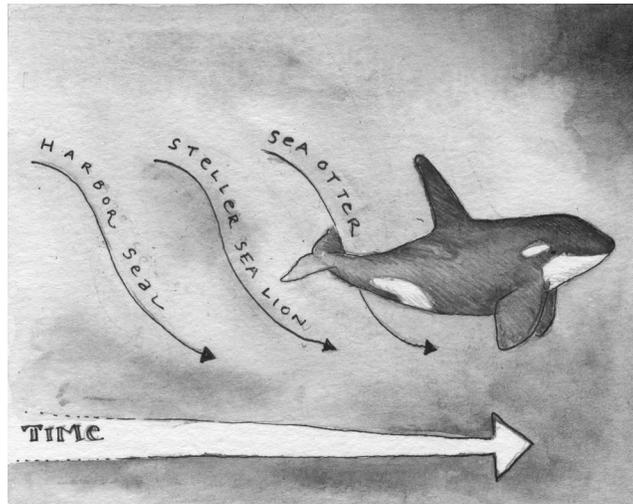


Mangel, M. and N. Wolf. 2006. Predator diet breadth and prey population dynamics. Pg 279-285 in **Whales, Whaling, and Ocean Ecosystems** (JA Estes, DP Demaster, DF Doak, TM Williams and RL Brownell, Jr. editors). University of California Press, Berkeley

Predator Diet Breadth and Prey Population Dynamics Mechanism and Modeling

MARC MANGEL AND NICHOLAS WOLF



The notion that the sequential megafaunal collapse of several subpopulations of harbor seal, Steller sea lion, and sea otter (sensu Springer et al. 2003) is due to killer whale predation relies on the assumption of expanding diet breadth for orcas. That is, the putative mechanism for the decline is a preference of killer whale for large whale species, but an inclusion of certain populations of harbor seal, fur seal, Steller sea lion, and sea otter as the preferred prey types become less available. When considering the observed sequential declines, a number of features need to be explained (Figure 2 of Springer et al. 2003): (1) the ordering of the declines (harbor seals first, Steller sea lions second, sea otters third), and (2) the apparent lack of inclusion of one prey type (as measured by a lack of decline) until the other prey types are nearly exhausted. For simplicity, we focus on harbor seals, Steller sea lions, and sea otters.

In this chapter, we use a combination of models from behavioral and population ecology to address these questions, and in doing so, elucidate these two points and certain other aspects of the community dynamics. Our goal is to show how the synthesis of two different scientific traditions (the literature on prey choice by predators and the literature on population dynamics) can lead to new understandings and new empirical challenges. Indeed, in anticipation of the meeting that led to this chapter, one of us (MM) asked a

colleague about this question and was told, “There is actually quite a large literature on body composition of pinnipeds although I can’t recall anybody looking at them from the perspective of the prey” (I. Boyd, personal communication to MM, February 25, 2003). Each of these scientific traditions has an enormous literature and in order to keep the paper of reasonable length, we provide minimal citation to that literature, but an interested reader will have no trouble finding entry points, some of which we point out at relevant moments in the chapter. An evolutionary understanding of feeding behavior turns out to be a good starting point for combining the traditions of prey choice by predators and population dynamics.

The Four Questions of Tinbergen and the Diet Choice Model

Niko Tinbergen (1963) observed that, regarding any behavior, four questions need to be considered:

1. How does behavior develop within an individual (ontogeny)?
2. What is the evolutionary history of the behavior (phylogeny)?

3. What is the physiological mechanism of the behavior (proximate mechanism)?
4. What is the survival and/or reproductive value of the behavior (ultimate mechanism)?

The classic diet choice model (Stephens and Krebs 1986; Mangel and Clark 1988; Clark and Mangel 2000) begins with the assumption that Darwinian fitness (the long-term number of descendants, often approximated by the expected lifetime reproductive success) is maximized when the rate at which energy is obtained is maximized. As we note below, killer whales often hunt in groups. Group hunting is a complicating factor, but it does not necessarily affect the validity of the assumption of rate maximization. For example, energy obtained from the prey may simply be divided among the individual predators in the group. The current formulation of our model assumes that group size is fixed with respect to prey type, and that food is divided equally among members of the group, at least on average. The numerical values of energy gain that we report correspond to the share of an individual. We recognize that the strategy killer whales use in hunting may depart from this assumption, but it seems a reasonable starting point in this paper. Subsequent research should investigate the robustness of our conclusions to this hypothesis (see Discussion).

In this classic model of diet choice (Stephens and Krebs 1986), prey are characterized by three values. These are (1) the energy, E_i (units, kcal), obtained by chasing, killing, and consuming a single individual of prey type i ; (2) the time, h_i (units, hours), needed to “handle” (chase, kill, and consume) a single individual of prey type i ; and (3) the encounter rate, λ_i (units, 1/hours), with prey type i . In the standard model of diet choice, the encounter rate is treated as fixed; in the analysis that we conduct next the encounter rate will vary according to the population dynamics. In particular, the encounter rates with a prey species will decline as its population declines.

We next assume that the only activities of the predator consist of searching for prey and handling prey. Thus, any long period of time T is divided into a total time spent searching S and a total time spent handling H . These assumptions are sufficient to compute the long-term rate of energy gain for any diet selection rule that the predator uses. We then choose the diet selection rule that maximizes the rate of energy return.

The key results of this theory are that items are ranked by profitability, E_i/h_i , that a prey species is either completely included in the diet or not (there are no partial preferences), and that only the most profitable prey species ($i = 1$) is included as long as

$$\lambda_1 > \frac{E_2}{E_1 h_2 - E_2 h_1} \quad (21.1)$$

where $i = 2$ corresponds to the next most profitable prey species. This equation may be derived in another manner,

assuming that at each moment the predators are maximizing the rate of energy gain from an encountered prey. If an individual of prey species type 2 is encountered and consumed, the rate of energy flow to the predator from this prey is E_2/h_2 . On average, taking into account both handling time and search time ($= 1/\lambda_1$), the rate of energy flow (the profitability) to the predator from the preferred prey species is $E_1/(h_1 + 1/\lambda_1)$, and we predict that the predator will take only the most profitable prey as long as $E_1/(h_1 + 1/\lambda_1) > E_2/h_2$, which can be rearranged to give Equation 21.1.

Equation 21.1 defines a *switching value* for the encounter rate with the most profitable prey species. Note that the right-hand side of this equation does not contain the encounter rate with the second most profitable prey species. That is, as long as the most profitable prey species is sufficiently abundant, we predict that it will be the only species selected by the predator, regardless of the abundance of other prey types. Thus, a predator foraging optimally, according to this description, on a high initial density of its most profitable prey species is predicted to eat only that species until it is sufficiently depleted. Once the most profitable prey species is sufficiently depleted, the predator is predicted to expand diet breadth and include the second most profitable prey species.

Equation 21.1 is generalized by considering the rate of energy return, R_k , when the most profitable k prey types are included in the diet:

$$R_k = \frac{\sum_{i=1}^k E_i \lambda_i}{1 + \sum_{i=1}^k h_i \lambda_i} \quad (21.2)$$

The first link between predator diet breadth and prey population dynamics is the assumption that the encounter rates are determined by prey abundance. That is, if $N_i(t)$ is the abundance of prey type i at the start of year t , we assume that

$$\lambda_i = q_i N_i(t) \quad (21.3)$$

where q_i is a measure of the search effectiveness of the predator for prey species i . It has units of rate per prey individual. We recognize that transient killer whales do not hunt as individuals but as pods of two to seven animals when preying on relatively small prey such as pinnipeds. Even so, this assumption is a reasonable starting point since any additions make the analysis more complicated (e.g., Mangel and Clark 1988, especially Chapter 3).

There is another interpretation of q_i , and it is this interpretation that allows us to couple the diet choice and prey population dynamics. For simplicity, consider a single, focal prey individual and a single predator. Equation 21.3 is equivalent to the assumption (Hilborn and Mangel 1997) that in a small interval of time, dt , the probability of the prey encountering the predator and being killed is approximately

$q_i dt$ (it is actually $q_i dt + o(dt)$, where $o(dt)$ represents terms that are higher-order powers of dt ; see Hilborn and Mangel 1997). This can be integrated (Hilborn and Mangel 1997) over a year to show that the probability that an individual of the focal prey avoids predation by a single orca is $\exp(-q_i)$. If there are $O(t)$ orcas present at the start of year t , and the predators do not interfere with each other, the probability that a focal prey escapes predation is $[\exp(-q_i)]^{O(t)} = \exp[-q_i O(t)]$, and we thus conclude that the fraction of prey experiencing predation will be $1 - \exp[-q_i O(t)]$. This assumes, of course, that the prey species we are discussing is included in the diet and that the predators are insatiable (we discuss the latter assumption later in the paper). As described above, the hunting of killer whales in pods may require reinterpretation of this derivation; in such a case $O(t)$ would represent the number of hunting groups and q_i would represent the hunting effectiveness of a group. (Once again, see Mangel and Clark 1988, Chapter 3.)

Coupling Diet Choice and Population Dynamics

We now couple prey dynamics and predator diet choice. To do this, we explicitly separate out the orca predation from other sources of regulation of the prey at the level of the population. In the absence of predation by orcas, we assume that the i th prey species grows according to the a-logistic model

$$N_i(t+1) = N_i(t) + r_i N_i(t) \left[1 - \left(\frac{N_i(t)}{K_i} \right)^a \right] \quad (21.4)$$

where we set the parameter $a = 2.4$ (Taylor et al. 2000), although the actual range may be 1–8 and 2.4 is used out of tradition (D. DeMaster, personal communication). In addition, r_i is the maximum per capita growth rate (corresponding to low population sizes), and K_i is the carrying capacity of species i .

Suppose now that predator diet breadth is fixed for the course of a year and we define an acceptance variable according to $S_i(t) = 1$ if the i th prey species is included in the diet and $S_i(t) = 0$ if the prey species is not included in the diet. Combining the result from the end of the last section with Equation 21.4, the prey population dynamics become

$$N_i(t+1) = N_i(t) + r_i N_i(t) \left[1 - \left(\frac{N_i(t)}{K_i} \right)^a \right] - S_i(1 - e^{-q_i O(t)}) N_i(t) \quad (21.5)$$

and these are the equations that will allow us to predict the population dynamics of the prey, as a function of the predator's diet choice behavior. Note that in deriving this equation we have assumed that all killer whales (or killer whale pods more specifically) behave similarly. This is likely not true in the sense that pods develop expertise for different prey

species and there is inertia when trying to learn how to forage on new species. But, once again, these are elaborations awaiting future work.

To begin, let us hold the orca population constant, so that $O(t)$ does not depend on time. We may then ask for the steady states of the prey population assuming that they are included in the diet, which are population sizes for which

$$r_i \bar{N}(t) \left[1 - \left(\frac{\bar{N}(t)}{K_i} \right)^a \right] = (1 - e^{-q_i O(t)}) \bar{N}(t) \quad (21.6)$$

and for which one solution always is $\bar{N}_i = 0$, corresponding to extinction of the prey. The other solution can be envisioned as the intersection of the line on the right-hand side with the parabola-like curve on the left-hand side (Figure 21.1). At this point of intersection, removals ("harvest") by the predators balance population growth ("production") by the prey.

Parameter Estimates and Sample Calculations

In the Chapter Appendix, we use the theory developed so far to determine the conditions of parameters in which a cascade is predicted. There we show that there are two sets of conditions, one involving 9 parameters and the other involving 14 parameters. Rather than conducting such a full analysis here to examine the plausibility of the diet breadth hypothesis, we will explore the numerical iteration of Equation 21.5. In order to use Equation 21.5 to explore prey population dynamics as a function of predator diet breadth, we need estimates of the various parameters. Some of these have simply not been measured, or can only be estimated for some of the species. Even so, it is instructive to choose parameters and estimate the dynamics.

Matkin et al. (2002) estimate about 200–300 transient killer whales in Alaska, so that we hold $O(t)$ constant at 200; and, lacking any information, we set $q_i = 0.002$ for each species. Note that it is the product $q_i O(t)$ that matters. In this case, the product is 0.4, implying that killer whales, once they have added a prey species to the diet, can take about 40% of the population per year. Although this appears to be a large fraction, the reader should recognize that there are no other sources of mortality in the model.

Regarding the information that is needed for diet choice calculation, Barrett-Lennard et al. (1995, p. 12) report the following data, based on multiple sources: killer whales take about 30 minutes to kill and consume harbor seals and about 1–2 hours to kill and consume Steller sea lions. Hence we set $h_1 = 0.5$ hr, $h_2 = 2.0$ hr. We lacked data for sea otters, so we set $h_3 = 0.25$ hr.

Barrett-Lennard et al. (1995) also report that when preying on harbor seals and southern sea lions, killer whales predominantly attack and take pups and juveniles (50–80% of the kills or attacks). We lack specific data on energy content of the prey species, which is required for the parameter E_i .

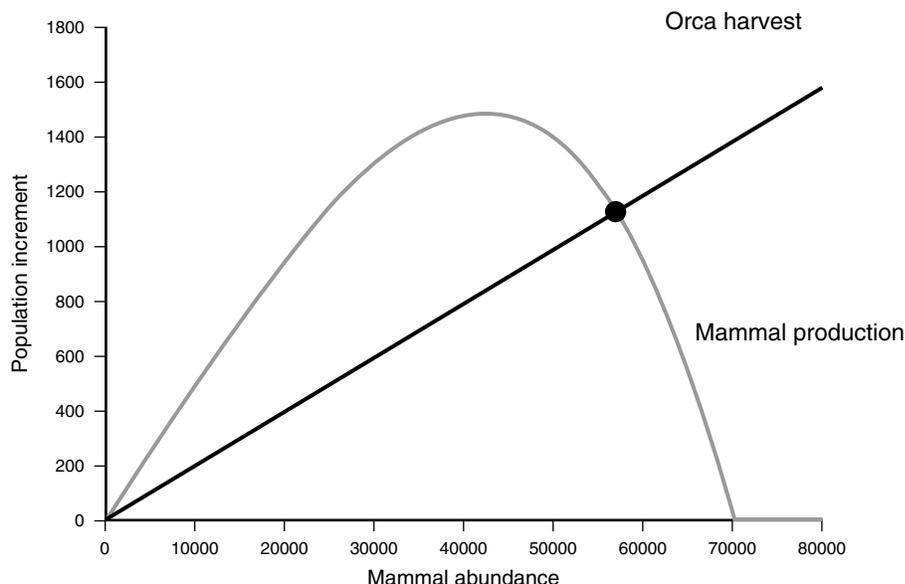


FIGURE 21.1. If the number of orcas is held constant, the steady-state population size of the prey species is determined by the balance between biological production (the curve) and the harvest taken by orcas (the line). Since the slope of that line is proportional to $q_i O$, increasing either the number of orcas or the efficiency with which they can find prey will rotate the line counterclockwise and will thus decrease the steady-state population size of the prey species. Furthermore, if the slope of the line is greater than the slope of the growth curve at the origin, the only potential steady state is that which corresponds to extinction of the prey. Here we have explicitly shown the case in which take by orcas leads to a steady state in which the prey species persist (at the intersection of the curve and the line). However, for the megafaunal collapse to occur, the parameters should be such that the only steady state is the origin.

However, we assume as a first approximation that body mass is a reasonable measure of energy content. Harbor seals are about 10 kg at birth and about 150 kg (males 170 kg, females 130 kg) at maturity; Steller sea lions about 20 kg at birth and 350 (female)–1100 (male) kg at maturity; and sea otters about 2 kg at birth and 40 kg (males 45 kg, females 33 kg) at maturity (Reeves et al. 2002). We do not know the mixture of pups, juveniles, and adults of any of the species taken by killer whales; this is another empirical question.

Lacking such information, we proceed as follows. We assume that E_i in Equations 21.1 and 21.2 is a fraction f of the mass of mature animals, where f is the assimilation efficiency divided by the killer whale group size. Note, however, that if this fraction is the same for all the prey species, then the particular value of the fraction has no effect on the diet choice rule in Equation 21.1 as it appears in both the numerator and the denominator. Furthermore, the relative variation in mass at maturity of harbor seals and sea otters is small, so we stipulate that $E_1 = 150$ kg and $E_3 = 40$ kg, respectively. On the other hand, Steller sea lions show a much greater size dimorphism, so we will treat E_2 as a parameter in our investigations.

Following Peters (1983), we assume that maximum per capita growth rate of species i , r_i , is related to female mass at maturity, W_i , according to $r_i = bW_i^{-0.26}$, where we picked the

constant b so that the maximum per capita growth rate of otters was 0.1/yr. The allometry then gives 0.07 and 0.05 for seals and sea lions, respectively. These may be a bit low; Taylor et al. (2000) indicate a value of 0.12 for harbor seals, and 0.2 and 0.09 may be more appropriate for otters and sea lions, respectively (D. DeMaster, personal communication). In the conditions that characterize the cascade (given in the Chapter Appendix), we show that these parameters are confounded with the number of orcas and the search efficiency of the orcas, so that determining the precise values of one set of parameters without knowing the others provides little advantage. Estimates of carrying capacities for any population of marine mammals are difficult to measure, and the carrying capacities themselves will surely change on a number of different time scales. For purposes of computation and illustration, we set the carrying capacities to be the maximum observed population sizes (about 20,500 in 1964, 70,000 in 1979, and 52,000 in 1959 for seals, sea lions, and otters, respectively).

We start each population at its carrying capacity, and we use Equation 21.2 to determine the diet breadth of the killer whales, and Equation 21.5 to iterate the population dynamics forward. The key result is shown in Figure 21.2, in which we have fixed all parameters in the model except E_2 (which is now a proxy for energy content of a sea lion). Because all

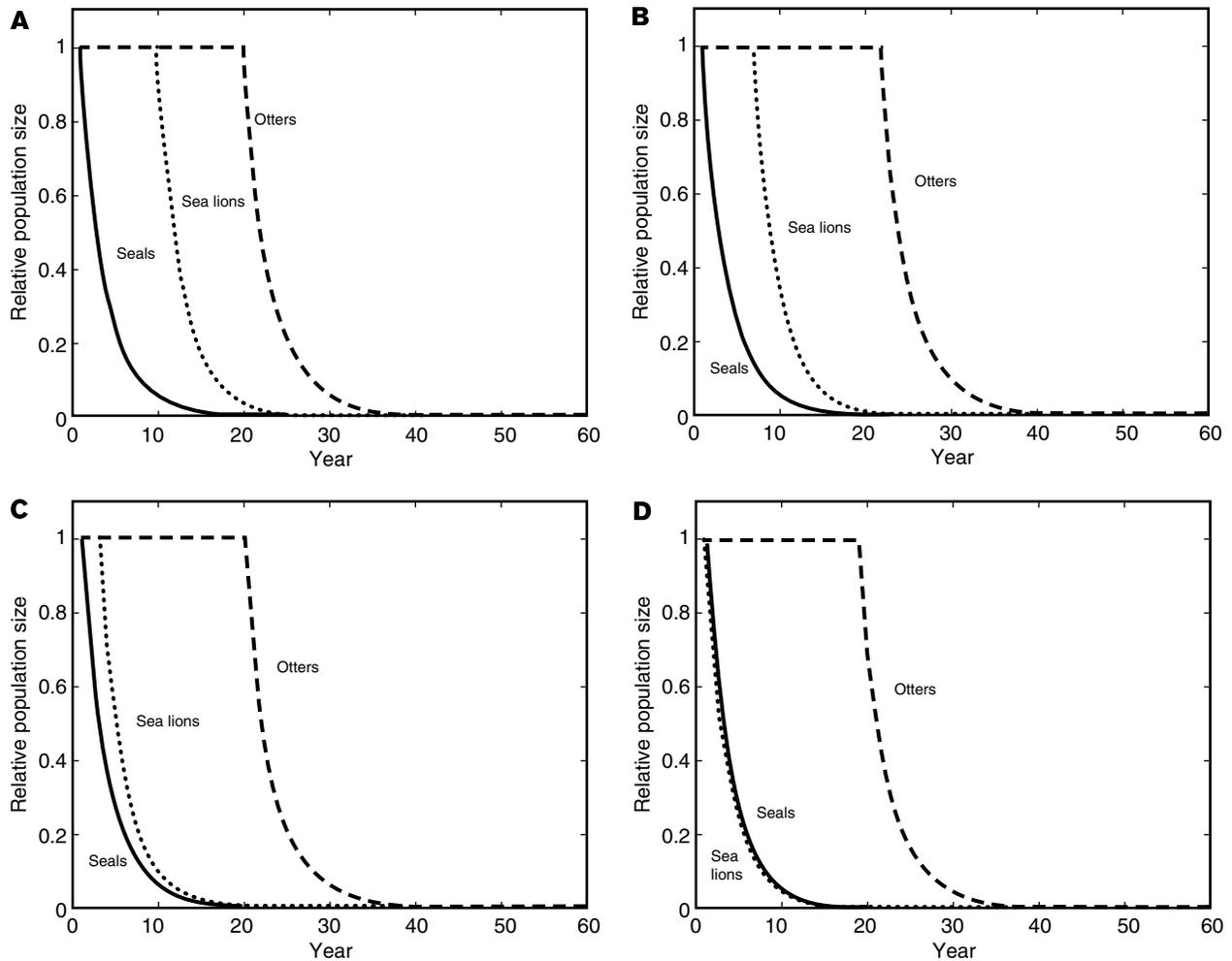


FIGURE 21.2. Predicted population dynamics of harbor seals, Steller sea lions, and sea otters, assuming the dynamics given by Equation 21.5, and diet breadth determined by Equation 21.2. We have held all parameters except E_2 constant ($h_1 = 0.5$ hr, $h_2 = 2$ hr, $h_3 = 0.25$ hr, $E_1 = 150$ kg, $E_3 = 40$ kg), for $E_2 = 350$ kg (panel a), 450 kg (panel b), 550 kg (panel c), or 650 kg (panel d).

parameters are fixed except this one, the profitability of sea lions changes as we vary it. If E_2 is not too large, our simple model captures the qualitative dynamics of the sequential collapse; but if E_2 is sufficiently large, then the prediction is that both seals and sea lions will be taken by the killer whales from the outset, or that sea lions would be depleted before harbor seals. Thus, to reproduce, at least qualitatively, the observed results, we required that E_2 is no more than about 450–500 kg. A similar calculation can be done to determine a minimum value for sea lions. That is, as E_2 becomes smaller, we reach a point (about 325 kg) at which sea lions and otters are predicted to be included in the diet simultaneously, rather than sequentially.

In summary, by coupling a model for predator diet choice and simple population dynamics for the prey, we have shown that predator diet breadth is a plausible mechanism for the megafaunal collapse. The question of how likely it is to be the cause requires an assessment of the weight of evidence for all potential mechanisms simultaneously (Wolf and Mangel 2006), but that is a different topic.

Summary

The modeling effort described here thus makes the notion of expansion of diet breadth a more plausible mechanism for the observed sequential decline, and leads to clear predictions and suggestions for empirical work. For example, three predictions are the following:

Prediction #1: The profitability of potential killer whale prey is ranked: harbor seals > Steller sea lions > sea otters; note that this refers to the profitability E_i/h_i of a single encounter.

Prediction #2: The energetic content of Steller sea lions taken by killer whales is no more than about three times greater than the energetic content of harbor seals taken by killer whales.

Prediction #3: All else being equal, at those Steller sea lion rookeries where harbor seal numbers are smaller, sea lions are more likely to decline than they are at sea lion rookeries where the harbor seal numbers are larger.

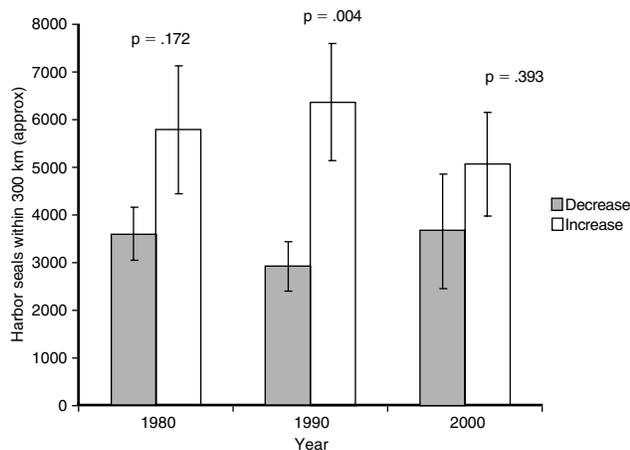


FIGURE 21.3. Estimates (± 1 SE) of the harbor seal populations within 300 km of rookeries with declining and growing Steller sea lion populations in 1980, 1990, and 2000. The significance test is a two-tailed *t*-test. See Wolf and Mangel (2006) for further details.

As a rudimentary test of this prediction, we estimated the number of harbor seals within the 300 km foraging radius (Gerber and Van Blaricom 2001) of each Steller sea lion rookery, and compared harbor seal numbers between rookeries where the sea lion population was declining and where the sea lion population was growing (Wolf and Mangel 2006). Harbor seal population time series for various large and small regions of Alaska were constructed by interpolating between published censuses and scaling the regional counts in proportion to “trend” data (counts from sub-areas containing an unknown fraction of the regional total) in years when only trend data were available. Estimates of the number of animals at a rookery before the earliest count or after the latest count were assumed to be fixed at the level of the earliest or latest count, respectively. The number of seals near each sea lion rookery was calculated as the sum of the counts from all regions multiplied by the fraction of their respective area (or linear extent) falling within 300 km of the rookery. The results (Figure 21.3) support the prediction: In all three of the years considered, rookeries with declining sea lion populations tended to have fewer seals within 300 km. The difference is statistically significant in the 1990 data (two-tailed *t*-test, $p = 0.0043$). The figure lends qualitative support to the idea that there is a threshold harbor seal density below which Steller sea lions become acceptable prey. The threshold is apparently somewhere around 4,500 seals per 283,000 km² (the area of a circle with a radius of 300 km), or about 0.016 seals per km².

Our work also suggests three important empirical tasks:

Empirical task #1: Determine the profitabilities of harbor seals, northern fur seals, Steller sea lions, and sea otters for killer whales.

Empirical task #2: Conduct studies to determine encounter rates of killer whales with different prey species.

Empirical Task #3: Determine the mixture of pups, juveniles, and adults taken by killer whales. Each of these will contribute further details in the investigation of the diet breadth hypothesis.

A Variety of Caveats

There is little chance of “validating” this model (for a fuller discussion of this point, see Stamps et al. 1998; Mangel et al. 2001). Clearly, with enough tunable parameters, one can make any model match a series of data points. Furthermore, in a stochastic world (which happens to be the kind in which we live) even if the model is exactly correct, it is possible for the model and the observed trajectory to differ considerably because of chance fluctuations. So what should we do? First, one should think about testing the assumptions that go into the model. Second, one should recognize that models are always approximations and that we use them to understand nature; so the question is, “what is the alternative model to explain the pattern of decline of seals, sea lions, and otters?”

Regarding the first point, there are key assumptions that we already know are wrong, but could be incorporated directly by using dynamic state variable models based on stochastic dynamic programming (Mangel and Clark 1988; Clark and Mangel 2000). We have ignored physiological state, both energetic reserves and gut content, of the killer whales and these can often affect the predictions of diet breadth in subtle ways. We know that killer whales hunt in groups and that there is individual variation in group formation and social interactions (Baird and Whitehead 2000). The classic diet choice model can be extended to include each of these, but such extensions are beyond the scope of this paper, and will not change the qualitative ideas developed here. To object that a model is not realistic because nature is more complicated than the model is a specious argument. Nature will always be more complicated than any model. We fully concur that physiology and social interactions are important, but also that theory becomes even more important in those circumstances.

Conclusion

Our goal in this paper has been to raise a variety of interlocking points. Understanding behavior is essential, not an add-on, for understanding population dynamics. In this area, theory plays a key and informative role. We have modeled a plausible mechanism and identified through that model a range of values for relevant parameters that allows us to provide a quantitative basis for the qualitative pattern of decline of several subpopulations of harbor seal, sea lion, and sea otter. The process of modeling, in addition to generally sharpening our thinking about the issues, helps identify what needs to be measured in the field and allows us to recognize the key assumptions that underlie the plausible mechanism

of diet breadth expansion. To be sure, the model described here is a simple one, but it demonstrates that the tools allowing us to connect behavioral and population ecology to determine insights into community ecology are available. We now need to use them.

Appendix: The General Conditions for a Cascade

In this appendix, we derive the general conditions for a cascade, under the assumptions of diet choice and population dynamics given in the text. The sequence of the cascade from harbor seal (prey species 1) to sea lion (prey species 2) to sea otter (prey species 3) requires that $E_1/h_1 > E_2/h_2$ and that $E_2/h_2 > E_3/h_3$. The cascade will proceed from harbor seal to sea lion if the harbor seal steady-state population size is sufficiently low so that Equation 21.1 of the text is violated. That is

$$q_1 K_1 \left(1 - \frac{1 - e^{-qO(t)}}{r_1} \right)^{\frac{1}{a}} \leq \frac{E_2}{E_1 h_2 - E_2 h_1} \quad (21.A1)$$

The cascade proceeds from sea lion to sea otter if both the harbor seal and sea lion steady-state population sizes are low enough that sea otter is predicted to be included in the diet. This condition is

$$q_2 K_2 \left(1 - \frac{1 - e^{-qO(t)}}{r_2} \right)^{\frac{1}{a}} \leq \frac{E_3 + q_1 K_1 \left(1 - \frac{1 - e^{-qO(t)}}{r_1} \right)^{\frac{1}{a}} (E_3 h_1 - E_1 h_3)}{E_2 h_3 - E_3 h_2} \quad (21.A2)$$

Equation 21.A1 involves 9 parameters, and Equation 21.A2 involves 14 parameters. Our results show that the cascade occurs for certain values of the parameters, so exploration of Equations 21.A1 and 21.A2 will allow us to determine the subsets of parameter space in which the cascade is predicted to occur. But that exploration is beyond the scope of this chapter.

Acknowledgments

For comments on the work, we thank members of the Mangel Research Group, and for very helpful comments on a previous version of the manuscript, an anonymous referee, Doug DeMaster, and Dan Doak.

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