



**Understanding the Decline of The Western Alaskan  
Steller Sea Lion: Assessing the Evidence Concerning  
Multiple Hypothesis**

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**For**

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Alaska Fisheries Science Center  
Seattle, Washington**

**#AB133F-02-CN-0085:**

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## Executive Summary

Although millions of dollars have been spent exploring the cause, and a wide variety of hypotheses have been proposed, the precipitous decline of the western population of Steller sea lions (*Eumatopias jubatus*) since the late 1970's has proven to be very difficult to explain. We view this as an opportunity for ecological detection, a process in which multiple hypotheses simultaneously compete and their success is arbitrated by the relevant data. The authors of a recent comprehensive review of the problem emphasized repeatedly that the system is in dire need of a modeling approach that takes advantage of the data available at small spatial scales (at the level of the rookery). Our approach is designed to do just that.

We begin by summarizing the biology of the Steller sea lion, including life history, prey base and relevant fisheries, and other marine mammals. The various competing hypotheses can be viewed in the context of different food webs of increasing complexity.

For the case of Steller sea lions, there exist sufficient data to explore the following ten hypotheses:

- H1: Total prey availability affects fecundity;
- H2: Total prey availability affects pup recruitment;
- H3: Total prey availability affects non-pup survival;
- H4: Pollock fraction in the environment affects fecundity;
- H5: Pollock fraction in the environment affects pup recruitment;

H6: Pollock fraction in the environment affects non-pup survival;

H7: Fishery activity affects pup recruitment;

H8: Fishery activity affects non-pup survival;

H9: Harbor seal density (predation) affects pup recruitment;

H10: Harbor seal density (predation) affects non-pup survival

We review a variety of previous studies, each of which has provided valuable insight into the problem. However, none made use of both spatial and temporal variation in sea lion counts as well as the environmental data. Most of the researchers pooled data across space, combining all rookery censuses within each year and performing their analyses using a composite time series representing the entire western population; and the remainder of the researchers effectively pooled data across time, fitting a single trend line to all the census data from each rookery.

We assembled, organized, and analyzed or re-analyzed databases at the spatial scale of the rookery and on an annual time scale concerning:

- Counts of sea lion pups and non-pups in various censuses of rookeries over the past 25 years;
- Commercial fisheries (both foreign and domestic) effort;
- The NMFS triennial trawl survey for the major prey species of Steller sea lions;
- Harbor seal counts (used as a proxy, via diet breadth theory, for the predation pressure from killer whales).

We obtained counts of Steller sea lions from the NMFS/AFSC/NMML online database. We assume that fisheries and survey haul data corresponding to locations within a 300-km foraging radius from a sea lion rookery are relevant to that rookery. We included eleven taxa that were described as “dominant,” “important,” or “most common” prey types in a review of Steller sea lion diet studies in the 2001 SSL restricted areas SEIS. We calculated estimates of fishing activity in minutes per year from the NMFS groundfish fishery observer database. Our estimates of harbor seal density came from online NMFS/AFSC marine mammal stock assessments and reports, a Marine Mammal Commission report, and eight journal articles. We developed new methods (space-time plots) for presenting the relevant data.

Pup counts should be fairly accurate, because pups are almost always on land during the summer surveys. Thus, in common with previous investigators, we use a sighting probability of 1 for pups. In contrast, the number of non-pups counted in any rookery census is nearly always smaller than the true number of individuals associated with the site, because an unknown fraction of the non-pups were at sea at the time of counting. To account for observation error in the counts of non-pups, we extended the traditional beta-binomial model for simultaneous estimation of the two parameters of a binomial distribution to account for the situation of summer censuses for non-pups. In particular, we assume that the probability of sighting in a given census is drawn from a beta density and that the number of observed animals follows a binomial distribution determined by the true number of non-pups present and the beta-distributed probability of sighting. We used data from rookeries that were censused multiple times within a single year to

calibrate the parameters in our observation error distribution. We estimate a mean sighting probability of about 60%.

To account for process uncertainty, we use a stochastic population model in which vital rates (non-pup fecundity and survival, pup survival) are functions of the local conditions determined by the abundance of food, the fraction of food that is pollock, the level of fishing activity, and the abundance of harbor seals. The local conditions modify base values of fecundity and survival. Each of the functions involving local conditions contains one unknown parameter, and we design these function in such a way that a value of the parameter equal to 0 means that the associated hypotheses has no effect on the population dynamics. We assume a Holling type III functional response for the relationship between local total prey availability and each vital rate, a power function for the relationship between local pollock fraction and vital rates, an exponential function for the relationship between minutes of local fishery activity and survival rates, and a knife-edge step function (as in standard diet selection theory) for the relationship between local harbor seal abundance (killer whale predation index) and survival rates.

We estimate the unknown parameters by comparing the predictions of the stochastic population model with the observed counts. To do this, we start with the beta-binomial observation error distribution and a two-life-stage stochastic population model employing the local vital rates and calculate the probability of observing the sequence of reported pup and non-pup counts at a particular rookery, given (1) relevant local conditions and (2) a particular set of parameter values in the hypothesized equations. We find this

probability using backwards iteration and by “thinking along sample paths,” adapting the method of path integration used in physics. Analogous probabilities are calculated for all rookeries and censuses and multiplied together to estimate the likelihood of the data given the hypotheses and a particular set of parameter values. We compute the maximum likelihood estimate (MLE) of each parameter and construct 10 one-dimensional profile likelihoods so that we can examine the support for each parameter, holding the others at their maximum likelihood estimates. For each parameter, we compute a profile likelihood interval by finding the area under the curve that contains 95% or 99% of the total area.

We consider that the data provide strong evidence for a hypothesis if the MLE of the parameter associated with that hypothesis is non-zero and the profile likelihood interval does not include 0. The data provide weak evidence for a hypothesis if the MLE of the parameter associated with that hypothesis is non-zero but the profile likelihood interval includes 0. If the MLE is 0, the data provide no evidence for the hypothesis.

Furthermore, we will classify the effects as strong effect, weak effect, or no effect, depending upon how the MLE value of the parameter affects the predicted population dynamics of Steller sea lions.

Our conclusions can be summarized in the following table:

	Strong Evidence	Weak Evidence	No Evidence
Strong Effect	H1: Total prey availability affects fecundity H5: Pollock fraction affects pup recruitment		
Moderate Effect	H10: Harbor seal density (predation) affects non-pup survival		
Weak or No Effect		H4: Pollock fraction affects fecundity	H2: Total prey availability affects pup recruitment H3: Total prey availability affects non-pup survival H6: Pollock fraction affects non-pup survival H7: Fishery activity affects pup recruitment H8: Fishery activity affects non-pup survival H9: Harbor seal density (predation) affects pup recruitment

Virtually all of the AIC weight (98.7%) is assigned to models with {H1, H4, H5, H10} or {H1, H5, H10} and the difference between these two models, hypothesis H4, is about 5%. These results are not unexpected (indeed, each of the 10 hypotheses is plausible and has been proposed at some point, with associated supporting data). What our work has

done is to guide the weight of the evidence, when all plausible hypotheses are competing, towards those that win the competition.

We compare non-pup census data to the results of forward simulations based on different model configurations for three rookeries in the western population and one in the eastern population (as a control). Such simulations are analogous to controlled laboratory experiments. Although both effects are statistically important, the effect of pollock on recruitment is stronger than the effect of total prey on fecundity in the sense that the slope of the predicted decline is much steeper in the case of pollock affecting recruitment.

Thus, the answer to the oft-asked question “Is it food” is yes and that it is both quality and quantity of food. The more recent question “Is it killer whale predation” can be answered too – sometimes, if harbor seal populations are sufficiently low, but not with a large reduction in survival.

Our results suggest a natural framework for adaptive management in which one designates the areas around some of the rookeries as experimental zones in which to make fishery quotas contingent upon the results of pre-fishing season survey trawls. The experimental treatments could be as follows:

- Rookeries around which fishing is not affected by the pre-season survey information (control type 1).
- Rookeries around which no fishing occurs (control type 2)

- Rookeries around which fishing is reduced or prohibited if the total prey biomass in the pre-season zone is below a critical threshold (which can be determined using the model we developed).
- Rookeries around which a directed pollock fishery occurs if the pre-season survey suggests that the fraction of pollock is above a critical threshold.

Our results also suggest a form of “adaptive observation”: Identify rookeries with high numbers and low numbers of harbor seals (regardless of the number of sea lions). The prediction of H10 is that the per-capita attack rate of killer whales on sea lions will be much higher around rookeries where harbor seals are low. The alternative would occur, for example, if H10 is false and environments that are bad for harbor seals are also bad for sea lions, and vice versa. In such a case, the prediction is that there will be no difference in the per capita rate of attack of killer whales.

## **1. Introduction: The Decline of Steller Sea Lions and The Method of Multiple Hypotheses**

The precipitous decline of the western population of Steller sea lions (*Eumatopias jubatus*) since the late 1970's has proven to be very difficult to explain. A significant problem is that most aspects of the population and the environmental variables proposed to explain its decline involve a combination of high spatial and temporal variability and limited data availability. As a result, researchers who have attempted to model the system have been forced to pool data across rookeries or across time, obscuring spatial and/or temporal patterns (compare Figures 1.1 and 1.2). An additional complication stems from the suggestion that the first decline in the 1980's and the continued decline in the 1990's may have had very different causes. Specifically, much of the evidence seems to point toward a "bottom-up" (food-related) problem in the initial decline and a "top-down" (predation or other mortality-related) control since 1989 or so, although even these general conclusions are contentious. This variation can be seen if one computes annual mortality rates based on non-pup counts (Figure 1.3).

The authors of a recent comprehensive review of the problem (NRC 2003) emphasized repeatedly that the system is in dire need of a modeling approach that takes advantage of the data available at small spatial scales. Our approach is designed to do just that. In this section, we give a broad overview of the biology of the organism (to ensure that our models have the correct assumptions) and frame the general approach. We begin (Section 1.1) with a review of the biology of the Steller sea lion that is relevant to the

modeling which we undertake here. We describe the fisheries with which the sea lions may interact (and thus their prey base). We then summarize the problem (Section 1.2) as one of competing hypotheses (mechanisms) that could explain the decline. Previous work by MRAG Americas helps frame the issues that must be addressed. We then (Section 1.3) explain the role of ecological detection (Hilborn and Mangel 1997) in understanding this particular problem. In contrast to traditional single-hypothesis statistical approaches, ecological detection is based on the notion of simultaneous competition among multiple hypotheses, with relative strength assigned to each hypothesis according to its ability to reproduce the data. Thus, in Section 1.4 we explain the various hypotheses that we investigate here and in Section 1.5 explain how previous studies have approached the problem.

Equipped with this background, we then (Section 2) describe the data that we acquired and how we treated those data in preparation for analysis. In Section 3, we describe the summarized versions of the data that underlie our work. We introduce the idea of space-time plots of the data, where space is indexed by rookeries. Such plots of the data immediately illuminate interesting aspects of the problem. The summarized data are available at the web site given in Section 3.

Our models involve both process uncertainty and observation error. The latter is introduced during summer counts of sea lions because, although all pups should be visible on the beach, some non-pups may be at sea foraging during the time of the survey. However, the sighting probability is also unknown. The problem of simultaneously

estimating the number of trials and the probability of success in a binomial process is an exceptionally difficult one (Hilborn and Mangel 1997). The best existing solution is still the beta-binomial model (Martz and Waller 1982; Evans et al 2000), in which the sighting probability is assumed to follow a beta probability density and, conditioned on that, the number of animals observed is binomially distributed with unknown true number of animals and beta-distributed sighting probability. However, even the best existing work was insufficient for our needs, so we have extended it appropriately in Section 4.

In Section 5, we introduce the vital rates that underlie our analysis. These are the probabilities of annual non-pup survival and reproductive success and the probability that a pup successfully recruits to the non-pup population. We also introduce the notion of local conditions; that is, we assume that the vital rates depend upon the local conditions within typical foraging range of a rookery. Then, in Section 6 we use a population model with vital rates determined by local conditions to connect the hypotheses and data. We adopt a method used in physics (path integration) to help us sort through the different hypotheses about the cause of the decline; hence we call this the method of thinking along sample paths.

In Section 6, we describe the details involved in computing likelihood to estimate parameter values, and in Section 7 we present the results. In Section 8, we provide a broad discussion about the implications of our work. In the Appendix, we explain what the next steps in this work might be.

## 1.1 The Steller Sea Lion

The Steller sea lion, *Eumatopias jubatus*, occupies the north Pacific coastline from central California to Japan. Evidence from mitochondrial DNA shows that the population east of 144° W longitude is genetically distinct from the population west of that line (Bickham et al. 1998), and an analysis of resightings of marked individuals confirms that there is very little exchange of breeding individuals between the two regions. Females tend to return either to their natal rookery (about 67% of the time in the western stock) or to a neighboring rookery (Raum-Suryan et al. 2002). Thus, the set of rookeries within each region qualifies as a metapopulation (York et al. 1996), a group of local populations linked by dispersal (Hanski 2000), although our models have no explicit migration parameter.

Rookeries are generally located on small, remote islands. Most pups (one per pregnant female) are born within a two-month period centered in June (Pitcher et al. 2002), and enter the water for the first time when they are 2-4 weeks old (Sandegren 1970). Mothers alternate between nursing on land and foraging at sea, leaving the pups behind to fend for themselves for 1-2 days at a time (NRC 2003). Pups depend on their mothers for nourishment throughout most the first year, during which time they gradually learn to forage and become proficient at diving. Dive depth increases from 70 m at 6 months of age to 140 m at 12 months (Rehberg et al. 2001). Most pups wean by the end of their first year, but a few nurse for a second year (Trites and Porter 2002; Pitcher and Calkins 1981).

The sex ratio at birth is approximately 50/50. Sexual maturity for females usually occurs at around 4.5 years (Harmon 2001, Holmes and York 2003), but females as young as 3 years old have been observed with pups (Raum-Suryan et al. 2002).

After they wean, but before they become proficient at deep diving and catching fast-swimming fish, pups may rely heavily upon slow-moving, easily captured prey, including shrimp (Hansen 1997) or crab (P. Dayton, pers. comm.). The abundance of such prey species could be important in determining the recruitment success of pups (Merrick and Loughlin 1997).

Mature sea lions typically dive to depths of 250 m or less (Merrick and Loughlin 1997) in search of their prey, which are mostly various kinds of groundfish. Time-depth recorder studies indicate that much of the foraging time is spent near the bottom (Merrick et al. 1994). Therefore, the shallower parts of the continental shelf, where the water is less than about 200 m deep, are generally assumed to be the most important foraging areas (e.g. Gerber and Van Blaricom 2001).

Steller sea lions are largely opportunistic foragers keying in on locally and temporally aggregated prey (including Walleye pollock, herring, eulachon, salmon and Pacific cod), although they may display some prey preference under certain conditions. Walleye pollock (*Theragra chalcogramma*) are currently the principal diet component for both the Western stock and the stocks in the Eastern Aleutians and southeast Alaska (Anderson and Blackburn 2002; Alverson 1992). Other important prey species include Atka

mackerel (*Pleurogrammus monopterygius*), Pacific cod (*Gadus macrocephalus*), and Pacific herring (*Clupea pallasii*).

Walleye pollock, Atka mackerel, and Pacific cod are harvested primarily using groundfish trawling gear. The largest groundfish harvests in the area occur in the Bering Sea. The peak catch was more than 2.1 million mt (metric tons) in 1972, followed by a decline in the late 1970's and a recovery in the mid-1980's. Total annual groundfish catch since about 1985 has hovered near 1.5 million mt. Pollock comprise the vast majority (over 76%) of the groundfish caught in the Bering Sea (NRC 2003). In the Gulf of Alaska, there was a major peak in the pollock catch between 1976 and 1985, when up to 300,000 mt per year were taken from the Shelikof Strait, between Kodiak Island and the mainland. Catch restrictions limited the Shelikof Strait fishery to about 80,000 mt starting in 1986, and total groundfish catch in the Gulf of Alaska has hovered around 200,000 mt per year since then (NRC 2003). Another fishery for groundfish developed in the Aleutian Islands in the late 1970's. Total annual catch grew slowly to about 180,000 mt between 1989 and 1996, dominated first by a pollock boom in the eastern Aleutians and later by a peak in Atka mackerel. The pollock fishery declined to 24,000 mt per year by 1998, when it was closed as a precautionary measure to protect the sea lions (NRC 2003).

Herring in Alaskan waters are currently harvested for their roe, using gillnets and purse seines. Catch effort in this fishery is closely associated with known spawning locations and timed to just precede the spawning period. A record catch of over 140,000 mt in

1970 declined to about 30,000 mt by the late 1970's and remained at approximately that level through the late 1990's, with most of the harvest occurring in the eastern Bering Sea. Catches have declined sharply since about 1997, resulting in closures of the fishery in Prince William Sound and Cook Inlet (NRC 2003).

The Steller sea lion decline in western Alaska was preceded by declines in the populations of Northern fur seals, *Callorhinus ursinus*, and Pacific harbor seals, *Phoca vitulina*, occupying the same region. The causes of these declines remain similarly unexplained (Merrick 1997). One possibility is the killer whale diet breadth hypothesis: The range of the sea lions' western population is also home to a large population of Killer whales, *Orcinus orca*. Of these, a substantial number (certainly more than 100) belong to the "transient" race (Barrett-Lennard et al. 1995), whose diet consists mainly of marine mammals, including Steller sea lions (Matkin et al. 2002). Unfortunately, very little is known about the spatial or temporal distribution of these whales. But if killer whales expand and contract their diets in an adaptive manner, then the abundance of alternative food sources (i.e. other marine mammals) may determine the magnitude of killer whale predation on Steller sea lions at local scales (Mangel and Wolf, submitted). This mechanism has recently received considerable attention (Springer et al 2003; Wade et al 2003). Our work allows one to separate plausibility and evidential weight in support of this and all other hypotheses considered.

## 1.2 Summary of the Problem

While estimates of the eastern population of Steller sea lions have been growing slowly since survey methods were standardized in the 1970's, the estimates of the size of the western population have fallen by more than 80%. The decline appears to have begun in the eastern Aleutians and spread in both directions from there. The initial decline was characterized by a loss of about 15% of the population per year (Figure 1.3), accompanied by reduced size-at-age and other symptoms of nutritional stress (Calkins et al. 1998; Castellini 1993). After 1989 or so, the rate of decline slowed to about 5% per year (Sease and Loughlin 1999), and the available evidence suggests that animals in the western population were actually in better condition than those in the growing eastern population (Andrews et al. 2002). The western stock was listed as Endangered in 1997.

Numerous competing hypotheses have been proposed to explain the decline of the western population. We explore these in more detail in subsequent sections and consider a subset of hypotheses for which sufficient data are available to apply appropriate analytical and statistical methods. Our approach is to compare the hypotheses using ecological detection (Hilborn and Mangel 1997), in which alternative models are confronted with the data and ranked according to their ability to produce it. From the outset, we do not subscribe to a particular hypothesis and set out to support our idea. Rather, we seek to understand the role of multiple mechanisms in the decline of the Steller sea lion.

The various competing hypotheses can be viewed in the context of a series of increasingly complicated food webs (MRAG Americas 2002). For example, the simplest model for the interactions between marine mammals and a fishery is shown in Figure 1.4a. In this case, the target fish are assumed to be prey for both the fishery and marine mammals. The interactions can be either indirect and thus bottom up, with the fishery removing prey that the mammals or birds would otherwise take, or else direct, and thus top-down, with incidental mortality of mammals or birds occurring during fishing operations. This food web is one used implicitly when changes in marine mammals or birds are assumed to be caused by fishery activities.

While Figure 1.4a may be a useful conceptual tool for framing interactions, it is overly simplified. Potential complexities of the primary interactions include:

- age-specific factors in the interactions between major species;
- temporal and spatial components to the interactions; and
- availability of target species.

These complexities are included in the food web in Figure 1.4b. The trophic level labeled “mammals and birds” makes no distinction between different life history stages, such as juveniles and adults. Both the direct and indirect effects of the fishery may differ between juveniles and adults, for a variety of reasons. Similarly, once this trophic level is separated into adults and juveniles, effects on growth (especially the transition from juvenile to adult) and reproduction (the production of new juveniles) may be different.

In addition, the simple web in Figure 1.4a is based on the assumption that the fishery targets a single stock that is also the sole prey source for the marine mammals and birds. However, marine mammals and birds often have cosmopolitan diets; thus the trophic level occupied by “target fish” may also be occupied by other fish species that are competitors of the target species and prey for the mammals and birds. In a similar way, the marine mammals and birds may themselves be prey for other marine organisms, such as toothed whales or sharks or marine diseases. These ideas are also captured in Figure 1.4b.

One should expect variation in ecosystems. Thus, the target species may be removed by the fishery (leading to interference competition with the marine mammals or birds), but it may also move in space relative to the location of the fishery and the marine mammals or birds. Although the enlarged food web in Figure 1.4b is more complex, it ignores environmental factors that affect the production of fish stocks. These factors may be biotic (e.g. the level of zooplankton or primary production) or abiotic (e.g. different temperature regimes). Figure 1.4c captures these ideas.

### 1.3 The Role of Ecological Detection

Each of the food webs in Figure 1.4 can be viewed as a pictorial model for the ecosystem and its interactions. Now confronted with the information that Steller sea lions have declined, different hypotheses could be generated by these models. We show some examples in Table 1.1, knowing that these are “nested” in the sense that more than one of them could apply.

Given a set of data concerning the decline of Steller sea lions, one view of the role of analysis is that its purpose is to confront each of these putative mechanisms of the decline with the data and allow the data to arbitrate between the different models. Hilborn and Mangel (1997) call this process ecological detection. Ecological detection recognizes that our understanding of the world will always be incomplete and that the goal should be to achieve the best understanding possible by working with multiple competing hypotheses and allowing the data to arbitrate the competition.

#### 1.4 The Hypotheses

Numerous competing hypotheses have been proposed to explain the decline of the western population (Ferrero and Fritz 2002). We will consider a subset of hypotheses for which sufficient data are available to apply appropriate analytical and statistical methods.

#### H1-H3: Acute Nutritional Stress (Food Limitation) hypotheses

Fecundity (H1), pup recruitment (H2), or non-pup survival probability (H3) is a positive function of the local encounter rate with groundfish prey. Specifically, starvation (H2, H3) or termination of pregnancy (H1) occurs if an animal experiences a long series of unsuccessful foraging attempts and fails to find enough to eat.

The motivation for these hypotheses is as follows. Prey availability is assumed to affect body condition. Under poor foraging conditions, animals may lose condition because they consume less prey, spend more time and energy hunting, or both. Body condition,

in turn, is known to be a significant determinant of the probability that a pregnant female Steller sea lion actually completes her pregnancy and produces a pup (Pitcher et al. 1998). Poor foraging conditions also increase the probability of starvation and expose the animals to additional predation risk during any extra time spent foraging, leading to elevated mortality rates. The probability of pup recruitment may be linked indirectly to prey availability if mothers are more likely to abandon pups under poor foraging conditions, or it may be linked directly if starvation is a serious concern when the inexperienced pups begin foraging for themselves near the end of their first year.

#### H4-H6: Chronic Nutritional Stress (Junk-food) hypotheses

Fecundity (H4), pup recruitment (H5), or non-pup survival probability (H6) is a positive function of the fraction of prey other than Walleye pollock in the environment. Specifically, starvation (H5, H6) or termination of pregnancy (H4) occur with higher probability where prey other than pollock are relatively scarce.

There is general agreement that high fractions of pollock in the environment correlate with poor performance by Steller sea lions, although the mechanism is still unclear. Some versions of the mechanism call for the sea lions to suffer ill effects from shifting their diet to consume too much pollock when it is abundant, while other versions propose that the sea lions do not shift their diet but rather starve because there is not enough of something other than pollock. We discuss several possibilities here, although our current model does not specify the exact mechanism.

The idea that a pollock-intensive diet might lead to poor body condition and depressed vital rates was first proposed by Alverson (1992) and supported by evidence showing a strong inverse correlation between diet diversity and population decline rate across rookeries (Merrick et al. 1997). Pollock do not contain as much fat as other prey species (Rosen and Trites 2000, 2002), and Rosen and Trites (2000) found that captive Steller sea lions lost weight on a pollock-only diet, even when fed ad-libitum.

Alternative mechanisms involve pups. For example, the limited dive depth and lack of experience of pups probably restricts them to a subset of easily caught prey that might be more difficult to find in environments where pollock dominate. Another possibility is that the stomachs of pups may be too small to ingest enough calories if their diet is composed primarily of pollock. Thus, pup recruitment probability may be especially sensitive to prey species composition, and in particular it might be negatively correlated with relative pollock abundance.

The approach that we develop is effective regardless of the particular mechanism as long as one agrees that a larger fraction of pollock in the environment is not good for Steller sea lions (i.e., the negative effect may derive either from too much pollock in the environment or else from too little of something else; and pollock consumption may be bad for the animals or it may have no effect).

## H7, H8: Anthropogenic Activity (Fishery-related mortality) hypotheses

Survival probability of pups (H7) or non-pups (H8) is a declining function of the local encounter rate with groundfish trawling operations.

The motivation for these hypotheses is as follows. Incidental mortality, usually resulting from the entanglement of sea lions in fishing gear, was recently estimated to be killing less than 100 animals per year now (Perez and Loughlin 1991; Loughlin and York 2002), but at certain times and in certain places (e.g. the Shelikof Strait trawl fishery in the late 1970's and early 1980's) it was much higher (NRC 2003). Deliberate shooting of sea lions by fishers may be another significant source of mortality, although its magnitude is not well known. It was legal to shoot sea lions in defense of gear until 1990, and there are anecdotal reports suggesting that shooting (even unrelated to defense of gear) may still occur (NRC 2003). It may be very difficult to determine whether incidental or deliberate mortality is the problem, since both might scale with fishing effort. However, it seems likely that entanglement would be a bigger problem for naïve pups (Loughlin et al. 1983), whereas adults are more likely to be targeted by shooters.

It is possible, of course, that fishing activity depletes food sources so that the effect of fisheries is felt not directly (as in H7 or H8) but indirectly (as in H1-H3).

## H9, H10: Predation mortality hypotheses

Survival probability of sea lions declines when local harbor seal density falls below a critical threshold.

The motivation for this hypothesis is as follows. Not all Killer whales eat marine mammals, but members of the transient race do. Steller sea lions in particular may comprise 5-20% of their diet (Matkin et al. 2002). The stomach of one Killer whale that washed up on a beach in British Columbia contained flipper tags from 14 different Steller sea lion pups, all of which had been tagged at the Marmot Island rookery 3-4 years before (Saulitis et al. 2000). If the transient Killer whale population is stable (as suggested by Barrett-Lennard et al. 1995), but its more profitable prey types (in the sense of classical diet choice theory) are being depleted (as suggested by Estes et al. 1998), then (according to the optimal prey switching argument) Killer whale predation upon sea lions is thus predicted to be more intense at sea lion rookeries around which there are few harbor seals. A form of this hypothesis was proposed by Hanna (1922) to account for ‘missing’ fur seals. In Section 5, we lay out very clearly the assumptions associated with this predation mortality/diet breadth hypothesis

We acknowledge that not all potential causes for the decline of Steller sea lions are accounted by this list. For example, arrowtooth flounder and halibut are both predators of pollock and prey of Steller sea lions and their populations have increased (especially arrowtooth flounder) as Steller sea lion populations declined (Hollowed et al 2000; Figure 1.5 here). Thus, for example, it might be that competition with these potential prey species for another prey species has contributed to the decline of Steller sea lions. Similarly, Hunt et al. (1999) show that a wide variety of marine birds increased during the period in which Steller sea lions declined, and we have not accounted for the

possibility that these birds have outcompeted Steller sea lions for the same prey, thus inhibiting the recovery of sea lions. Finally, we have not accounted for environmental change hypotheses explicitly (Ferrero and Fritz 2002), although that could also be done with our methods (see the Appendix).

### 1.5 Previous studies

Many attempts have been made over the years to determine why the population has declined. These include:

- 1.) Construction of a Leslie matrix model for a stable population, followed by perturbation of various transition rates in order to find the most parsimonious way to produce a trajectory matching the observed decline. Using this method, York (1994) determined that the initial decline could be explained most easily by a 10-20% decrease in juvenile survival. Pascual and Adkison (1994) went a step further and estimated the effective mortality and fecundity rates for six individual rookeries by maximum likelihood methods. Adkison et al. (1993) and Pascual and Adkison (1994) also modified the matrix model by allowing vital rates to vary according to alternative hypotheses, in order to see which of them could produce the observed decline.
  
- 2.) Assumption of a fixed set of underlying vital rates (Leslie matrix) and calculation of the number of animals that would have to be removed in order to match the observed census data (e.g. Blackburn 1990, cited in Castellini 1993; Loughlin and York 2002;

NRC 2003). The time series of “missing” animals may be compared with other available time series.

3) Analysis of trends across space rather than across time. Using linear regression, Merrick et al. (1997) observed a correlation between population growth rate and diet diversity (a factor hypothesized to be an important determinant of survival and/or fecundity rates) among different rookeries.

4) Estimation of vital rates across time using age-structured data and maximum likelihood estimation. Holmes and York (2003) re-examined aerial census photos to produce a metric for the juvenile fraction of the broad non-pup age class. Using these data, they concluded that low juvenile survival drove the early decline, whereas low fecundity was the major factor after about 1990.

5.) Construction of a simulation model that includes the hypothesized effect (e.g. Barrett-Lennard et al. 1995), followed by assessment of its ability to match the census data.

6) Use of Ecopath or Ecosim models (e.g. Trites et al 1999, NRC 2003) to capture the flow of trophic interactions at a highly aggregated scale.

Each of the above studies has provided valuable insight into the problem. However, none made use of both spatial and temporal variation in sea lion counts as well as the environmental data. Most of the researchers pooled data across space, combining many

rookery censuses within each data point and performing their analyses using a composite time series representing the entire western population (Figure 1) or a large fraction of it. The remainder (Pascual and Adkison 1994, Merrick et al. 1997) effectively pooled data across time, fitting a single trend line to all the census data from each rookery.

The general conclusion from previous work is that it is hard to determine which of the hypotheses is most likely when one is working with pooled data. The recent NRC (2003, pg 7) report asserts that “Finer-scale spatial analysis of Steller sea lion populations and environmental conditions will be required to uncover potential region-specific determinants that are affecting sea lion survival” and calls for new modeling approaches that are both spatially and temporally explicit. Our work is aimed squarely at this gap.

#### Captions for Figures

**Figure 1.1.** When we only consider data from years in which population estimates are available for the entire western population, there are only eleven data points for non-pups. The sheer magnitude of the decline is obvious, but its spatial structure is not.

(Source: Merrick et al. 1987, and NMFS 2002)

**Figure 1.2.** Even though not every population is censused in every year, many more data are available when we consider individual rookeries. a) Non-pup census data from six individual rookeries in the Aleutians. b) Non-pup census data from ten individual rookeries in the Gulf of Alaska.

**Figure 1.3.** Annual mortality rates across different intervals for the data shown in Figure 1.1 computed according to  $S(t_i) = S(t_{i-1})e^{-M(t_i-t_{i-1})}$  where M is the mortality rate over a census interval, S(t) is the non-pup count in year t, and  $t_i$  is the year of the  $i^{\text{th}}$  census. Note that in some years mortality is considerably different; we seek to understand the origins of this difference. (Sources: 1956-85, Merrick et al. 1987; 1990-00, Angliss & Lodge 2002; 2002, Sease 2002.)

**Figure 1.4.** a) The simplest model for the interaction between marine mammals and birds and a fishery. In this case, the target fish are assumed to be prey for both the fishery and marine mammals or birds. The interactions can be either indirect, in which the fishery removes prey that the mammals or birds would otherwise take, or direct, in which there is incidental mortality of mammals or birds during fishing operations. b) An elaboration of the simplest food web to account for age-specific factors in the interactions between major species, temporal and spatial aspects of the interactions, and availability of target species. c) A food web that includes environmental factors.

**Figure 1.5.** Our list of hypotheses does not account for all possible mechanisms. For example, arrowtooth flounder and halibut are both predators of pollock and prey of sea lions (right hand panel). In consequence, their increase (left hand panel) may be a mechanism for the decline of sea lions. The left hand panel is reproduced from Hollowed et al (2000).

**Table 1.1.** Hypotheses About the Cause of a Decline in Marine Mammals or Birds

Food Web	Primary Hypothesis
Figure 1.4a	The decline is caused by incidental mortality in the course of fishing operations
Figure 1.4a	The decline is caused by removal of target fish by the fishery
Figure 1.4b	The decline is caused by a diet shift in toothed whales (increased predation) or the prevalence of marine disease
Figure 1.4b	The decline is caused by a shift in the mixture of target fish and other fish, which differ in catchability or else provide different levels of nutrients to the mammals and birds
Figure 1.4c	The decline is caused by a shift in the distribution or abundance of zooplankton, thus affecting the resource base for the fish
Figure 1.4c	The decline is caused by a shift in abiotic components, either temporally or spatially, that affect the distribution of fish stocks and their accessibility to marine mammals and birds.

## **2. Acquisition and Treatment of Data**

We acquired various data concerning prey availability, harbor seal abundance and commercial fishery activity.

Prey availability and fisheries activity were tallied from July 1 in one year to June 30 in the next and assumed to affect sea lion survival probabilities across that period and annual fecundity at the end of the period. These dates are chosen to fall just after new pups are born, and right around the time that censuses are done. Therefore, the CPUE and fishery activity estimates averaged across those 12 months should affect survival rates between two breeding seasons (or for the duration of a pup's first year of life) and/or fecundity at the end of the 12 months.

Harbor seal counts (which do not include pups) are generally done around the same time as sea lion censuses, raising the question of whether a harbor seal count in late June/early July is more representative of conditions in the 12 months prior to the count, or the 12 months after the count. One could probably argue either way, but we chose to assume the former, reasoning that the non-pup harbor seal count reflects the level to which the population was depleted in the 12 months prior to the count. That level seems most relevant to the predation hypotheses. The alternative, i.e. assuming that the harbor seal count reflects numbers in the 12 months after the count, seems less accurate because we don't know how many pups were added to the mix right after the count. To be clear, we estimated the harbor seal non-pup total for a calendar year (using numbers from June and

July, or occasionally August) and applied this estimate to the sea lion survival rates in the 12 months leading up to June 30 of that year.

### *The Foraging Radii*

We assume that fisheries and survey haul data corresponding to locations within a 300-km foraging radius from a sea lion rookery are relevant to that rookery. The 300-km cutoff was also used by Gerber and Van Blaricom (2001) in their study, and it is intended to encompass a typical SSL home range. When there were no major land masses between the rookery and the location, we calculated the intervening distance as the length of the great-circle arc connecting the two points using their latitudes and longitudes. When there was a large island (Kodiak or Unimak) or a peninsula (Alaska or Kenai) in between, we calculated the distance as the sum of the great-circle lengths of the shortest two legs required to connect the points without going over land. We assume that False Pass, between Unimak Island and the Alaska Peninsula, is navigable by sea lions.

The specific criteria for including or excluding data by location for all rookeries, from west to east, are based on the following notation:

$d_1$  = GC (Great Circle) distance between each rookery and Cape Sarichef: 164.947 W, 54.572 N

$d_2$  = GC distance between each rookery and False Pass: 163.409 W, 54.854 N

$d_3$  = GC distance between each rookery and Nagahut Rocks: 151.772 W, 59.100 N

The Alaska Peninsula line is a set of four segments separating Bering Sea and Gulf of Alaska locations:

$$\text{for } (W. \text{ Longitude}) > 163.25: \quad (N. \text{ Latitude}) = 84.757 - 0.183(W. \text{ Longitude})$$

$$\text{for } 163.25 > (W. \text{ Longitude}) > 162.95: \quad (N. \text{ Latitude}) = 55.15$$

$$\text{for } 162.95 > (W. \text{ Longitude}) > 161.20: \quad (N. \text{ Latitude}) = 78.45 - 0.143(W. \text{ Longitude})$$

$$\text{for } 161.20 > (W. \text{ Longitude}): \quad (N. \text{ Latitude}) = 124.07 - 0.426(W. \text{ Longitude})$$

The Kenai Peninsula line separates Cook Inlet locations from Gulf of Alaska locations. It is:

$$(N. \text{ Latitude}) = 163.064 - 0.685(W. \text{ Longitude})$$

With this notation, the criteria for determining whether a location falls within the 300-km foraging radius of each rookery are:

Attu/Cape Wrangell to Ugamak Complex:

Include all points that are within 300 km of the rookery.

Sea Lion Rock (Amak):

Include all points that are both within 300 km and one or more of the following:

- (1) North of the Alaska Peninsula line (defined below);
- (2) within  $(300-d_1)$  km of Cape Sarichef: 164.947 W, 54.572 N;
- (2) within  $(300-d_2)$  km of False Pass: 163.409 W, 54.854 N.

Clubbing Rocks, Pinnacle Rock:

Include all points that are both within 300 km and one or more of the following:

- (1) South of the Alaska Peninsula line;
- (2) within (300-d<sub>1</sub>) km of Cape Sarichef: 164.947 W, 54.572 N;
- (3) within (300-d<sub>2</sub>) km of False Pass: 163.409 W, 54.854 N.

Chernabura, Atkins:

Include all points that are both within 300 km and one or more of the following:

- (1) South of the Alaska Peninsula line;
- (2) within (300-d<sub>2</sub>) km of False Pass: 163.409 W, 54.854 N.

Chowiet, Chirikof:

Include all points that are both within 300 km and south of the Alaska Peninsula line.

Sugarloaf, Marmot, Outer (Pye):

Include all points that are within 300 km of each rookery.

Wooded (Fish):

Include all points that are both within 300 km and one or more of the following:

- (1) South of the Kenai Peninsula line (defined below);
- (2) within (300-d<sub>3</sub>) km of Nagahut Rocks: 151.772 W, 59.100 N.

Seal Rock:

Include all points that are both within 300 km and south of the Kenai Peninsula line.

White Sisters, Hazy, Forrester Complex:

Include all points that are within 300 km of each rookery.

*Local conditions matrices: Prey abundance and Pollock fraction*

We calculated total prey availability and Pollock availability, both in CPUE units of kg per km<sup>3</sup> trawled, from NMFS/AFSC (National Marine Fisheries Service/Alaska Fisheries Science Center) GOA/AI (Gulf of Alaska/Aleutian Islands) triennial groundfish survey data. We included eleven prey taxa that were described as “dominant,” “important,” or “most common” prey types in a review of Steller sea lion diet studies in the 2001 SSL restricted areas SEIS (Supplemental Environmental Impact Statement, available at <http://www.fakr.noaa.gov/sustainablefisheries/seis/sslpm/final/>). The eleven prey types are listed in Table 2.1.

The GOA/AI database we used covered the period from 1980 to 2001. We estimated CPUE values for each rookery/year combination by averaging across all survey hauls that either began or ended within the 300 km foraging radius from the rookery. When there were no data for certain rookery/year combinations, we used linear interpolation to estimate the missing value from reported values in earlier and later years for the same rookery. The volume trawled was calculated as the product of the net’s width and height multiplied by the distance trawled. When one or more of the net dimensions was missing

from a haul record, we used an average value from other hauls made by the same ship in the same year. We calculated the pollock fraction as pollock CPUE divided by total prey CPUE before interpolation.

*Local conditions matrices: Fishery activity*

We calculated estimates of fishing activity in minutes per year from the NMFS groundfish fishery observer database. This database covers foreign and joint-venture groundfish fisheries from 1973 to 1991 and domestic fisheries from 1986 to 2001. The estimates of total haul time that we used include foreign, joint-venture, and domestic fisheries and do not distinguish between different types of fishing gear or target species. As above, the total haul time for each rookery included only those hauls conducted within 300 km of foraging distance from the rookery.

*Local conditions matrices: Harbor seal abundance*

Our estimates of harbor seal density came from online NMFS/AFSC marine mammal stock assessments and reports (Angliss and Lodge 2002; Withrow et al. 2000, 2001, 2002), a Marine Mammal Commission report (Hoover-Miller 1994), and eight journal articles (Boveng et al. 2003; Small et al. 2003; Pitcher 1990; Jemison and Kelly 2001; Frost et al. 1999; Bailey and Faust 1980; Everitt and Braham 1980; and Mathews and Pendleton 2000). Whenever possible, we used mean counts from June and July, when the seals are onshore for breeding. We constructed time series for nine regions: Aleutian Islands, Otter Island, N. side AK Peninsula west (Unimak I. - Herendeen Bay), N. side AK Peninsula east (Pt. Moller - Kvichak Bay), S. side AK Peninsula, Kodiak

Archipelago, Cook Inlet/Kenai Peninsula, Prince William Sound/Copper River Delta, and SE Alaska. We used region-wide counts when they were available, and estimated them in other years by scaling up from trend route or sub-area counts using the ratio of the total count to the sub-count as calculated in years when both were reported. When counts from multiple sub-areas were available in a single year, we scaled up from the one representing the largest fraction of the region total. Region totals for years in which no data were available were linearly interpolated from earlier and later counts for the same region.

We then estimated harbor seal abundance near each sea lion rookery as the sum of all nine region totals, each multiplied by the fraction of its seals estimated to be within 300 km of swimming distance from the rookery. This fraction was determined from detailed maps of harbor seal count locations whenever possible; otherwise, it was estimated as the fraction of the region's total area or linear extent that fell within the 300-km foraging radius of the rookery, subject to the geographical constraints outlined above.

#### *Sea lion data*

The Steller sea lion counts are from the NMFS/AFSC/NMML (National Marine Mammal Laboratory) online database (<http://nmml.afsc.noaa.gov/AlaskaEcosystems/sslhome/stellerhome.html>). We limited our consideration to year/rookery combinations in which counts from June or July were available for both pups and non-pups, and to rookeries for which such censuses from at least two different years were available. When more than one count was available for a

particular rookery in a single year, we took the average. Several sets of adjacent rookeries were censused as one large rookery early in the data set and as separate rookeries in later years. In some of these cases, we combined the counts from the separate rookeries in later years in order to extend the time series for the “joint” rookery.

**Acknowledgement:** We thank Jason Melbourne for his help with the larger data sets.

**Table 2.1.** Major Prey Species of Steller Sea Lions (Based on Sinclair and Zeppelin 2002).

<b>Common name</b>	<b>Species name(s)</b>
Walleye Pollock	<i>Theragra chalcogramma</i>
Atka Mackerel	<i>Pleurogrammus monopterygius</i>
Pacific Salmon	<i>Oncorhynchus spp.</i>
Pacific Cod	<i>Gadus macrocephalus</i>
Arrowtooth Flounder	<i>Atheresthes stomias</i>
Pacific Herring	<i>Clupea pallasii</i>
Pacific Sand Lance	<i>Ammodytes hexapterus</i>
Irish Lords	<i>Hemilepidotus spp.</i>
Cephalopods	Class <i>Cephalopoda</i>
Capelin	<i>Mallotus villosus</i>
Rockfishes	Family <i>Scorpaenidae</i>

### 3. The Summarized Data

In summary, then, we have the following sources of data at the scale of individual rookeries:

- Counts of pups and non-pups in various censuses;
- Fisheries effort;
- The NMFS triennial trawl survey for the major prey species; and
- Harbor seal counts as a proxy for orca predation pressure.

In contrast to the highly aggregated data (Figure 1.1), we now have an enormous amount of data. In this section, we describe the summarized data that underlies our computations.

In addition to organizing these data and making them available at a public web site

<http://www.ams.ucsc.edu/projects/sealion/>

we have developed two methods for presenting the information that has spatial and temporal components. We illustrate the first, the ‘space-time’ plot, in Figure 3.1. In this plot, the 38 Steller sea lion rookeries are arranged along the abscissa in order from West to East (one column per rookery; not to scale). The list of rookeries is given in Table 3.1. The ordinate in each plot indexes years, with time increasing from bottom to top. The color of each cell reflects the value of the local condition estimated for the corresponding rookery/year combination (blue = low; red = high). Gray shading indicates that no data are available for the cell.

For example, in Figure 3.2 we show counts of non-pups (panel a), counts of pups (panel b) and the derived quantity of pups per non-pup (panel c). Simply creating this plot allows us to recognize possible spatial and temporal patterns in the population dynamics (Figure 3.3).

Our second tool for the presentation of data are the latitude-longitude locations of commercial fishing effort, with approximate 300-km foraging radii (introduced earlier) indicated around each rookery (Figure 3.4). The resulting space-time plot of fishery effort is shown in Figure 3.5.

For the space time plots of triennial survey data, we report presence/absence (displayed as the fraction of trawls that were successful), the average catch per trawl, and the average weight of the fish trawled, by species (Figure 3.6), for all species combined, and for the pollock catch as a fraction of the total (Figure 3.7).

As described previously, there are insufficient distributional data on the abundance of Killer whales. As a proxy for the predation pressure induced by orcas, we use the spatial and temporal abundance of harbor seals (Figure 3.8). The justification proceeds as follows (Springer et al 2003; Mangel and Wolf, submitted): If Killer whales are assumed to include Steller sea lions in their diet only if the encounter rate with harbor seals is sufficiently low (because local harbor seal density is low), then the seal population within the foraging radius of a rookery should indicate whether or not sea lions are included in the diet of Killer whales. Thus, low harbor seal density is a proxy for predation risk.

### *A word about Accuracy*

By most standards, it was asking a lot of the available data to extract the spatially and temporally detailed tables (described above) that went into our model. Much of the data were collected sporadically, and certainly without our purposes in mind. Our use of interpolation to fill in the gaps probably amplified some inaccuracies. But our sacrifice of accuracy in favor of detail was, we believe, a necessary compromise, without which we could never have attempted the novel analyses presented here.

### **Captions for Figures**

**Figure 3.1.** A space time plot, used to represent the summarized data. Details are explained in the text and in Table 3.1.

**Figure 3.2.** Space time plots of counts of non-pups (panel a), counts of pups (panel b), and the derived quantity of pups per non-pup (panel c).

**Figure 3.3.** The space time plot of pups per non-pup allows us to recognize a variety of spatial and temporal patterns, including local peaks and declines, apparent cyclic behavior, and a cline of recovery in the Aleutians (a wave of increasing “fecundity” moving from east to west).

**Figure 3.4.** Latitude-longitude plots for foreign and domestic fishery effort. The circles represent approximate 300-km foraging ranges around each rookery. Each dot indicates the starting location of a commercial haul.

**Figure 3.5.** The resulting space-time plot of fishery effort.

**Figure 3.6.** Space-time plots of the NMFS Triennial Survey Data. a) We show the fraction of successful hauls by location/year in the upper panel, the average haul ( $\text{kg}/\text{km}^3$ ) in the middle panel, and the average weight per fish in the lower panel. The results for b) arrowtooth flounder, c) Atka mackerel, d) capelin, e) cephalopods, f) Irish Lords, g) Pacific cod, h) Pacific herring, i) Pacific salmon, j) Pacific sand lance, k) rockfish (*Sebastes* spp.), and l) walleye Pollock follow.

**Figure 3.7.** We combine the data in Figure 3.6 to obtain space time plots for the biomass trawled ( $\text{kg}/\text{km}^3$ ) for all species (upper panel) and for the pollock catch as a fraction of the total (lower panel).

**Figure 3.8.** The space-time plot of harbor seal abundance, used to index the predation pressure from killer whales.

**Table 3.1:** Rookery locations, in order from west to east, as used in the space time plots.

<b>Rookery (W to E)</b>	<b>N. Latitude</b>	<b>W. Longitude</b>	<b>Years of SSL census data</b>
1. Attu/Cape Wrangell	52.91667	187.54083	98, 02
2. Agattu	52.38567	186.4695	79, 88, 89, 90
3. Buldir	52.3615	184.09351	79, 88, 89, 90, 98, 02
4. Kiska/Cape St. Stephen	51.88334	182.79416	79, 89, 90, 94, 98, 02
5. Kiska/Lief Cove	51.95333	182.65884	79, 85, 89, 90, 94, 98, 02
6. Ayugadak	51.756	181.595	79, 85, 90, 94, 98, 02
7. Amchitka/Column Rock	51.53867	181.17867	79, 90, 94, 98, 02
8. Semisopchnoi/Pochnoi	51.955	180.23334	94, 98
9. Ulak/Hasgox Point	51.31334	178.98752	79, 85, 90, 94, 98, 02
10. Tag	51.55833	178.575	85, 90, 94, 98, 02
11. Gramp Rock	51.48117	178.343	85, 90, 94, 98, 02
12. Adak	51.6075	176.9725	85, 90, 94, 98, 02
13. Kasatochi/North Point	52.18517	175.51666	79, 85, 90, 94, 98, 02
14. Amlia/Sviech. Harbor	52.03	173.39833	90, 98
15. Agligadak	52.1015	172.90384	90, 98
16. Seguam/Saddleridge	52.35058	172.56667	79, 85, 89, 90, 94, 98
17. Yunaska	52.69	170.60583	79, 85, 90, 94, 98, 00, 02
18. Adugak	52.91167	169.175	85, 90, 94, 98, 00, 02
19. Ogchul	52.99517	168.40402	85, 94, 98
20. Bogoslof/Fire Island	53.92822	168.03416	73, 79, 85, 89, 90, 91, 98, 00, 02
21. Akutan/Cape Morgan	54.05906	166.02777	85, 90, 92, 94, 98
22. Akun/Billings head	54.29321	165.53142	85, 90, 91, 94, 98, 00, 02
23. Ugamak Complex	54.21767	164.78799	85, 86, 89, 90, 91, 96, 97, 98
24. Sea Lion Rock (Amak)	55.46367	163.20166	98, 02
25. Clubbing Rocks	54.706	162.4455	78, 79, 92, 94, 98
26. Pinnacle Rock	54.76758	161.76422	78, 79, 91, 94, 98, 00, 02
27. Chernabura	54.75867	159.57278	78, 79, 86, 90, 92, 94, 98
28. Atkins	55.05333	159.28999	78, 79, 86, 90, 91, 94, 96, 98, 00, 02
29. Chowiet	56.007	156.69183	78, 79, 89, 90, 92, 94, 98
30. Chirikof	55.7745	155.69133	78, 79, 89, 90, 91, 94, 98, 00, 02
31. Sugarloaf	58.8875	152.03999	76, 78, 79, 89, 90, 92, 94, 97, 98
32. Marmot	58.19625	151.83176	78, 79, 86, 88, 89, 91, 94, 96, 97, 98
33. Outer (Pye)	58.84583	150.39583	76, 78, 79, 89, 90, 91, 94, 97, 98, 00, 02
34. Wooded (Fish)	59.88167	147.34416	94, 96, 98, 00
35. Seal Rocks	60.163	146.83833	76, 78, 79, 89, 90, 91, 94, 96, 98
36. White Sisters	57.635	136.25667	90, 91, 92, 94, 96, 98
37. Hazy	55.86666	134.56667	79, 89, 90, 91, 94, 96, 98
38. Forrester Complex	54.83833	133.52667	73, 79, 82, 90, 91

#### 4. Treating Observation Error

Pup counts should be fairly accurate, because pups are almost always on land during the summer surveys. Thus, following Pascual and Adkison (1994), we use a sighting probability of 1 for pups. In contrast, the number of non-pups counted in any rookery census is nearly always smaller than the true number of individuals associated with the site, because an unknown fraction of the animals were at sea at the time of counting. We now show how to account for this observation error.

We estimate the distribution of observation error (the probability distribution for the observed count given the “true” number of individuals present) using multiple censuses conducted within the same season at the same site (available for three rookeries; see below).

We only consider females in the model (Sections 5,6). Since about 75% of the non-pup sea lions on rookeries are females, and about 50% of the pups are females (NRC 2003), we multiply all non-pup counts by 0.75 and pup counts by 0.5 before using them.

Our likelihood-based approach requires us to calculate the probability of observing  $N_{\text{obs}}$  non-pups given that  $N_{\text{true}}$  are actually present. We use a beta-binomial distribution (Martz and Waller 1982, Evans et al 2000) to describe the number of individuals sighted in a non-pup survey. In this approach, the probability of sighting an individual,  $P_{\text{obs}}$ , varies from census to census according to a beta distribution defined by the parameters  $\alpha$  and  $\beta$  (Evans et al. 2000), so that the average value of the probability of sighting an

individual is  $\alpha/(\alpha+\beta)$ . The values of these two parameters are unknown but assumed constant across time and space. The variance of  $P_{\text{obs}}$  between censuses is given by  $\alpha\beta/((\alpha+\beta+1)(\alpha+\beta)^2)$ , and the coefficient of variation is:

$$\sqrt{\frac{\beta}{\alpha(\alpha + \beta + 1)}} \quad (4.1)$$

The number of animals observed in a census is a binomial random variable conditioned upon  $N_{\text{true}}$  and the beta-distributed  $P_{\text{obs}}$  value:

$$\Pr\{N_{\text{obs}} | N_{\text{true}}, \alpha, \beta\} = \int_{p=0}^1 \Pr\{P_{\text{obs}} = p\} \binom{N_{\text{true}}}{N_{\text{obs}}} p^{N_{\text{obs}}} (1-p)^{N_{\text{true}}-N_{\text{obs}}} dp \quad (4.2)$$

where

$\Pr\{P_{\text{obs}} = p\}$  is short-hand for the probability that  $P_{\text{obs}}$  falls between  $p$  and  $p+dp$ . We model this as the beta density,

$$p^\alpha (1-p)^\beta \frac{\Gamma(\alpha + \beta + 2)}{\Gamma(\alpha + 1)\Gamma(\beta + 1)} \quad (4.3)$$

In Figure 4.1, we show some examples of beta densities corresponding to different values of  $\alpha$  and  $\beta$ .

We estimate the parameters of the beta distribution using maximum likelihood based upon counts from three rookeries (Outer/Pye Island, White Sisters, and Hazy) that were each censused eight times within a single season. For each of these rookeries, we assume that the only source of variation between the repeated counts at a single site is

observation error. Since the true non-pup population numbers that produced the counts are unknown, we need to integrate across a range of possible  $N_{\text{true}}$  values at each rookery in order to calculate the likelihood for each set of  $\alpha$  and  $\beta$  values. We do not know the prior probability distribution for  $N_{\text{true}}$ , but our choice of error structure implies that the expected ratio of  $N_{\text{true}}$  to  $N_{\text{obs}}$  at any rookery, given particular values of alpha and beta, is the inverse of the mean of the beta distribution. Thus, the expected distribution of true non-pup numbers among rookeries in a single year has the same shape as the distribution of observed counts, and the distribution of  $N_{\text{true}}$  can be estimated (given  $\alpha$  and  $\beta$ ) by horizontally expanding the  $N_{\text{obs}}$  distribution by a factor of  $(\alpha+\beta)/\alpha$ .

We construct prior probability distributions for  $N_{\text{true}}$  corresponding to each combination of  $\alpha$  and  $\beta$  values by fitting a log-normal distribution to the  $N_{\text{obs}}$  values from all rookery counts recorded in a single year (1998: Fig. 4.2) and scaling it up by a factor of  $(\alpha+\beta)/\alpha$ . We chose the data from 1998 for this purpose because more rookeries were censused in that year than in any other. The  $N_{\text{true}}$  prior distribution is factored into the likelihood calculations for  $\alpha$  and  $\beta$  according to Bayes' theorem (Hilborn and Mangel 1997).

The likelihood is calculated as follows:

$\Pr\{N_{\text{true}} = n\}$  is the prior probability distribution for  $N_{\text{true}}$  (see Fig. 4.1)

$\Pr\{P_{\text{obs}} = p|\alpha,\beta\}$  is shorthand for the Beta density, as in Eqn 4.3

$\text{data}_{i,k}$  is the  $k^{\text{th}}$  count recorded at the  $i^{\text{th}}$  rookery

and

$$\Pr\{\text{data}_{i,k}|N_{\text{true}} = n, P_{\text{obs}} = p\} = \binom{n}{\text{data}_{i,k}} p^{\text{data}_{i,k}} (1-p)^{n-\text{data}_{i,k}} \quad (4.4)$$

We then have

$$\text{Likelihood}(\text{data}|\alpha, \beta) = \prod_{i=1}^3 \sum_{n=0}^{\infty} \left[ \Pr\{N_{\text{true}} = n\} \prod_{k=1}^8 \int_{p=0}^1 \Pr\{P_{\text{obs}} = p|\alpha, \beta\} \Pr\{\text{data}_{i,k}|N_{\text{true}} = n, P_{\text{obs}} = p\} dp \right] \quad (4.5)$$

In practice, the summation in Eqn 3 is carried out over the range from  $n=242$  to  $3000$ , with the lower limit set at the smallest of the 24 counts and the upper limit selected to greatly exceed the highest count (1852) while still allowing the computer to complete all necessary calculations within a reasonable amount of time. The integral in the equation is approximated using numerical integration. The binomial probabilities are estimated using a Gaussian approximation. In the population model (Section 6), we use only the maximum-likelihood estimates of  $\alpha$  and  $\beta$ , not their posterior probability distributions.

### Captions for Figures

**Figure 4.1.** Some examples of the beta density  $p^\alpha (1-p)^\beta \frac{\Gamma(\alpha + \beta + 2)}{\Gamma(\alpha + 1)\Gamma(\beta + 1)}$ , which we use to compute the distribution of the probability of observing a non-pup.

**Figure 4.2.** The log-normal distribution fit to observed values from all rookery counts in 1998.

**Table 4.1.** Repeat counts from rookeries used for fitting the beta-binomial model of observation error.

Rookery (Year)	Outer/Pye (1992)	White Sisters (1991)	Hazy (1991)
	242	1040	1582
	481	1153	1521
	319	857	1562
	477	905	1852
	370	1011	1413
	371	1041	1382
	369	932	1375
	391	860	1278
Mean	377.5	974.875	1495.625
SD	78.14638	103.826	177.7486
CV	0.20701	0.106502	0.118846

## 5. Vital Rates and Local Conditions

Our investigatory approach is based upon the assumption that sea lion vital rates vary from rookery to rookery and year to year according to the local conditions around each rookery in each year. Each of the competing hypotheses that have been raised to explain the sea lions' decline can be interpreted as a generalized linear model (Stefansson 1996) relating mortality or fecundity rates to local conditions.

### *Population Model: Two Age Classes, Three Vital Rates*

We assume that the population dynamics can be satisfactorily described in terms of 2 age classes: pups and non-pups. We follow York (1994) in considering only females and assume a 50-50 sex ratio (NRC 2003). Thus, the underlying variables are:

$$\begin{aligned} J(i,t) &= \text{Number of female pups at rookery } i \text{ in year } t. \\ N_{\text{true}}(i,t) &= \text{Number of female non-pups at rookery } i \text{ in year } t. \end{aligned} \quad (5.1)$$

We assume that the number of pups observed equals  $J(i,t)$  but that the number of non-pups observed,  $N_{\text{obs}}(i,t)$ , is less than or equal to the actual number of non-pups,  $N_{\text{true}}(i,t)$ , and use the model developed in Section 4 to relate the two.

Because the breeding season is relatively compressed, we assume discrete time dynamics and no density dependence. In that case, there are three fundamental parameters at rookery  $i$  in year  $t$ :

$\rho_{i,t}$  = Probability of pup survival (recruitment to the non-pup population) from year t to year t+1

$$\sigma_{i,t} = \text{Probability of non-pup survival from year t to year t+1} \quad (5.2)$$

$\phi_{i,t}$  = Per capita probability for non-pups of successful reproduction in year t.

We set fixed background values for these parameters (denoted by  $\rho_0$ ,  $\sigma_0$ , and  $\phi_0$ ) that are modified by local conditions according to parameterized functions reflecting each hypothesis. We estimate the background values from life tables based on data collected on the Marmot Island rookery (Calkins and Pitcher 1982) and used by Pascual and Adkison (1994) and York (1994), with corrections in Holmes and York (2003). The annual growth rate of a population using the original life table is slightly more than 1%. Since our model lumps together all age classes above 1 year, we calculate  $\sigma_0$  and  $\phi_0$  by integrating the survival and fecundity probabilities across all non-pup classes in the stable age distribution produced by the life table:

$$\rho_0 = 0.776$$

$$\sigma_0 = 0.858$$

$$\phi_0 = 0.197$$

(5.3)

This fecundity estimate accounts for only about 50% of the pups being female (York 1994, NRC 2003) and for about 45% of the non-pup population being juvenile (Holmes and York 2003). Our estimate is a little lower than the value used by York (1994), 0.315.

However, she only included the sexually mature age classes (3+) in her average, whereas our simpler model lumps together all non-pup age classes (1+), including non-reproductive juveniles.

### *Vital Rates as Functions of Local Conditions*

Each hypothesis corresponds to a generalized linear model that produces a scaling factor between 0 and 1 to modify the fecundity, recruitment, or survival rate at any rookery in any year according to the corresponding local conditions. The relevant local conditions may include prey abundance, fishing activity, predator abundance, or other factors, depending on the hypothesis being tested.

We let  $\omega_n$  denote the symbol for the value of the vital rate modifier produced by the function corresponding to hypothesis  $n$ . Each function contains a parameter,  $c_n$ , that is unknown, but which we assume is constant across all rookeries and years and which we intend to estimate from the data. The local value of each vital rate ( $\rho_{i,t}$ ,  $\sigma_{i,t}$ , or  $\phi_{i,t}$ ) is calculated by multiplying the maximum potential rate ( $\rho_0$ ,  $\sigma_0$ , or  $\phi_0$ ) by all the relevant scaling factors. We consider ten unknown parameters, one per hypothesis. In each case, a parameter value of zero indicates that the corresponding hypothesis has no effect. The ten hypotheses and their functional forms are described in detail below, and summarized in Table 5.1.

*H1-H3: Acute Nutritional Stress (Food Limitation) hypotheses*

Low abundance of groundfish and other prey causes local fecundity (Hypothesis 1), pup recruitment (Hypothesis 2), or non-pup survival probability (Hypothesis 3) to be diminished. Specifically, we assume that the probability with which an animal avoids starvation ( $\omega_2$ ,  $\omega_3$ ) or successfully produces a pup ( $\omega_1$ ) follows a Type III functional response (Holling 1959) with respect to the average total prey biomass,  $\lambda_{total}(i,t)$ , recovered per unit volume of standardized trawling effort within the foraging area around rookery  $i$  during year  $t$  (Figure 5.1a):

$$\omega_n(i,t) = \frac{\lambda_{total}^2(i,t)}{c_n^2 + \lambda_{total}^2(i,t)} \quad (5.4)$$

where the subscript  $n$  indicates that hypothesis  $n$  is being considered, and  $c_1$ ,  $c_2$ , and  $c_3$  are the (unknown) parameters corresponding to each hypothesis. We refer to these parameters as the half-saturation constant, since when  $\lambda_{total}(i,t) = c_n$ ,  $\omega_n(i,t) = 0.5$ .

Our choice of a sigmoid function (a Holling Type III functional response, Turchin 2003) implies that sea lions are unlikely to find enough to eat when prey are scarce, and unlikely not to find enough to eat when prey are abundant. The negative effect is increasingly severe at lower food abundance levels. One could argue whether the Type II or Type III functional response is more appropriate. This is an empirical, rather than theoretical, question and a variety of papers in Boyd and Wanless (in prep – ZSL

Symposium 22/23 April 2004 “Management of Marine Ecosystems: Monitoring Change in Upper Trophic Levels”) support the choice of a Type III functional response.

*H4-H6: Chronic Nutritional Stress (Junk-food) hypotheses*

As described in Section 1, there is general agreement that an abundance of walleye pollock is not ‘good’ for sea lions, although the mechanism is still not fully understood. Consequently, we assume that a high proportion of walleye pollock in the environment causes local fecundity (Hypothesis 4), pup recruitment (Hypothesis 5), or non-pup survival probability (Hypothesis 6) to be diminished.

We make no assumption about the fraction of walleye pollock in the diet, but do assume that a higher fraction of pollock in the environment means a smaller value for the multiplier characterizing the local conditions. We model this as the fraction of non-pollock prey raised to an unknown power,  $c_n$  (Figure 5.1b):

$$\omega_n(i, t) = \left( \frac{\lambda_{total}(i, t) - \lambda_{pollock}(i, t)}{\lambda_{total}(i, t)} \right)^{c_n} \quad (5.5)$$

If the unknown parameter is 0, then the average biomass (measured by CPUE) of pollock in standardized survey trawls has no effect. If the parameter is 1, the effect is linear between the two extremes, with the vital rate of interest unaffected at 0% pollock and completely suppressed at 100% pollock (Figure 5.1b). Values greater than 1 indicate

strong suppression of the vital rate whenever pollock represents a significant fraction of the total biomass (assessed via CPUE) in the environment:

*H7, H8: Anthropogenic Activity (Fishery-related mortality) hypotheses*

As described in Section 1, fisheries may have indirect effects on survival or fecundity by removing prey or direct effects through entanglement in gear or shooting. For these hypotheses, we assume that survival probability of pups (Hypothesis 7) or non-pups (Hypothesis 8) is diminished in areas where there is more commercial fishery activity. Specifically, the probability with which a pup or non-pup avoids having a fatal encounter with a fishing boat is the Poisson probability of zero fatal encounters in a single year, where the rate of fatal encounters is proportional to the total duration (minutes) of commercial haul activity reported near the rookery,  $\mu(i,t)$ . The unknown proportionality constant (= mortality rate per encounter) is  $c_n$  (Figure 5.1c):

$$\omega_n(i,t) = e^{-c_n \mu(i,t)} \quad (5.6)$$

Equation 5.6 can be derived from first principles of random search (Hilborn and Mangel 1997), but has also been found (Washburn 1981) to effectively characterize encounters that are non-random.

*H9, H10: Predation mortality hypotheses*

The notion that the sequential collapse of populations of harbor seals, Steller sea lions, and sea otters (sensu Springer et al 2003) is due to killer whale predation relies on the assumption of expanding diet breadth for orcas. We approach this from the viewpoint of rate-maximizing diet choice theory (Stephens and Krebs 1986), which we now briefly review.

The classic diet choice model 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 (Mangel 1992). The suite of prey species is characterized by 1) the net 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  $r_i$  (units, 1/hours) with prey type  $i$ . One then assumes that the major 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. One then chooses the diet selection composition that maximizes the rate of energy return.

The key results of this theory are that items are ranked by profitability  $\frac{E_i}{H_i}$ , that an item is completely included in the diet or not (there are no partial preferences), and that only the most profitable prey type is included as long as

$$r_1 > \frac{E_2}{E_1 H_2 - E_2 H_1} \quad (5.7)$$

Eqn 5.7 defines a ‘switching value’ for inclusion of the second most profitable prey type according to the encounter rate with the most profitable prey item. Note that the right hand side of this equation does not contain the encounter rate with the second most profitable prey item. That is, as long as the most profitable prey item is sufficiently abundant, the predator is predicted to select only it for the diet, regardless of the abundance of other prey types. Analogous equations show that the decision to include or exclude the third most profitable prey type (or the fourth, etc.) depends only on the densities of the more profitable prey types. Within this framework, the complicated food habits and trophic guild structure of killer whales become simplified to a ranking of their prey species by profitability. We assume that harbor seals are: a) more profitable than Steller sea lions, and b) such a large component of the transient Killer whale diet that we may neglect the densities of other prey more profitable than Steller sea lions, so that the relevant mechanism reduces to Eqn. 5.7.

To be sure, 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 (Mangel and Clark 1988, Mangel 1992, Clark and Mangel 2000) in subtle ways. We also know that killer whales hunt in groups and that there is individual variation in group formation and social interactions (Baird 2000). The classic diet choice model can be extended to include each of these, but such extensions are beyond the scope of this work (Mangel 1992), and rate maximizing has proven itself to be a reasonable, if not totally realistic, starting point for many questions in behavioral ecology (Stephens and Krebs 1986).

Thus, we assume that pup survival (Hypothesis 9) and/or non-pup survival (Hypothesis 10) decrease(s) when harbor seal numbers at rookery  $i$  in year  $t$ ,  $h(i,t)$ , fall below a critical level,  $h_{crit}$ . Below this harbor seal density, the encounter rate between Killer whales and harbor seals is so low that the average profitability of a sea lion exceeds the average intake rate of a Killer whale searching only for seals, and a rate-maximizing whale is predicted to begin to hunt sea lions as well as seals. In particular, if Killer whales expand their diets when harbor seal numbers are too low, then  $\omega_n(i,t)=1$  if  $h(i,t)>h_{crit}$  and  $\omega_n(i,t)=1-c_n$  otherwise, with  $h_{crit}$  and  $c_n$  to be determined.

Thus, if Killer whale predation is a significant source of mortality for Steller sea lions, the average density of harbor seals around sea lion rookeries with rising populations should be higher than that around rookeries with falling populations. The critical harbor seal density is predicted to lie in between these two distributions. We therefore estimate

$h_{crit}$  as the midpoint between the harbor seal density averages for sea lion rookeries with rising and falling populations (Section 7).

*Putting it all together*

The ‘full’ model, which accounts for all 10 hypotheses, is one in which the life history parameters take the form:

$$\begin{aligned}
 \phi(i,t) &= \phi_0 \omega_1(i,t) \omega_4(i,t) \\
 \rho(i,t) &= \rho_0 \omega_2(i,t) \omega_5(i,t) \omega_7(i,t) \omega_9(i,t) \\
 \sigma(i,t) &= \sigma_0 \omega_3(i,t) \omega_6(i,t) \omega_8(i,t) \omega_{10}(i,t)
 \end{aligned}
 \tag{5.8}$$

As mentioned previously, we assume that the parameters  $c_1$ - $c_{10}$  in the ten hypothesized functions are constant across space and time and we estimate them from the relevant data. Note that if  $c_n=0$ , then  $\omega_n(i,t)=1$  and we conclude that Hypothesis  $n$  has no effect on the relevant life history parameter; this gives a prelude of what is to come in the statistical analysis: If, as a result of our confronting the models with data we conclude that the best estimate for  $c_n=0$ , then the associated particular mechanism is unlikely to play a significant role in the dynamics of the Steller sea lions. If, on the other hand, we conclude that  $c_n \gg 0$ , then the associated mechanism is likely to play a critical role in the dynamics. In Section 6, we make these ideas more precise in terms of the Maximum Likelihood Estimate (MLE) of the parameter and the 95% confidence interval for that parameter.

We can also investigate any particular combination of sub-models by setting the associated  $c_n=0$ , or (equivalently),  $\omega_n(i,t)=1$ .

### Caption for Figure

**Figure 5.1.** The functional forms that we use to calculate vital rates from the local conditions matrices according to the acute nutritional stress hypotheses (panel a), the chronic nutritional stress hypotheses (panel b) and the anthropogenic mortality hypotheses (panel c).

**Table 5.1.** The ten hypotheses and their respective parameters.

Hypothesis	Parameter
H1: Prey CPUE → fecundity	c1, prey density at which fecundity is half of potential rate
H2: Prey CPUE → pup recruitment	c2, prey density at which recruitment is half of potential rate
H3: Prey CPUE → non-pup survival	c3, prey density at which non-pup survival is half of potential rate
H4: Pollock fraction → fecundity	c4, exponent of non-pollock prey fraction in fecundity multiplier
H5: Pollock fraction → pup recruitment	c5, exponent of non-pollock prey fraction in recruitment multiplier
H6: Pollock fraction → non-pup survival	c6, exponent of non-pollock prey fraction in non-pup survival multiplier
H7: Fishing activity → pup recruitment	c7, pup mortality rate per minute of haul time
H8: Fishing activity → non-pup survival	c8, non-pup mortality rate per minute of haul time
H9: HS density → SSL pup recruitment	c9, fraction of potential recruitment lost when harbor seals < $hs\_crit$
H10: HS density → SSL non-pup survival	c10, fraction of potential non-pup survival lost when HS < $hs\_crit$
H9, H10	hcrit, harbor seal density below which sea lions become prey

## 6. A Model that Connects the Hypotheses and the Data

In previous sections, we have defined functional forms for our ten hypotheses, outlined our population model, and shown how to account for observation error. We must now connect the observed census data and the unknown local vital rate function parameters with each other through the stochastic population dynamics of the stock.

The basic approach is as follows: Starting with the beta-binomial observation error distribution and a two-life-stage stochastic population model employing the local vital rates, we calculate the probability of observing the sequence of reported pup and non-pup counts at a particular rookery, given (1) relevant local conditions and (2) a particular set of parameter values in the hypothesized equations. We find this probability using backwards iteration and by “thinking along sample paths,” which essentially amounts to averaging across many possible true population trajectories that each could have produced the observed sequence of census data.

Analogous probabilities are calculated for all rookeries and censuses and multiplied together to estimate the likelihood of the data given the hypotheses and each possible set of parameter values. The likelihood profile for each parameter is calculated while holding all the other parameters at their respective MLEs (Maximum Likelihood Estimates). Using Bayes’ theorem (Hilborn and Mangel 1997) and a uniform prior probability distribution for each parameter, we convert the likelihoods into posterior probability distributions and estimate confidence intervals from them, allowing us to

quantify the relative strengths of the corresponding hypotheses. Strictly speaking, each parameter's posterior distribution calculated in this way is contingent upon an assumption that the MLE values of the other nine parameters are approximately correct. However, our data set is sufficiently large that we can neglect this issue (Kalbfleisch and Sprott 1970).

In contrast to all previous modeling approaches, we do not require a complete data set, and we make use of variation both between rookeries and across time. The details of our approach are outlined below.

### *The Basic Population Dynamics*

As already noted, we assume that the population dynamics can be described by two age classes: pups ( $J(i,t)$ , age <1 year) and non-pups ( $N(i,t)$ , age 1+). We follow York (1994) in considering only females. The three relevant vital rates are:

$\rho_{i,t}$  = Probability of pup survival (recruitment to non-pup class) from year  $t$  to  $t+1$

$\sigma_{i,t}$  = Probability of non-pup survival from year  $t$  to year  $t+1$

$\phi_{i,t}$  = Probability of successful pup production by a non-pup in year  $t$ . (6.1)

In the absence of stochasticity, the population dynamics would be given by:

$$N(i,t+1) = \rho_{i,t}J(i,t) + \sigma_{i,t}N(i,t) \quad (6.2a)$$

$$J(i,t+1) = \phi_{i,t}N(i,t+1) \quad (6.2b)$$

If all parameters were constant, then the dynamics in Eqn 6.2 would generate population growth or decline according to the dynamics

$$N(i,t+1) = [\rho \phi + \sigma]N(i,t) \quad (6.3)$$

For the base case parameters given in Eqn 5.3, this corresponds to a growth rate of just over 1% per year. However, the parameters are not constant (they vary according to local conditions), and the transitions in Equation 6.3 are stochastic, not deterministic. Thus, we must deal with process uncertainty.

#### *Accounting for Process Uncertainty*

Each of the life history parameters is bounded by 0 and 1, so that we can think of them as binomial transition probabilities of non-pup survival and reproduction and pup survival.

The probability distributions for true numbers of non-pups and pups at time  $t$ , given the numbers at  $t-1$ , are therefore computed from the associated binomial distributions. In the equation for the non-pup distribution, we sum across all possible numbers of pups

( $j=0,1,2\dots N(t-1)$ ) at time  $t-1$ , multiplying the probability associated with each  $j$  value by a convolution of binomials that accounts for all the possible permutations of surviving non-pups ( $s = 0,1,2\dots N(t-1)$ ) and recruiting pups ( $r = N(t)-s$ ) that could have produced  $N(t)$  non-pups at time  $t$ , given  $N(t-1)$  non-pups and  $j$  pups at time  $t-1$ . If we let

$\Pr\{N(t)|N(t-1)\}$  denote the probability that the non-pup population in year  $t$  is  $N(t)$  given that the non-pup population in year  $t-1$  was  $N(t-1)$ , then

$$\Pr\{N(t)|N(t-1)\} = \sum_{j=0}^{N(t-1)} \left[ \binom{N(t-1)}{j} \phi^j (1-\phi)^{N(t-1)-j} \sum_{s=0}^{\min(N(t-1), N(t))} \left[ \binom{N(t-1)}{s} \sigma^s (1-\sigma)^{N(t-1)-s} \binom{J(t-1)}{N(t)-s} \rho^{N(t)-s} (1-\rho)^{J(t-1)-(N(t)-s)} \right] \right] \quad (6.4)$$

Alternatively, one might consider that at time t-1 there were N(t-1) non-pups and N(t-1) “potential pups,” reflecting the fact that each non-pup can produce a pup. In this interpretation, we multiply the fecundity and recruitment probabilities together rather than dealing with them separately. The resulting equation

$$\Pr\{N(t)|N(t-1)\} = \sum_{s=0}^{\min(N(t-1), N(t))} \left[ \binom{N(t-1)}{s} \sigma^s (1-\sigma)^{N(t-1)-s} \binom{N(t-1)}{N(t)-s} (\phi\rho)^{N(t)-s} (1-\phi\rho)^{N(t-1)-(N(t)-s)} \right] \quad (6.5)$$

is therefore equivalent to Equation 6.4.

If the number of pups at time t-1 is known, then we do not need to sum across possible pup numbers, and Eqn 6.5 becomes:

$$\Pr\{N(t)=n|N(t-1), J(t-1)\} = \sum_{s=0}^{\min(N(t-1), N(t))} \left[ \binom{N(t-1)}{s} \sigma^s (1-\sigma)^{N(t-1)-s} \binom{J(t-1)}{N(t)-s} \rho^{N(t)-s} (1-\rho)^{J(t-1)-(N(t)-s)} \right] \quad (6.6)$$

Finally, the probability distribution for pups given the number of non-pups at time t is a single binomial:

$$\Pr\{J(t)|N(t)\} = \binom{N(t)}{J(t)} \phi^{J(t)} (1-\phi)^{N(t)-J(t)} \quad (6.7)$$

What remains is to connect the probabilistic dynamics given by these equations to the observed data. We do this next.

### *Thinking Along Sample Paths*

We want to find the values of the parameters in the local condition matrix that give the highest probability of observing all the reported SSL counts, using all of the data at hand. To do this, we take advantage of the rules of probability. In particular, if  $\Pr\{A|B\}$  indicates the probability of the event A, given the event B, then (Mangel and Clark 1988)

$$\Pr\{A | B\} = \sum_C \Pr\{A | C\} \Pr\{C | B\} \quad (6.8)$$

where the sum is taken over all the events (or states) C that can occur between B and A. In physics, this approach is known as path integration (Shulman 1981) and was first made very useful by Richard Feynman in his formulation of quantum mechanics (Feynman 1948). For that reason, we call it the method of ‘thinking along sample paths’.

We illustrate the ideas in Figure 6.1. We begin with a series of censuses, not necessarily in consecutive years (Figure 6.1a). Associated with each census (represented by the solid dot in Figure 6.1a) is a probability distribution for the true number of non-pups, which is larger than the observed number (as discussed in the previous section). We now recognize (Figure 6.1b) that there is a very large number of trajectories of population size that might connect the census values. In actual fact, the situation is a bit more complicated than Figure 6.1b, because we must consider counts of both pups and non-pups (Figure 6.1c, in which we show one trajectory ).

### *Looking Backward*

The likelihood associated with a particular set of parameter values is estimated as the product of the likelihoods for all rookeries. Likelihood for an individual rookery is calculated using backwards iteration, which is an efficient way to consider many different possible “sample paths” simultaneously. First, we consider a range of possible values for  $N_{\text{true}}(T)$ , the true number of non-pups at the time of the latest available census, and calculate, for the given combination of parameters, the probability of observing the reported non-pup and pup counts ( $N_{\text{obs}}(T)$  and  $J(T)$ ), using Eqns 4.2 and 4.3 for non-pups and assuming no observation error for pups. Second, we move to the previous year ( $T-1$ ) and use Equations 6.5 and 6.7 to calculate, for a range of possible  $N_{\text{true}}(T-1)$ , the probability of making the transition to each  $N_{\text{true}}(T)$  value considered in the first step. This involves integrating over all the possible combinations of recruiting pups and surviving non-pups that could produce each  $N_{\text{true}}(T)$  value, as in Equation 6.4 or 6.5. For each  $N_{\text{true}}(T-1)$ , the likelihood of observing  $J(T)$  and  $N_{\text{obs}}(T)$  is the sum of the probabilities calculated in the first step, weighted by the integrated binomial probabilities corresponding to each possible transition from  $N_{\text{true}}(T-1)$  to  $N_{\text{true}}(T)$ . Formally expressed, we have:

$$\begin{aligned} & \Pr\{J(T), N_{\text{obs}}(T) | N_{\text{true}}(T-1)\} \\ &= \sum_{n=N_{\text{obs}}(T)}^{\infty} [\Pr\{N_{\text{obs}}(T) | N_{\text{true}}(T) = n\} \Pr\{N_{\text{true}}(T) = n | N_{\text{true}}(T-1)\} \Pr\{J(T) | N_{\text{true}}(T) = n\}] \end{aligned} \quad (6.9)$$

*where*

$\Pr\{N_{obs}(T)|N_{true}(T)=n\}$  is calculated using numerical integrations of Eqns 4.2 and 4.3,  
 $\Pr\{N_{true}(T)=n|N_{true}(T-1)\}$  is calculated using a Gaussian approximation of Eqn 6.5, and  
 $\Pr\{J(T)|N_{true}(T)=n\}$  is calculated using Eqn 6.7.

In practice, the summation in equation 6.9 is carried out in steps of 20 over the range from  $N_{obs}(T)$  to 11417, with this upper limit set to the highest estimated female non-pup count (6380) multiplied by a factor of  $(\alpha+\beta)/\alpha$ . We chose a step size of 20 for  $N_{true}$  in order to minimize computer run-time without noticeably altering the shape of the output likelihood curves.

If T-1 was a census year, we also multiply by the probability of observing  $N_{obs}(T-1)$  and  $J(T-1)$ , given each possible true non-pup count at T-1. That is,

$$\begin{aligned} & \Pr\{J(T-1), N_{obs}(T-1), J(T), N_{obs}(T)|N_{true}(T-1)\} \\ &= [\Pr\{N_{obs}(T-1)|N_{true}(T-1)\}\Pr\{J(T-1)|N_{true}(T-1)\} \\ & \cdot \sum_{n=N_{obs}(T)}^{\infty} [\Pr\{N_{obs}(T)|N_{true}(T)=n\}\Pr\{N_{true}(T)=n|N_{true}(T-1), J(T-1)\}\Pr\{J(T)|N_{true}(T)=n\}]] \quad (6.10) \end{aligned}$$

where

$\Pr\{N_{obs}(T-1)|N_{true}(T-1)\}$  is calculated using numerical integrations of Eqns 4.2 and 4.3,

$\Pr\{J(T-1)|N_{true}(T-1)\}$  is calculated using Equation 6.7,

$\Pr\{N_{obs}(T)|N_{true}(T)=n\}$  and  $\Pr\{J(T)|N_{true}(T)=n\}$  are calculated as above, and

$\Pr\{N_{true}(T) = n | N_{true}(T-1), J(T-1)\}$  is estimated using a Gaussian approximation of Eqn 6.6.

Analogous procedures are used to calculate the probabilities of observing all reported counts from T-2 onwards, given a range of possible values for  $N_{true}(T-2)$ . Then the process is repeated for T-3, T-4, etc. until we reach the earliest recorded census at  $t_{start}$ .

Model likelihood for a single rookery is calculated as the average of the likelihoods of all possible trajectories starting at each possible combination of observed true pup and unknown non-pup numbers,  $J(t_{start})$  and  $N_{true}(t_{start})$ . The equal weight given to each trajectory likelihood in this average reflects our use of a flat (uniform) prior probability distribution for the unknown  $N_{true}(t_{start})$ . Overall model likelihood is calculated as the product of the likelihoods from all rookeries.

The likelihood of a model with parameters  $\{c_n, n=1..10\}$  given the census data is then:

$$L\{c_1, c_2, \dots, c_{10} | data\} = \sum_{\substack{\text{all\_possible} \\ N_{true}(t_{start})}} \left[ \Pr\{N_{true}(i, t_{start})\} \prod_{\substack{\text{all} \\ \text{censuses}}} \Pr\{N_{obs}(i, t), J(i, t) | N_{true}(i, t_{start}), c_1, c_2, \dots, c_{10}, \alpha, \beta, etc\} \right] \quad (6.11)$$

We now view the data as fixed (which it is), so that  $L\{c_1, c_2, \dots, c_{10} | data\}$  is a 10-dimensional function of the unknown parameters. In many other settings, some parameters are known a priori to be of interest and other parameters not; they are often

called nuisance parameters. There exists a considerable literature that explores how likelihood methods can deal with nuisance parameters (e.g. Kalbfleisch and Sprott 1970; Edwards 1992; Royall 1997; Sorensen and Gianola 2002). The situation that we consider is somewhat different, because we are a priori interested in all of the 10 parameters, but seek a practicable way to envision the output. Based on examination of the literature, we have settled on the following procedure to estimate the values of the parameters and the evidence that the data provide about the strength of the effect associated with each parameter. Royall (1997) notes that there is no general solution to this problem and no existing approach that is theoretically unassailable, but that “there are a variety of quite satisfactory *ad hoc* methods for many important applications” (pg 152).

We searched the 10-dimensional parameter space for the values of the constants that maximize the likelihood function. We denote these maximum likelihood estimates (MLEs) by  $c_i^*$ . Next, we constructed 10 one-dimensional functions by holding 9 of the parameters at their maximum likelihood value and systematically varying the 10<sup>th</sup> across the range of values where likelihood is appreciable. Thus, for example, for the parameter associated with hypothesis H1, the function we consider is  $L(c_1 | c_2^*, \dots, c_{10}^*, data)$  (for purposes of presentation in figures, we use log-likelihoods). This is called the profile likelihood for parameter  $c_1$ ; the definitions of the other 9 profile likelihoods are similar. In the next section, we will show plots of the 10 profile likelihoods.

We will also introduce the profile likelihood interval, defined as the upper and lower limits of the shortest segment under the likelihood curve that contains 95% or 99% of the total area under the curve. These points are often approximated as the intersections

between the log-likelihood curve and a horizontal line drawn several units below the maximum likelihood (Hudson 1971). However, because many of our curves are asymmetrical and/or have their peak at or near zero, we calculate the confidence intervals more precisely using numerical integration (with the range of values considered for each parameter divided into 20 steps) and interpolation. To the extent that the profile likelihood can be considered a true likelihood curve (see below), this interval can be interpreted as a true posterior confidence interval given a uniform prior probability distribution for each parameter.

Kalbfleisch and Sprott (1970) and Sorensen and Gianola (2002) note that problems arise when the number of parameters to be estimated is large relative to the number of data points, but that if the number of parameters is relatively small, then the profile likelihood can be viewed as a true likelihood function. In our case, we have 10 parameters and 167 censuses (123 census intervals), so that the number of parameters is indeed small relative to the amount of data.

We will say that the data provide strong evidence for a hypothesis if the MLE of the parameter associated with that hypothesis is non-zero and the profile likelihood interval does not include 0. The data provide weak evidence for a hypothesis if the MLE of the parameter associated with that hypothesis is non-zero but the profile likelihood interval includes 0. If the MLE is 0, the data provide no evidence for the hypothesis.

Furthermore, we will classify the hypotheses as having a strong effect, a weak effect, or no effect, depending upon how the MLE value of the parameter affects the predicted

population dynamics of Steller sea lions. Specifically, for each possible formulation of the model, we look at the difference between the deterministic annual population growth rate calculated from Eqn 6.3 according to the model and that calculated from the same equation using the background vital rates (about 1.1%).

### **Caption for Figure**

**Figure 6.1.** The method of ‘thinking along sample paths’ allows use to connect censuses in different years (panel a) with underlying population trajectories (panel b), even in the more complicated case of both pups and non-pups (panel c). Further details are given in the text.

## 7. Results and Interpretations

### *Observation Error*

The maximum-likelihood estimates of  $\alpha$  and  $\beta$  are approximately 19 and 15, respectively (Figure 7.1). Our characterization of the distribution for observation error (Figure 7.2) results in a mean probability of observing a non-pup of about 56%.

### *Critical Harbor Seal Density*

Harbor seal densities around rookeries with rising or falling sea lion populations are shown in Figure 7.3 for three different years: 1980, 1990, and 2000. Consistent with the prey switching hypotheses (H9, H10), all three years show higher mean harbor seal densities ( $> 5000$ ) where the sea lion population is growing, and lower densities ( $< 4000$ ) where the sea lion population is falling. The difference is statistically significant in 1990 ( $p = 0.004$ ). We chose an intermediate harbor seal density (4500) as the threshold parameter below which killer whales and/or other predators switch to consuming Steller sea lions.

### *Confronting the Hypotheses With Data*

The log-profile likelihood plots for the parameters associated with each hypothesis are shown in Figure 7.4. In Table 7.1, we provide the MLE values for these parameters along with their 95% confidence intervals. The evidence can be summarized as follows:

	Strong Evidence	Weak Evidence	No Evidence
Strong Effect	H1: Total prey availability affects fecundity H5: Pollock fraction affects pup recruitment		
Moderate Effect	H10: Harbor seal density (predation) affects non-pup survival		
Weak or No Effect		H4: Pollock fraction affects fecundity	H2: Total prey availability affects pup recruitment H3: Total prey availability affects non-pup survival H6: Pollock fraction affects non-pup survival H7: Fishery activity affects pup recruitment H8: Fishery activity affects non-pup survival H9: Harbor seal density (predation) affects pup recruitment

We consider that H4 only has weak evidence because the 95% and 99% confidence intervals both include 0.

In Table 7.2, we give the Akaike Information Criterion (AIC) and AIC Weight for thirteen of the most likely model configurations. Two models, one including H1, H4, H5, and H10 and the other including only H1, H5, and H10, have very similar AIC weights and together comprise almost 99% of the total weight. The third most likely model,

including H1 and H5, brings the cumulative total to 99.5%.

### *Forward Comparisons*

In Figure 7.5, we compare non-pup census data to the results of forward simulations based on different model configurations for three rookeries in the western population and one in the eastern population. In Figure 7.5a, the simulation uses the fixed background vital rates measured at the Marmot Island rookery (Calkins and Pitcher 1982, York 1994, Holmes and York 2003). In panels b, c, d, and e, the vital rates are modified according to hypotheses H1, H4, H5, and H10 alone, using the MLE values of their respective parameters. Panel f includes both of the significant effects acting simultaneously. The solid line in each graph shows the annual median value from 10,000 Monte Carlo simulations starting at a single non-pup count chosen to minimize the sum-of-squares difference between the observed censuses and the mean of the simulated trajectories. The dotted lines correspond to the 2.5 and 97.5 percentiles of the simulated observed counts.

If we compare Figures 7.5b, c, d, and e, we see that H5 has by far the strongest effect, followed by H1, H10, and finally H4. A comparison of Figures 7.5d and f reveals that H5 can nearly explain the entire decline by itself.

## Captions for Figures

**Figure 7.1.** Likelihood contours for the parameters of the beta distribution used to characterize the observation error.

**Figure 7.2.** The resulting distribution for the probability of sighting a non-pup has a peak at about 60%, and essentially all of the probability is contained between 40% and 80%.

**Figure 7.3.** When we compare the harbor seal populations around rookeries where Steller sea lion populations were increasing (clear) or declining (grey) we see a clear (and sometimes statistically significant) division with more harbor seals around those rookeries that are increasing. We choose a density of 4500 harbor seals within the 300 km foraging radius of a rookery as the threshold for inclusion of Steller sea lions in the diet of killer whales.

**Figure 7.4.** Profile likelihoods for the parameters associated with each of the hypotheses. The weight of the evidence supports only H1 (that fecundity is a function of total prey availability), H4 (that fecundity is a function of pollock fraction), H5 (that pup recruitment is a function of pollock fraction), and H10 (that non-pup survival is a function of harbor seal density).

**Figure 7.5.** Forward simulations at three Western rookeries and a ‘control’ Eastern rookery (Marmot Island). Points represent the census data, the solid line the median value from 10,000 simulations, and the dotted lines the 2.5 and 97.5 percentiles. Panel a): Results using the base parameters; Panel b): Using H1 alone; Panel c): Using H4 alone, Panel d): Using H5 alone; Panel e): Using H10 alone; and Panel f): all four nonzero effects at once.

**Table 7.1:** Maximum-likelihood estimates and Confidence Intervals (based on area under curve) for the parameters associated with each hypothesis

	<b>Hypothesis</b>	<b>MLE</b>	<b>95% weight interval</b>	<b>99% weight interval</b>
H1	total prey -> fecundity	900000	805000, 987000	750000, 996000
H2	total prey -> recruitment	0	0, 138000	0, 173000
H3	total prey -> non-pup survival	0	0, 77600	0, 90000
H4	pollock -> fecundity	0.04	0, 0.0826	0, 0.0996
H5	pollock -> recruitment	5	4.61, 5.39	4.54, 5.46
H6	pollock -> non-pup survival	0	0, 0.00776	0, 0.00900
H7	fisheries -> recruitment	0	0, 0.00000000255	0, 0.00000000349
H8	fisheries -> non-pup survival	0	0, 0.000000000896	0, 0.00000000148
H9	seals/orcas -> recruitment	0	0, 0.0339	0, 0.0479
H10	seals/orcas -> non-pup survival	0.01	0.00597, 0.0138	0.00469, 0.0149

**Table 7.2:** Model likelihoods and AIC weights

<b>Model</b>	<b>Log-likelihood</b>	<b>parameters</b>	<b>negative AIC</b>	<b>AIC weight</b>	<b>Cumulative</b>
c1,c4,c5,c10	-5183.74	5	-10377.5	0.520969	0.520969
c1,c5,c10	-5184.85	4	-10377.7	0.467161	0.98813
c1,c5	-5191.08	2	-10386.2	0.006814	0.994943
c1,c4,c5	-5190.77	3	-10387.5	0.003427	0.99837
c1,c5,c9	-5190.96	4	-10389.9	0.001037	0.999408
c1,c4,c5,c9	-5190.52	5	-10391	0.000592	1
c5,c10	-5436.45	3	-10878.9	6.88E-110	1
c4,c5,c10	-5438.04	4	-10884.1	5.17E-111	1
c5	-5463.73	1	-10929.5	7.23E-121	1
c5,c9	-5463.11	3	-10932.2	1.81E-121	1
c1,c4,c10	-6575.22	4	-13158.4	0	1
c1,c10	-6749.27	3	-13504.5	0	1
c1	-7840.38	1	-15682.8	0	1

## 8 Discussion

The strong message of ecology is that the world changes and that the reasons for change are manifold. Thus, rather than trying to ‘prove’ one mechanism, we should recognize that multiple mechanisms will almost always be at work, and we should ask how to weigh the importance of different mechanisms. It is this approach that we’ve taken in understanding the decline of the western population of Steller sea lions. Based on the best set of data examined to date, we conclude that:

There is good evidence for two strong effects

H1: Total prey availability affects fecundity

H5: Pollock fraction in the environment affects pup recruitment.

and one moderate effect,

H10: Harbor seal density (predation) affects non-pup survival

marginal evidence for one weak effect,

H4: Pollock fraction in the environment affects fecundity

and no evidence at all for any of the other six effects considered:

H2: Total prey availability affects pup recruitment

H3: Total prey availability affects non-pup survival

H6: Pollock fraction in the environment affects non-pup survival

H7: Fishery activity affects pup recruitment

H8: Fishery activity affects non-pup survival

H9: Harbor seal density (predation) affects pup recruitment

Virtually all of the AIC weight (98.7%) is assigned to two models (one with H1, H4, H5, and H10 and the other with H1, H5, and H10), suggesting that these three or four hypotheses (or analogous ones that have the same apparent behavior) are sufficient to explain the decline.

These results are not unexpected (indeed, each of the 10 hypotheses is plausible and has been proposed at some point, with associated supporting data). What our work has done is to guide the weight of the evidence, when all plausible hypotheses are competing, towards those that win the competition.

However, the predicted population trajectories at Hazy (in the eastern stock) in Figure 7.5f are far too low. This suggests that the current model formulation has not yet captured some important factor that differs between the western and eastern stocks. This and a range of other possible follow-on projects are discussed in Appendix A.1.

### **Implications**

Although we use the word mechanism, we recognize that a study such as this one cannot demonstrate causality. But our work can suggest key empirical studies. To see this, let us return to the deterministic version of the population model:

$$\begin{aligned}
N(i,t+1) &= \rho(i,t)J(i,t) + \sigma(i,t)N(i,t) \\
J(i,t+1) &= \phi(i,t)N(i,t+1)
\end{aligned}
\tag{8.1}$$

for which we now have life history parameters

$$\begin{aligned}
\phi(i,t) &= \phi_0 \omega_1(i,t) \omega_4(i,t) \\
\rho(i,t) &= \rho_0 \omega_5(i,t) \\
\sigma(i,t) &= \sigma_0 \omega_{10}(i,t)
\end{aligned}
\tag{8.2}$$

Eqn 8.1 can also be rewritten as

$$N(i,t+1) = [\phi(i,t) \rho(i,t) + \sigma(i,t)]N(i,t)
\tag{8.3}$$

which gives us a simple way of measuring the decline or growth of the population.

Combining the various data described in Section 3 with these life history parameters allows us to construct space-time plots for the decline rate, which we show in Figure 8.1.

Were we to speculate, it would seem that H1 is a relatively clear and simple mechanism: that lower abundance of all prey types leads to lower fecundity through the direct effect of reduced resource accumulation by adults and thus reduced storage for reproduction. H10 also has a clear mechanism, but note that its MLE is about 0.01, so that the effect of adaptive diet breadth by killer whales leads to only a 1% reduction in non-pup survival, and then only in cases where harbor seal numbers are sufficiently low.

On the other hand, H4 and H5 are more complicated. A high pollock fraction can result either from high pollock or from low non-pollock, and either of these could be the underlying factor. Furthermore, the mechanism might be something completely different for which pollock fraction is only a correlate. For example, juveniles may require some easily caught subset of prey species because they are unable to dive deep enough or swim fast enough to catch the prey that is better for them. (In the current data set the fish biomass is not broken down by size class of fish. However, the really small fish and the really big ones are probably not useful to sea lions. Thus, some additional thinking is required about how to modify the survey data to address this question.)

Our results also suggest an adaptive management plan in which one designates the areas around some of the rookeries as experimental zones in which to make fishery quotas contingent upon the results of pre-fishing season survey trawls. We envision a series of treatments:

- Rookeries around which fishing is not affected by the pre-season survey information (control type 1).
- Rookeries around which no fishing occurs (control type 2)
- Rookeries around which fishing is reduced or prohibited if the total prey biomass in the pre-season zone is below a critical threshold (determined by  $c_1$ ).
- Rookeries around which a directed pollock fishery occurs if the pre-season survey suggests pollock fraction is above a critical threshold (determined by  $c_5$ ).

This combination of rookery types would allow sufficient variation in treatment, which is crucial in adaptive management (MRAG Americas 2002). Sea lion vital rates would be monitored in the same areas to see if the management plan is having a positive effect. Before organizing any adaptive management, it would be possible to use our model to simulate forward and suggest a time scale over which results might be expected to appear.

Our results also suggest a form of “adaptive observation”: Identify rookeries with high numbers and low numbers of harbor seals (regardless of the number of sea lions). The prediction of H10 is that the per-capita attack rate of killer whales on sea lions will be higher around rookeries where harbor seal densities are low. Careful monitoring of killer whale attack rates would provide a natural test of Hypothesis 10: If low harbor seal numbers are associated with declining sea lions, but not with elevated Killer whale attack rates, then there must be some other factor to explain the observed correspondence between low harbor seals and declining sea lions (Figure 7.3; also see Appendix).

The question “Is it food” has been asked a number of times in the context of the decline of Steller sea lions. As with most questions in biology, we shall never be able to ‘prove’ that it is food. However, we conclude that the weight of the current evidence is that it is indeed food – and both the quantity and quality of the food matters. The more recent question “Is it killer whale predation” can be answered too: Sometimes, if harbor seal populations are sufficiently low, but not with a large reduction in survival.

### **Caption for Figure**

**Figure 8.1.** Space time plots of the decline rate based on Eqn 8.3 for H1 (total food affecting fecundity) alone (Panel a), H4 (pollock fraction affecting fecundity) alone (Panel b), H5 (pollock fraction affecting pup recruitment) alone (Panel c), H10 (harbor seal density affecting non-pup survival) alone (Panel d), or all four effects together (Panel e). Note that the warmer colors correspond to greater rates of decline.

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## **Appendix: Additional hypotheses and other follow-on possibilities**

*Possible extensions of the work presented here:*

1. Either remove or expand the eastern population data set. Currently, the data set covers 35 rookeries in the western population and 3 in the east. The poor fit of simulated trajectories to the eastern-population data (e.g. Hazy in Figure 7.5f) suggests that the mechanisms may be different there. Perhaps a larger set of eastern rookeries would force the model to match them better, or perhaps the two populations should simply be treated separately.
2. Solve for  $h_{crit}$  (the critical harbor seal density below which SSL become Killer whale prey) rather than assuming it's 4500.
3. Try using a “foraging radius” other than 300 km.
4. Investigate alternative explanations for the correlation between low harbor seal densities and falling sea lion populations. One explanation for the pattern shown in Figure 7.3 is that declining sea lions and low harbor seals are correlated simply because poor local conditions depress both species. This can perhaps be tested more directly. The strategy would be to compare sea lion population trajectories in different areas where the harbor seal population is either low and rising, or low and falling. Falling sea lion populations in locations where harbor seal densities are low but rising would support H10.
5. Divide non-pups into two age classes, following Holmes and York (2003).
6. Run forward simulations to predict how long it might take to get conclusive results from experimental/adaptive management strategies.

7. Add new effects to the model:

- a. Consider using the probability of non-zero catch instead of CPUE in H1-H3.
- b. Consider making prey availability a function of prey size (biomass per individual)
- c. Refine H5 to tease apart the issue of whether the problem derives from too much pollock or too little non-pollock. Focusing on availability of crabs or other easily caught prey (perhaps needed by juveniles) would be one possibility.
- d. Test for a negative impact of Arrowtooth Flounder due to competition.
- e. Use local small boat registration locations or "fish tickets" as a proxy for small boat activity, which might correlate with sea lion mortality for a variety of reasons.
- f. Consider direct effects of the climate shift. For example, elevated water temperatures may alter metabolism, leading to a change in minimum caloric intake.
- g. Add metapopulation dynamics, either as a diffusion kernel or as a simple probability of moving to a neighboring rookery.

**Table A.1:** A summary of hypotheses as to causes of declines in marine mammals or birds, the effect those causes have on individuals, the role of the environment in driving those changes, variables of the marine mammals and birds that would need to be monitored in addition to abundance, and the expectation of how those variables would be altered if fishing was reduced.

Hypothesis	Immediate effect on individual marine mammals or birds	Environmental driver (other than target species being reduced)	Variables to measure (in addition to abundance)	Expectation given a reduction in fishing (including temporal scale)
The decline is caused by incidental mortality in the course of fishing operations	Death	None	Age-specific mortality	Mortality rate declines (immediately)
The decline is caused by removal of target fish by the fishery	Starvation	None	Body weight Reproduction Age-specific mortality	Body weight increases (one year) Reproduction increases (two years) Mortality rate declines (one to two years)
The decline is caused by a diet shift in toothed whales (increased predation)	Death	Alternative toothed whale prey – decreased	Age-specific mortality	No change
The decline is caused by the prevalence of marine disease	Ill health	Production – None Prevalence of disease – increased	Health Body weight Reproduction Age-specific mortality	No change
The decline is caused by a shift in the mixture of target fish and other fish, which differ in catchability or nutritional value to the mammals and birds	Starvation	Non-target fish – increase	Body weight Reproduction Age-specific mortality	No change
The decline is caused by a shift in the distribution or abundance of zooplankton, thus affecting the resource base for the fish	Starvation	Production – decrease	Body weight Reproduction Age-specific mortality	No change
The decline is caused by a shift in abiotic components, either temporally or spatially, that affect the distribution of fish stocks and their accessibility to marine mammals and birds.	Starvation	Production – displaced from foraging areas	Body weight Reproduction Age-specific mortality	No change