologically speaking, r represents per-capita contributions to population growth, which is simply the difference between births and deaths for an average individual in the population, $r = b - d$. If the number of births per individual per unit time (b) exceeds the number of deaths per individual per unit time (d), r will be positive and the population will grow; if deaths exceed births, r will be negative and the population will shrink. We can also re-express Eq. (10.4) in a different form to predict the population size at any time in the future:

$$N_t = N_0 \times e^{rt} \tag{10.5}$$

In Eq. (10.5), N_0 represents the initial population size, and e^{rt} means to take the exponential function of the product of r and t (where t is the number of time steps into the future). Note that the exponential function of a number means to raise the natural logarithm base e, which is approximately 2.718, to the power of that number. Equation (10.5) seems simple enough, but there is a slight problem: this simple model would suggest that any population with a positive value of r, however small, will eventually grow to massive size. For example, try plugging in an initial population size of 100 and an instantaneous growth rate of $r = 0.2$ (a pretty typical maximum growth rate for a large mammal). Assuming our time step is a year, you will find that after just 100 years our population would number about 48,517,000,000! Thus the exponential population growth described by Eqs. (10.4)–(10.5) may be useful for predicting dynamics over short time intervals, but clearly we need to add a little bit more realism to this model before it is useful for longer periods. Biologically speaking, we have to account for the fact that individuals in a population can have negative impacts on other individuals, frequently referred to as "negative density dependence"; for example, they may compete for limited resources, or spread diseases to each other. We can represent this mathematically by adding a new term, α, representing the incremental amount by which each new individual added to the population reduces the rate of births (or increases the chance of death) of every other individual in the population. As more and more individuals are added these tiny

(*Continued*)

Box 10.2 (Continued)

incremental effects add up and reduce the per capita birth rate (or increase the death rate), so that the realized rate of population growth will slow over time:

$$\frac{dN}{dt} = rN_t(1 - \alpha N_t) \tag{10.6}$$

Equation (10.6), the logistic growth equation, is one of the simplest but most powerful ways of modeling the long-term dynamics of population growth. With a bit of algebra one can solve Eq. (10.6) to find the value of N_t at which the rate of change = 0, that is, the abundance at which growth will stop and the population will stabilize. It turns out this happens when $N_t = 1/\alpha$, so we can define the value $1/\alpha$ as the equilibrium abundance of N_t, also known as the carrying capacity or "K" (thus $K = 1/\alpha$ = the point at which births and deaths cancel each other out). Another way to express Eq. (10.6) is as a "discrete equation," meaning that time is represented as discrete steps (e.g., 1-year steps) rather than as a continuous process:

$$N_{t+1} = N_t e^{r(1-(N_t/K))} \tag{10.7}$$

Equation (10.7) tells us that the abundance of the population next year can be calculated from three pieces of information: (a) the abundance this year, (b) the intrinsic rate of growth, r, and (c) the carrying capacity, K. When population abundance is very low, the fraction N/K is approximately 0 and so drops out of the model, with the result that Eq. (10.7) becomes effectively identical to Eq. (10.5), the exponential growth model. This implies that the per capita growth rate of the population will be at its maximum, r, when N is very small, and indeed in this context it is common to refer to the parameter r as "r_{max}," the maximum possible rate of growth.

population status and/or population impacts of various perturbations. Gerrodette (1987) developed a statistical model for gauging the effectiveness of survey data for estimating r, and demonstrated that a long-term time series of regular counts can be an extremely powerful means of detecting even subtle changes in growth. Estes (1990) used this approach to analyze time series from multiple sea otter populations across the North Pacific, including Amchitka Island (where the population had apparently reached carrying capacity by the early 1970s), Attu Island (which sea otters had only recently recolonized), California, and three populations established by translocation, Washington, British Columbia, and southeast Alaska. The results were fascinating: populations at Attu, Washington, British Columbia, and southeast Alaska were all growing at remarkably high rates, with estimated values r of 0.17–0.25, in contrast to a slower growth rate of 0.05 in California. Estes (1990) also employed a life table model derived by Cole (1954) to estimate the theoretical maximum rate of growth (r_{max}) for an age-structured population, given a specified age at first reproduction (a = 2–4 years for sea

otters), age of last reproduction ($w = 12-18$ years for sea otters), female birth rate ($b = 0.43-0.49$ female pups per year), and assuming near-perfect survival of females up until the age of last reproduction:

$$1 = e^{-r_{max}} + be^{-r_{max}a} - be^{-r_{max}(w+1)} \tag{10.8}$$

By solving Eq. (10.8) with the parameter values listed above, it can be shown that the theoretical value of r_{max} for sea otters is somewhere between 0.20 and 0.25. Thus the recovering population at Attu and the translocated populations at Washington, British Columbia, and southeast Alaska were found to be increasing at (or near to) the theoretical r_{max}, while the recovering population in California was growing at only one quarter of that rate, at best. This result has been taken to suggest that the California population has experienced a chronically higher mortality rate than northern populations, although an alternate explanation for the difference may be related to the narrow, almost one-dimensional configuration of habitat in California, which, when combined with the high degree of spatial structure of the population (Tinker et al., 2008b), results in more constrained range expansion and thus slower population growth (this is the case because a larger proportion of the population more quickly becomes resource limited than northern populations where there is a two-dimensional matrix of available habitat for range expansion).

The other key parameter of the logistic model shown in Eq. (10.7) is of course K, the carrying capacity. Estes (1990) used a qualitative assessment of the time series at Amchitka to conclude that the population at that island had reached a carrying capacity of between 5245 and 6597 otters by the early 1970s. A similar qualitative assessment was made by Laidre et al. (2001) to identify areas in central California assumed to be at or near carrying capacity. Laidre and colleagues then used a spatial habitat model, developed in a geographic information system (GIS), to extrapolate these equilibrium densities to areas of similar habitat type throughout the rest of coastal California and thereby estimate a potential *total* carrying capacity for southern sea otters (assuming that sea otters were to eventually recolonize all nearshore habitat between the Oregon border and Mexico). Gregr and colleagues (2008) used a similar spatial habitat model to estimate potential carrying capacity for sea otters in British Columbia. Coletti (2006) developed an even more elaborate model for Prince William Sound, using stepwise logistic regression to describe relationships among behavior, diving activity, and habitat attributes, including both nearshore and offshore habitat, and then applied those relationships to predict equilibrium densities throughout the Sound, and in particular to those areas affected by the EVOS in order to determine the potential for further post-spill recovery.

All the population models discussed to this point have focused on predicting changes in population abundance overall, while effectively ignoring

any details about the animals that make up the population. Often such simplified models are sufficient and appropriate for addressing the questions of interest. But what if we are interested in learning about a specific segment of the population, or we want to know about the impacts of a factor that only affects certain animals (i.e., a disease that primarily affects juveniles or females). Accounting for this complexity requires a different kind of population model, one which explicitly incorporates "population structure," or differences within the population (see Box 10.3).

Box 10.3 Primer on Matrix Models of Structured Populations

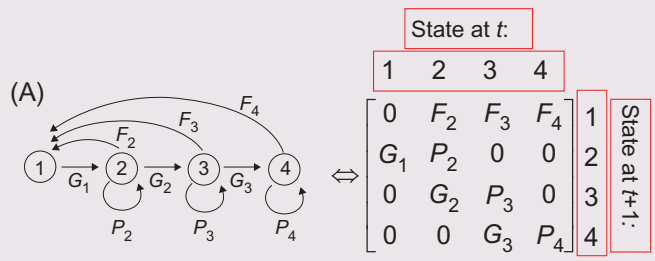
The most common type of model used to investigate structured populations is the projection matrix model (a thorough treatment of this subject is provided by Caswell, 2001). A projection matrix is a mathematical tool for describing "transitions between states," and is basically a series of linear equations organized to simplify algebraic operations such as multiplication. If we were to classify all the individuals from a population into one of a limited number of "states" (where states could be defined by sex, age, size, or any other attribute deemed to be important), then the matrix describes all the ways that individuals of a given state can transition to (or contribute to) other possible states over the course of a single time-step (the time-step is usually assumed to be 1 year, but could also be a month, or a week, or any other appropriate interval). For example, if we decide that it is important to classify individuals by age, where the possible state values are juvenile, sub-adult, adult, and old adult, then our matrix will reflect the fact that it is possible for a juvenile to make a transition to sub-adult simply by surviving and growing a year older. Conversely an adult cannot grow into a sub-adult (so this transition will not be allowed in our matrix); however, an adult *can* contribute to the juvenile age class by reproducing and successfully rearing an offspring to become a juvenile. These examples illustrate the three main types of transition that are described by a projection matrix: growth, survival, and reproduction (Figure 10.4A).

The values that are actually stored in the matrix are "per capita transition rates": in the case of survival, this corresponds to the probability that a typical individual of a given state (e.g., age class) will survive from 1 year to the next, while for reproduction this corresponds to the average number of offspring produced by a typical individual over the course of 1 year. The value of the matrix in column j and row i (which we will refer to as a_{ij}) represents the annual transition rate from state j to state i (a population projection matrix is always square, so both i and j take on values from 1 to the number of different possible states). If we know the number of individuals in the population assigned to each state value at the start of this year, we can use *matrix multiplication* (or matrix projection) to calculate the expected number of individuals in each state at the start of next year, and similarly for all future years: this operation is illustrated in Figure 10.4B. Additional matrix algebraic operations can be used to obtain useful properties of the population such as the asymptotic annual population growth rate, usually represented by the symbol λ (not to be mistaken with the

(*Continued*)

Box 10.3 (Continued)

instantaneous growth rate r discussed previously, but which is related to r by the equation $\lambda = e^r$). In Figure 10.4B, $\lambda = 1.018$, meaning that a population with these vital rates will grow at an annual rate of 1.8%. Other advantages include the ability to determine which state transitions are most responsible for causing λ to go up or down. This latter property of population matrices, referred to as *sensitivity analysis*, is clearly a useful property, because it allows us to identify the demographic segments of the population that are most important to focus conservation efforts on if we wish to ensure population recovery.



(B)
$$\begin{pmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \\ n_4(t+1) \end{pmatrix} = \begin{pmatrix} 0 & F_2 & F_3 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix} \times \begin{pmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ n_4(t) \end{pmatrix}$$

$$\begin{pmatrix} 480 \\ 676 \\ 1238 \\ 389 \end{pmatrix} = \begin{pmatrix} 0 & 0.15 & 0.25 & 0.20 \\ 0.80 & 0.45 & 0 & 0 \\ 0 & 0.40 & 0.80 & 0 \\ 0 & 0 & 0.10 & 0.70 \end{pmatrix} \times \begin{pmatrix} 471 \\ 664 \\ 1216 \\ 382 \end{pmatrix}$$

FIGURE 10.4 Illustration of population projection matrix methods. (A) Loop diagram showing the possible life history transitions between each of four demographic "states," in this case age-classes (1 = juveniles, 2 = sub-adults, 3 = adults, 4 = aged adults), and a matrix formulation of this same life history. The three types of transition at each time-step include survival and growth to next age-class (G), survival without growth (P), and contribution to the first age-class via reproduction (F). In the matrix formulation, a transition from state j at time t to state i at time $t + 1$ is entered into row i and column j. (B) The operation of matrix multiplication (also called matrix projection) is demonstrated, whereby the number of animals in each age-class at time $t + 1$ is calculated based on the number of animals in each stage at time t, given the particular combination of vital rate estimates used to parameterize the matrix model.

Demographic models of sea otter populations have commonly used age as the state variable (generally modeling only the females in the population), although a few models have used both sex and age. Eberhardt (1995) was one of the first to apply an age-structured demographic model to sea otters, using a Lotka-Leslie age-structured matrix (see Box 10.3) within a re-sampling

simulation to develop a method for estimating reproductive rates (and associated variance estimates) that accounted for the fact that sea otters give birth year round. Eberhardt concluded that the matrix model approach could be used to evaluate population recovery from events such as the EVOS, and his model integrated previously published information on sea otter vital rates (e.g., Jameson and Johnson, 1993; Siniff and Ralls, 1991) and laid the groundwork for a number of later matrix models used to analyze sea otter population dynamics. For example, Estes and colleagues (1998) used a similar projection matrix model to estimate the number of sea otters that would have to have been lost to killer whale predation over a 6-year period (1990–1996) to account for the dramatic decline in sea otter populations that occurred throughout southwest Alaska. In this case, the model projections were used as part of a simulation analysis to determine whether it was feasible for killer whale predation to account for the 70–90% decline in sea otters that occurred over this period across the Aleutian Archipelago and the Alaskan Peninsula. Amazingly, the model results indicated that just 3–4 killer whales consuming 3–5 sea otters per day (the number of otters required to meet energetic requirements of an adult killer whale) would have been sufficient to drive the observed decline. It is worth noting that the estimates of sea otter vital rates (age-specific survival and reproduction) used for this feasibility analysis were taken from the literature, but matrices can also be useful for estimating vital rates from empirical data sets using standard data fitting techniques.

The use of maximum likelihood or Bayesian methods to fit age-specific survival rates to empirical data on the ages of either living animals or those that have died (in many areas it is possible to retrieve dead sea otters when they wash up on beaches) is one of the most powerful applications of projection matrices. Although this may sound intimidating if you are unfamiliar with data fitting techniques, the concept is actually quite simple, and can be summed up as follows: a key property of projection matrices is the ability to calculate the expected proportion of the population that can be found in each age class, as well as the proportional age distribution of the animals that die (the "death assemblage"). The precise nature of this output depends on the survival rate estimates in the matrix itself: tweaking these values will have the effect of changing the expected proportion of animals in each age class in both the living population and the death assemblage. If we were to systematically tweak all the survival rate values (and birth rate values) in the matrix model, running through the almost infinite set of possible permutations, we would eventually stumble upon the exact combination of values that result in the projected age distributions we find in nature. This may sound like a lot of work for us, but that is essentially what maximum likelihood and Bayesian analyses do. Udevitz and Ballachey (1998) developed a novel method for conducting this type of data fitting, using the ages of both living animals and beach cast carcasses from a population where the growth rate was varying over time (the assumption of

stable growth rates was a limitation of earlier techniques). Monson and colleagues (2000) used this type of age-structured model to assess whether there were lingering population effects from the 1989 EVOS. By using maximum likelihood methods to fit time-varying age-specific survival rates to age distributions of sea otters found dead on beaches of western Prince William Sound, Alaska, they found strong support for continued reductions in survival in the areas impacted by the oil spill. This model was rerun and elaborated upon 10 years later (Monson et al., 2011), to determine whether the oil spill effects had dissipated. This updated model indicated a gradual reduction of the survival effects over time; however, it was also shown that the oil-affected areas represented a "sink" population, where there was a net reduction in abundance, but that this was counterbalanced by the "source population" of unaffected areas, with the net result of slow recovery of the population of western Prince William Sound. A similar methodological approach was used by Tinker and colleagues (2006a) to examine the spatial and temporal shifts in demographic rates that were responsible for the period of decline seen in the California population in the late 1990s. The California model built on the approach of Udevitz and Ballachey (1998) and Monson et al. (2000, 2011), fitting survival rates to a time series of annual census counts as well as age at death data, and incorporating two sexes and spatial structure into the projection matrix. The results indicated that the period of decline that occurred between 1995 and 2000 was the result of decreased survival of sub-adult and prime-age adult females, particularly in the north and center of the sea otter's range (Figure 10.5).

Projection matrix models have also been used to answer an even wider range of applied conservation questions about sea otter populations. For example, Gerber et al. (2004) used a matrix model to assess the relative contribution of various causes of death to variation in the growth rate of the California sea otter population. Their sensitivity analysis revealed that infectious disease and emaciation had the greatest impact on population growth during the period of decline in the late 1990s, although shark bite wounds and human-caused trauma also had substantial impacts. Another common application of projection matrices includes the broad category of models known as "population viability analyses," or PVA. PVA models are used to assess the future viability of a given population under specific management scenarios, or to assess the potential impacts of a new threat or perturbation on the viability of a population. A PVA was developed by Tinker and colleagues for the southwest Alaska sea otter population, and is included as part of the recovery plan for this population (USFWS, 2010, 2013). As part of that analysis, trend data from skiff surveys of index sites across the Aleutian Archipelago were combined with data on vital rates collected during telemetry studies at Amchitka, Adak, and Kodiak Islands, and these were used to estimate mean and variance in per-capita mortality rates in southwest Alaska over the period of 1992–2007. Simulations were then run to investigate the

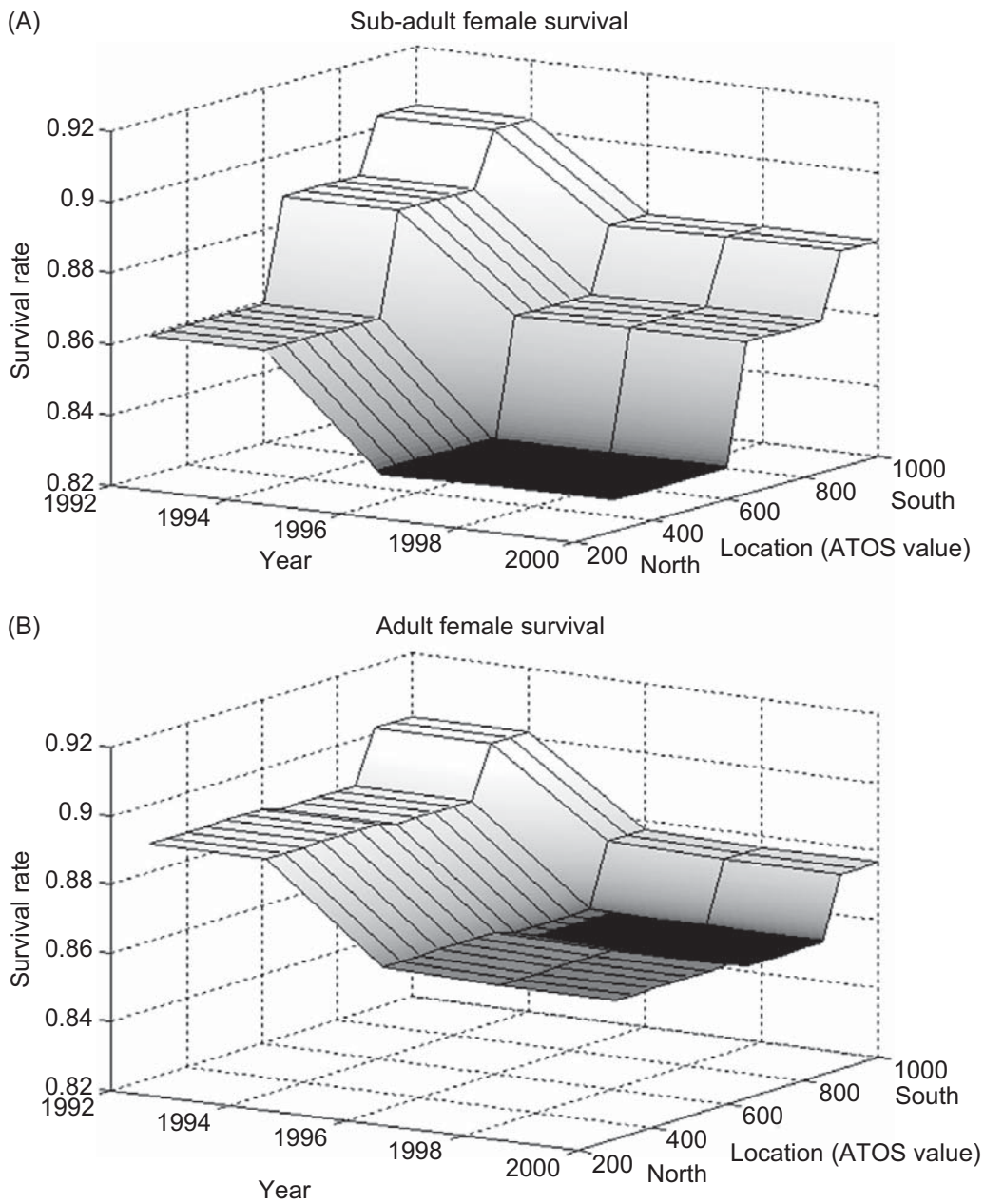


FIGURE 10.5 Spatial and temporal variation in sea otter survival rates in California during the 1990s plotted for sub-adult females (A) and adult females (B). The two horizontal axes are time (in yearly increments, 1992–2000) and geographic location within the range (units are 500 m increments along the coastline, ranging from Santa Cruz in the north to Pt. Conception in the south). The vertical axis is the model-estimated annual rate of survival for the indicated life-stage. *(Figure from Tinker et al. (2006a). Used by permission of The Ecological Society of America.)*

probability of persistence under various scenarios about initial population size and the nature of predator-induced mortality. The results of these simulations provided guidance on appropriate abundance thresholds for the up-listing and de-listing criteria (i.e., the abundance at which up-listing from

"Threatened" to "Endangered" status should be considered, and the abundance at which de-listing from "Threatened" status should be considered). Another PVA for Alaskan sea otters was developed by Bodkin and Ballachey (2010), designed to investigate the potential impacts of human harvests on local sea otter populations in southeast Alaska (Chapter 4). By parameterizing a matrix-based model with vital rates derived from stable, slowly growing and rapidly growing populations, and then simulating harvests of varying magnitudes and sex ratios, Bodkin and Ballachey determined what levels of take would be sustainable (i.e., would not drive the population to decline). They found that the level of additional mortality from harvest that was sustainable varied considerably, from just 0.5% increased mortality in stable populations with 1:1 harvest sex ratio, up to 27% increased mortality in rapidly growing populations with a 3:1 ratio of males to females in the harvest. Interestingly, although they found that male-only mortality maximized annual harvest in stable populations, they also noted that highly male-biased mortality in all simulations eventually led to low proportions of males in localized areas, leading to instability in projected populations over time. This result highlighted the need to account for localized sources of mortality in sea otter PVA models, due to the fact that sea otter populations tend to be structured at relatively small spatial scales.

The above examples demonstrate that it can be important to include spatial differences in population density and vital rates in conservation models. Another aspect of spatial dynamics that has been explored using models is changes in the distribution of sea otter populations. This was the focus of an analysis by Lubina and Levin (1988), who used a diffusion-based model to describe the rate with which the sea otter population in California was spreading northwards and southwards along the coast. This relatively simple model combines behavior (movement) and population growth, treating population spread as a diffusion process, more or less equivalent to the outward diffusion of a gas cloud released into a vacuum. The diffusion model estimates "invasion speed," V, or the rate at which the "population front" moves into unoccupied habitat:

$$V = 2(r_{\max} D)^{1/2} \tag{10.9}$$

Equation (10.9) predicts the rate of invasion into new habitat with only two parameters: $r_{\max}$ and D, the diffusion parameter, which has units of km^2 per unit time, and is a property of the relative mobility of individuals within the population. Specifically, in the case of population diffusion along a one-dimensional axis (i.e., the California coastline), D can be estimated as one half of the mean square net displacement per unit time of a typical individual (the net displacement of an individual is calculated as the straight-line distance between its location at time $t = 0$ and its location at time $t = 1$, and this is then squared to estimate mean square displacement). The diffusion

model of Lubina and Levin provides a good first approximation of how sea otter populations spread into unoccupied habitat, generally matching observed patterns at large scales although omitting many details. Some of the important details that the diffusion model does not incorporate include differences in how sea otters utilize different types of habitat, and the fact that male and female sea otters, and otters of different ages, tend to have different patterns of habitat use, mobility, and survival rates. Many of these sources of variation were later included in more elaborate integrodifference equation models of population spread in California (Krkosek et al., 2007; Smith et al., 2009; Tinker et al., 2008b). As with the simple diffusion models, integrodifference equation models are used to estimate the asymptotic wave speed, the rate at which a population front will advance into unoccupied habitat, based on the mobility and demographic rates of individuals within the population. Unlike the diffusion models, however, integrodifference equations can accommodate differences in the mobility, survival, and/or reproductive rates between individuals of different ages (or sexes), and also can handle frequency distributions of individual movement distances that are not normally distributed (e.g., skewed distributions where a few individuals move very great distances: Kot et al., 1996; Neubert and Caswell, 2000). By applying integrodifference equation models to the California sea otter population it was found that a skewed distribution of net displacement distances could explain the accelerating nature of range expansion in the earlier part of the twentieth century (Krkosek et al., 2007), and that differences between northern and southern rates of range expansion were potentially explained by differences in survival rates (Smith et al., 2009). A specific management application of an integrodifference equation model will be discussed below in "Applied Conservation Questions."

MODELS OF COMMUNITY DYNAMICS

Sea otters have long been recognized as keystone predators in nearshore ecosystems (Estes and Palmisano, 1974), which means that their presence and abundance in the ecosystem has inordinately strong impacts on the structure and dynamics of sub-tidal and inter-tidal community assemblages (see Chapter 2). The substantial ecosystem impacts of sea otters can be attributed to both direct and indirect effects of their predator–prey interactions with other species. Note that in ecology, the terms "direct effect" and "indirect effect" have very specific meanings: a species has a *direct effect* on another species if it actually eats (or is eaten by) that species, or otherwise directly affects the abundance of that species through a non-feeding interaction (e.g., parasitism and pollination). A species is said to have an *indirect effect* on another species if it affects the abundance of that species without actually eating (or being eaten by) that species, but the effect is mediated through one or more other species interactions (e.g., if species A eats species B, and species

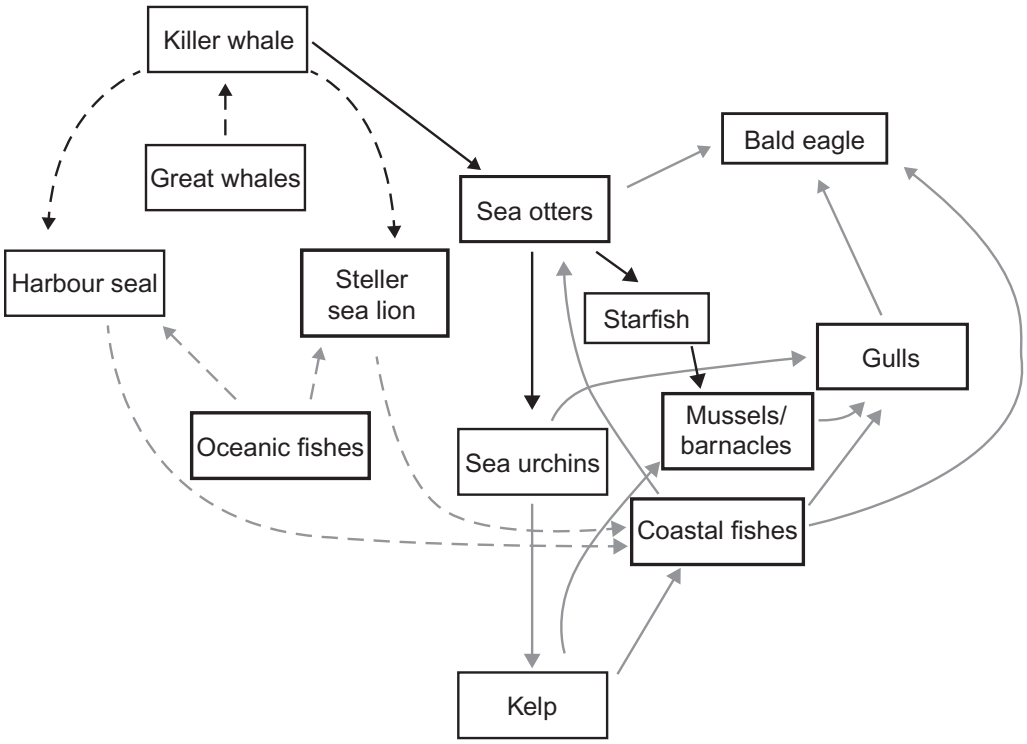


FIGURE 10.6 Food-web relationships among selected species in the North Pacific Ocean and southern Bering Sea. The arrows represent feeding linkages for which there are known (solid lines) or suspected (dashed lines) dynamic interactions. See text for explanations. *(Figure from Estes et al. (2009). Used by permission of the authors.)*

C also eats species B, then species A can affect species C indirectly via its impacts on species B). Direct and indirect effects can best be pictured using a food web (Figure 10.6), a graphical representation of the network of feeding interactions occurring within a specified community of plants and animals. The direct effects in a food web are represented by the arrows that indicate a feeding link between two species. Indirect effects are represented as the connections between two species that can be made by following a pathway through more than one arrow: for example, in Figure 10.6 an indirect effect between sea otters and coastal fish can be traced through links from sea otters to sea urchins to kelp to coastal fishes. If one begins to describe all possible indirect effects in a food web, it quickly becomes apparent that this kind of interaction network contains a great deal of potential complexity. How, then, do we begin to predict which interactions will be most important for maintaining stability of the community (or conversely, which interactions are most likely to de-stabilize the community)? This is exactly the type of question posed by a community ecologist, and multi-species interaction models have been used for many years as tools to help answer such questions.

One of the simplest and most well-known multi-species models to be applied to sea otters is a "trophic cascade" model, consisting of a vertical

cascade of feeding links across two or more "trophic levels" (e.g., a primary consumer feeds on a herbivore that feeds on a plant). In most rocky-substrate habitats across the North Pacific, sea otters tend to prey heavily on sea urchins, a relatively abundant and energy-rich invertebrate, and sea urchins in turn are one of the most voracious herbivores to consume the various algal species that make up kelp forests. The quantitative predictions of the three species trophic cascade model are straightforward and easy to test: when the primary consumer (sea otters) increases in abundance, we expect to see a decrease in the herbivore (urchins) and an increase in the primary producer (kelp), because sea otters have a negative *direct effect* on urchins and thus a positive *indirect effect* on kelp (Estes and Palmisano, 1974). These predictions have been tested repeatedly through "opportunistic experiments" (specifically, the reintroduction or natural recolonization of sea otters into unoccupied habitat) in many regions, from Alaska's Aleutian Islands to Vancouver Island in British Columbia, with results generally supporting the model predictions (Estes and Duggins, 1995; Watson and Estes, 2011). The trophic cascade model can be extended by adding additional levels: for example, adding a fourth trophic level (a secondary consumer) is predicted to reduce the abundance of the primary consumer, increase herbivore abundance, and thus decrease plant biomass. An opportunity to test the predictions of this model occurred in the early 1990s, when killer whales began to prey upon sea otters in southwest Alaska (Estes et al., 1998). Consistent with the model predictions, sea otters declined, sea urchins proliferated, and kelp forests across the Aleutian Archipelago were dramatically reduced, all within a period of 5–10 years (Estes et al., 2004).

While the trophic cascade model has been very useful for predicting changes in kelp forest habitat caused by the addition or loss of sea otters, it is obviously somewhat limited in scope because it accounts for just a handful of species. More elaborate food web models, such as the one depicted in Figure 10.6, are more difficult to interpret in terms of their predictions because of the vast number of possible indirect effects. In some cases qualitative interpretations of model dynamics are possible, such as the review by Estes et al. (2009) of the cascade of indirect effects that occurred after killer whale predation reduced sea otter populations across the Aleutian Islands: this strong direct effect apparently resulted from a dietary shift of certain mammal-eating killer whales, presumably in response to earlier declines in their preferred prey of Steller sea lions and harbor seals (Estes et al., 1998, 2009). Indirect effects of the killer whale–sea otter interaction included a two- to threefold decrease in the growth rates of barnacles and mussels (Duggins et al., 1989), a 10-fold decrease in abundance of some kelp forest fish such as greenling (Reisewitz et al., 2006), and a shift in the diet of bald eagles from largely fish and mammals to largely gulls and other marine birds (Anthony et al., 2008). These particular indirect effects were interpretable because the mechanisms were well understood (Estes et al., 2009); however, because the number of

potential indirect effects increases geometrically with the number of species in a food web, qualitative interpretations of more species-rich food web models can be problematic. There are mathematical tools for analyzing more rigorously the expected dynamics of multi-species assemblages (Allesina et al., 2008; Dunne, 2006; McCann and Hastings, 1997; McCann et al., 1998; Pascual and Dunne, 2006; Wootton, 2001), although these tools can also become overwhelmed by complexity and the uncertainty associated with quantifying each direct species interaction (Novak et al., 2011). One such multi-species model is "Ecopath," which traces the flow of energy through a food web using a series of mass-balance equations that describe the production, consumption, and loss of biomass for each species in the system at equilibrium (Pauly et al., 2000). An Ecopath model that included sea otters was assembled for the Prince William Sound ecosystem (Okey and Pauly, 1998); however, that model was focused primarily on the open-water food-web interactions in order to predict fisheries dynamics, and so the treatment of sea otters and their invertebrate prey was cursory at best.

SOME EXAMPLES: APPLIED CONSERVATION MODELS

In the history of sea otter conservation there have been a number of particular challenges for which very specialized models have been designed and brought to bear. These applied models often incorporate more than one element of the subjects discussed above (e.g., both behavior and population dynamics) as well as other subject areas, and were generally designed to address a very specific question. I will briefly discuss two examples—understanding oil spills and predicting population spread—to provide a flavor of some of the ways in which specialized models can be designed to explore and help answer challenging conservation questions.

One of the most devastating anthropogenic impacts to sea otters, and to coastal ecosystems more generally, has been the occurrence of large oil spills. Perhaps the most well known of these to affect sea otters was the 1989 EVOS. Sea otters are particularly susceptible to coastal oil spills because of their nearshore distribution, but also because of idiosyncratic aspects of their biology that make them particularly vulnerable to oil in two ways: (1) they are dependent upon the integrity of their fur for thermoregulation, and oiling of their fur compromises its integrity as an insulator (Davis et al., 1988) and can lead to hypothermia and death (thermal challenges can be exacerbated by acute poisoning when they groom their fur and incidentally ingest and inhale oil); and (2) they feed on bottom-dwelling invertebrates in the subtidal and inter-tidal zones, which often require extraction from the substrate by digging, and this makes them susceptible to direct exposure to and ingestion of oil while foraging, potentially leading to chronic health effects. The first of these impacts tends to manifest itself immediately after an oil spill and can result in extensive mortality over large areas (Bodkin et al., 2002; Bodkin and Weltz, 1990; Degange and Lensink, 1990; Garshelis, 1997;

Williams et al., 1988). The second of these impacts, toxicological effects from oil ingestion, can continue to affect sea otters for months or years after the oil spill because oil can remain in the environment in inter-tidal sediments and sea otters may be repeatedly exposed during foraging (Ballachey et al., 2002). Using archival time depth recorder data and models to assign dive types, Bodkin et al. (2012) estimated sea otters foraging in oiled areas of Prince William Sound were exposed to lingering oil from 2 to 24 times per year, more than 15 years after the spill. Effects of such exposure can be difficult to measure and the health effects may be sub-acute and effectively "invisible," yet they can still have population-level impacts by reducing survival. To address this conservation concern, Harwell and colleagues (2010) developed a risk assessment model to assess the potential for toxicological harm to sea otters from buried EVOS subsurface oil residues (SSOR). Their model was an "individually based model," meaning that they used computer-based simulations of individual behavior, iterated many times. They incorporated multiple pathways of potential exposure to SSOR into their model, including oil that becomes suspended in the water column and is taken up by filter feeding invertebrates (and thus otters are exposed through diet); otters are directly exposed to SSOR as they dig pits in the inter-tidal zone to extract clams and other infaunal prey. To parameterize their model they used data on sea otter behavior (specifically activity budgets, diet composition, and feeding dive locations) as well as environmental data on shoreline substrate composition and oil residue levels in different substrate types. They ran 500,000 simulations of individual foraging otters, estimated exposure levels to SSOR for each simulated otter, and compared these to chronic toxicity reference values approved by the US Environmental Protection Agency. They concluded that although sea otters continued to be exposed to oil, the maximum exposure rate would not result in sufficient exposure to cause any health effects (Harwell et al., 2010). These results suggest that direct exposure to residual oil from EVOS should not be a factor in limiting sea otter populations in western Prince William Sound. This conclusion was contradicted by the results of Monson et al. (2000, 2011), summarized above in the discussion of population models, which found evidence for continued demographic impacts from EVOS. Further complicating the picture are analyses conducted by Ballachey et al. (2003), which examined the relation of various blood parameters to survival rates of juveniles in eastern and western Prince William Sound, and by Miles et al. (2012), which examined relations between oil exposure and the expression of genes. These authors found that differences in blood parameters and gene transcription in the area affected by EVOS were consistent with continued exposure to oil, and also possibly contributed to the lower survival rates in this group. So how should we proceed when different models produce contradictory findings? This is perhaps a good time to bear in mind the famous quote by the late George Edward Pelham Box: "Essentially, all models are wrong, but some are useful." None

of these models should be confused with reality, though all of them seek to provide useful explorations of some specific aspect of the real world. In this case there are empirical data which suggest some continued biological exposure to oil (Ballachey et al., 2003), contradicting at least some of the predictions of the risk assessment model developed by Harwell et al., but the question of actual population-level effects is more complex. Both the Harwell et al. (2010) model and the Monson et al. (2000, 2011) models make a number of simplifying assumptions, and these must be examined closely in order to evaluate the degree of reliability in the results of each paper. Ultimately, when two models that appear to be founded on reasonable assumptions produce contradictory results, the safest conclusion is that additional investigation into the question is warranted.

Despite continued debate over the long-term impacts of EVOS on sea otters in Prince William Sound, the EVOS has resulted in an enormous amount of baseline information about the Prince William Sound ecosystem, as well as the short-term and long-term effects of oil spills on ecosystems in general (Peterson et al., 2003). Some of this information has been used to inform conservation efforts aimed at sea otter populations elsewhere, particularly in California. Brody et al. (1996) used data on how EVOS had affected sea otter survival in Prince William Sound, specifically how those impacts varied with time and distance from the point of origin of the spill, to parameterize a simulation-based risk assessment model for California sea otters. Their model sought to estimate the population-level impacts of oil spills of similar magnitude if they should occur at different locations along the California coast, predicting morality of sea otters as a function of how an oil slick would disperse along the coast, how many otters it would encounter, duration of oil-otter encounters, and time since the spill. They found that an oil spill occurring at the Monterey peninsula could expose some 90% of the California sea otter population at that time to oil and kill at least 50% of individual otters (Brody et al., 1996). These model results supported an earlier, somewhat unusual model by VanBlaricom and Jameson (1982), which took advantage of an accidental lumber spill off central California during the winter of 1978, and spread to cover most of the sea otter's distribution within 4 weeks. These authors noted that the movement rates of lumber were very similar to those of oil slicks observed elsewhere, and their observations indicated that a major oil spill could expose most of the population to oil contamination within a month of a spill. These sobering findings were considered by the Endangered Species Recovery Team in setting de-listing criteria for southern sea otters, and in advising the US Fish and Wildlife Service on Management options (USFWS, 2003).

Management and conservation of wildlife species nearly always demands that we try to forecast the future based on past events, to gauge how a population will respond to some anticipated conservation challenge. The PVA described above represent one type of forecasting model, one that seeks to

assess the future viability of a population given a range of known or anticipated threats. A more specific management question in California required a more specialized forecasting model, one that combined information on population vital rates and individual behavior in order to forecast the future range expansion of southern sea otters. In particular, as part of the Environmental Impact Statement on the translocation of southern sea otters to San Nicolas Island (USFWS, 2012), the US Fish and Wildlife Service requested a model to forecast the future spatial extent of the sea otter population in southern California, and the number of animals projected to be south of Pt. Conception at various future times. This information was required as part of the Services' re-evaluation of the "No Otter Zone" policy that, in theory, would restrict sea otter range expansion south of Pt. Conception. Tinker and colleagues (2008b) developed a spatially structured integrodifference equation model with which to produce such a forecast. As discussed above (see "Population Models"), integrodifference equations can be used to estimate the rate at which a population will "spread" by making use of data on stage-specific vital rates and mobility. This matrix-based model utilized previously published estimates of survival and reproductive rates from various parts of the sea otter distribution (Tinker et al., 2006a) and combined these with data on individual movement behavior collected from radio telemetry studies, to predict both the speed with which the population would spread into habitat south of Pt. Conception, as well as the growth in numbers in this region. The model was initiated using data from the 2004 census, and predicted that by 2014 there would be 112 sea otters southeast of Pt. Conception (95% confidence limits = 69 − 163) and the southern range limit would be between Goleta and Carpentaria, California. These forecast estimates were used by Fish and Wildlife to estimate biological and socioeconomic impacts of allowing sea otters to naturally recolonize habitat south of Pt. Conception (USFWS, 2012), and factored into the decision to end the "No Otter" zone (Chapter 12).

CONCLUSION

The examples described above (and summarized in Table 10.1) are by no means an exhaustive review of all models developed by researchers investigating sea otters and their ecosystems; however, they do provide an overview of the diversity of topics and sea otter studies in which models have played an important role. At this point it may be useful to take a figurative step back and evaluate some of the more general lessons that may be gleaned from these examples and applied to other species and other systems. Models are an important tool for wildlife conservation, and when one considers the sea otter models described above, some little pearls of wisdom emerge that explain why they were possible and often successful, and what we learned from them.

TABLE 10.1 A Summary of Select Modeling Studies in Sea Otter Conservation

Published Paper (see References for Full Citations)	Subject Area Addressed									
	Behavior		Population				Community		Applied	
	Foraging	Movement Habitat Use	Growth/K	Demography Matrices	PVA	Spatial	Trophic Cascade	Food Web	Oil Spill	Risk Assessment
Ballachey et al., 2003, Can. J. Zool. 81	X			X					X	
Bodkin and Ballachey, 2010, USGS Report 2010				X	X					
Bodkin et al., 2012, Marine Ecology-Progress Series 447	X	X								X
Brody et al., 1996, Marine Mammal Science 12				X					X	
Coletti, 2006 Masters Thesis, U. New Hampshire		X								
Dean et al., 2002, Marine Ecology-Progress Series 241	X									

Eberhardt,1995, Journal of Wildlife Management 59				X						
Estes et al., 1981, Worldwide Furbearer Conference	X									
Estes et al., 1998, Science (Washington DC) 282							X	X		
Estes et al., 2003, Journal of Animal Ecology 72	X									
Estes et al., 2004, Bulletin of Marine Science 74							X	X		
Estes et al., 2009, Phil. Trans. Royal Soc. 364							X	X		
Estes, 1990, Journal of Animal Ecology 59			X							
Garshelis, 1997, Conservation Biology 11				X						
Gerrodette, 1987, Ecology 68			X							

(*Continued*)

TABLE 10.1 (Continued)

Published Paper (see References for Full Citations)	Subject Area Addressed									
	Behavior		Population				Community		Applied	
	Foraging	Movement Habitat Use	Growth/K	Demography Matrices	PVA	Spatial	Trophic Cascade	Food Web	Oil Spill	Risk Assessment
Gregr et al., 2008, JWM 72		X								
Harwell et al., 2010, Hum. Ecol. Risk Assess. 16									X	X
Johnson et al., 2009, PNAS 106		X								X
Kage, 2004, Masters Dissertation, UC Santa Cruz		X								
Krkosek et al., 2007, Theor. Popul. Biol. 71						X				
Kvitek and Oliver, 1992, MEPS 82	X									
Laidre et al., 2009, J. Mammal. 90		X								
Laidre and Jameson, 2006, J. Mammal. 87	X									

Lubina and Levin, 1988, American Naturalist 131						X				
Monson et al., 2000, PNAS 97				X					X	
Monson et al., 2011, Ecol. Appl. 21				X		X			X	
Ostfeld, 1982, Oecologia 53	X									
Siniff and Ralls, 1991, Marine Mammal Science 7				X						
Smith et al., 2009, Ecology 90						X				
Tinker et al., 2006, Ecol. Appl. 16				X						
Tinker et al., 2008b, Ecol. Appl. 18		X		X		X				
Tinker et al., 2008a, PNAS 105	X	X								
Tinker et al., 2009, Evol. Ecology Research 11	X									

(*Continued*)

TABLE 10.1 (Continued)

Published Paper (see References for Full Citations)	Subject Area Addressed									
	Behavior		Population				Community		Applied	
	Foraging	Movement Habitat Use	Growth/K	Demography Matrices	PVA	Spatial	Trophic Cascade	Food Web	Oil Spill	Risk Assessment
Tinker et al., 2012, Ecology Letters 15	X									
Udevitz and Ballachey, 1998, JWM 62				X						
USFWS, 2010, SWAK sea otter Draft Recovery Plan				X	X			X		
VanBlaricom and Jameson, 1982, Science 215									X	

1. Long-term data sets are powerful. One of the most rewarding aspects of working in the world of sea otter conservation is that our predecessors in this field had the foresight to initiate long-term monitoring programs, and as a result there is an embarrassment of riches when it comes to long-term data sets. Models are most useful in conservation if they are based on a solid understanding of the system in question AND can be parameterized with values that reflect something close to the full range of variation and uncertainty that exists in that system. For example, having 5 years of data on which to base a population growth model is certainly better than nothing; however, it is unlikely that those 5 years will provide a full picture of the range of variation in growth rates (i.e., really good years and really bad years). In contrast, many of the examples discussed above were based on >30 years of sequential population estimates, and in many cases time series of similar duration for other components of the ecosystem (e.g., kelp and urchins). Instinctively we tend to place more confidence in the projections of models that are built on such long-term data sets, and for good reason. What if that type of data set is simply not available for a species of concern? For species in which long-term data sets simply don't exist, it is often appropriate to look at closely related species where data may be more plentiful and use these data sets to parameterize models. As long as one allows for suitable amounts of uncertainty (either explicitly in the model, or implicitly in terms of interpretation of results), this approach can be useful for designing conservation models for data-poor species.
2. Combining multiple data types can be a good thing. Particularly in the modern age of information theory and Bayesian estimation techniques, it is very possible and indeed desirable to bring together and integrate multiple data types, as doing so can make model results more robust and often provide more insight. For example, estimation of vital rate parameters used in the matrix projection models developed for Alaska and California (Monson et al., 2011; Tinker et al., 2006a) was based on multiple independent data sets (in the case of the Alaska model, age distributions of both living and dead animals and survey estimates of population size; in the case of the California model, age distributions of dead animals, survey estimates of population size, and mark-recapture data from tagged animals). Maximum likelihood methods were used to extract far more information from these combined data sets than could be gained from any one by itself. The synthesis of diverse data types is indeed one of the main advantages provided by mechanistic models, in contrast to more traditional statistical analyses of single data sets, and in many cases the results that emerge can be surprising and non-intuitive.
3. In complex systems, models can be invaluable for elucidating mechanisms. Community models such as those discussed above provide an excellent illustration of how models can provide insights into complex

and otherwise intractable systems. In the Aleutian Island example, many apparently unrelated phenomena had been observed independently: declines in Steller sea lions and other pinnipeds in the pelagic realm, sea otter declines in the nearshore zone, reductions in kelp abundance, and declines in certain fish populations. Because none of these species have direct interactions with each other, it was a stretch to imagine that they were all connected; however, a food web model provided the conceptual and quantitative means of describing the network of indirect effects that linked them all together. In this sense models provided a feasibility test, answering the question of how likely or unlikely it was that killer whales could cause the sea otter decline, or that reductions in sea otters could lead to the observed changes in kelp and fish abundance. Just as importantly, models can be critical in understanding and interpreting "emergent dynamics" of complex systems. Emergent dynamics are, as the name suggests, phenomena that emerge from the complex suite of interactions of the system as a whole and are not predictable from examining any individual part of the system. It is generally not possible to examine a single pair of interacting species and predict whether impacts of that species' interaction on the community as a whole will be large or small. However, a food web model that incorporates multiple species (and thus includes both direct and indirect effects) can be used to assess emergent properties such as the relative importance of each pairwise interaction, and how the loss of any one species will affect the stability and resilience of the entire community. Although such model predictions obviously need to be empirically tested, they are nonetheless an important tool in conservation because they provide insight into when and how a threat to a single species will propagate throughout the community and have ecosystem-level impacts.

4. Models designed to answer questions about basic biology can provide unexpected insights into conservation questions. Some of the sea otter models described above would not initially seem to be tools for conservation. For example, models used to understand foraging ecology might seem interesting from a purely academic standpoint, but are perhaps less so when it comes to species conservation. And indeed, many models are initially designed to answer basic questions about organismal biology or ecology: how does an individual sea otter select prey, how does diet change as competition for food increases, how far away will a sea otter move over the course of a year? However, it is well known that effective conservation strategies are built on a solid understanding of natural history, and in addition to answering the ecological questions for which they were designed, such models may also provide unexpected but important insights into conservation challenges. For example, models designed to investigate individual foraging decisions (Tinker et al., 2009) and the network structure of predator–prey interactions at the individual level (Tinker et al., 2008a,

2012) showed that sea otters in high-density populations exhibited pronounced diet specialization, with individuals falling into one of a number of distinct diet modules. Making use of this information, Johnson et al. (2009) developed an epidemiological model to investigate whether diet specialization was a risk factor for exposure to land-based disease pathogens. The results of this model showed that certain prey specializations, including a diet high in marine turban snails, greatly increased risk of infection with protozoan parasites. Thus models initially developed to understand foraging behavior unexpectedly led to information that is helping conservation biologists determine how disease-causing parasites on land are finding their way into coastal marine food webs.

As computing capabilities become ever greater, along with technological innovations that increase our ability to collect and access large amounts of data, it is inevitable that quantitative models will become more and more critical for synthesizing and making sense of this information in order to solve conservation problems. The examples discussed here from the field of sea otter conservation provide a synopsis of how models have been used in the past, and many of the basic principles and lessons learned will apply to future models as well. However, more computationally intensive techniques such as individually based or agent-based models will likely become more widespread. Future directions in quantitative models also promise to bridge multiple conceptual levels, linking cellular-level processes to physiological and behavioral dynamics at the organismal level, and linking these to population-, community-, and ultimately landscape-level phenomena. Such models will play a crucial part in solving some of the most challenging conservation problems we now face, such as climate change, loss of bio-diversity, invasive species, and other large-scale environmental drivers. And given their important role as an apex predator in nearshore ecosystems, and their tractability for scientific study, sea otters will likely continue to provide an excellent model system for developing new conservation models.

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