Review of the November 2000 Biological Opinion and Incidental Take Statement with Respect to the Western Stock of the Steller Seal Lion, with Comments on the Draft August 2001 Biological Opinion

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Executive Summary

The November 30, 2000 Biological Opinion (Nov2000BiOp) prepared by the National Marine Fisheries Service (NMFS) resulted in a finding of jeopardy to the Endangered western stock of Steller sea lions (SSL; *Eumetopias jubatus*) relative to fisheries for pollock, Atka mackerel, and Pacific cod under management jurisdiction of the North Pacific Fisheries Management Council (Council). The Nov2000BiOp set forth a set of management measures (termed reasonable and prudent alternatives or RPAs) intended to alleviate jeopardy if implemented in the 2001 fishing season. There is continuing scientific debate about the evidence regarding food competition between SSL and these commercial fisheries, and the role of other factors that might be limiting the recovery of SSL, and the implications of this evidence for the conclusions of the Nov2000BiOp.

The Council initially tasked this team to review the Nov2000BiOp with particular focus on the following three tasks:

- 1) determine the types of information that should be collected and analyses necessary to demonstrate an unequivocal adverse affect of commercial groundfish fisheries on SSL mortality,
- 2) recommend an appropriate experimental design to improve our understanding of the interactions between fisheries and SSL, and the efficacy of imposed management measures to promote recovery of the SSL population, and
- 3) review reports of stressed pinniped populations worldwide.

Subsequent to the team's interim report to the Council, NMFS released a new draft Biological Opinion in August 2001 (Aug2001BiOp) as Appendix A to a Supplemental Environmental Impact Statement. The team was asked to review both the new biological information on SSL and the analyses used in the development of the new RPAs. We refer to this as Task 4.

Task 1 - Review of the Nov2000BiOp

The overall conclusion of the Nov2000BiOp is that there is great uncertainty about the effects of the groundfish fisheries on SSL, but it is possible that these effects could be negative. However, the evidence presented in the Nov2000BiOp is almost entirely circumstantial. With respect to many of the key hypotheses (e.g., local depletion of prey by fishing, effects of local depletion on SSL) there are essentially no direct data bearing on the specific mechanisms for the effects of fishing on SSL. For the most part, the arguments in the Nov2000BiOp are constructed on the basis that such effects are possible, biologically imaginable, and are not contradicted by the available data.

There is no question that the number of SSL in the western stock has declined dramatically since the 1970s. However, there has been a marked decrease in the overall rate of decline and the rates of decline in different parts of the range over the past decade. These changes suggest that the factors that contributed most strongly to the more rapid declines in the several decades prior to the 1990s may not be the most significant factors operating today.

The hypothesis of the Nov2000BiOp that some aspect of food availability may be responsible for the declines in SSL is based largely on inferences drawn from a comparison of measurements from samples of SSL taken during the 1970s and another sample taken during the 1980s. These samples indicated, or in some cases simply suggested, a reduction in body growth rate, in late-term pregnancy rates, and in juvenile survival that were consistent with food limitation hypotheses. But these inferences are based on vital rates that applied more than 15 years ago, when the oceanographic regime, the fishery activities, and the rate of decline of the SSL population were quite different from now. There are good reasons for suspecting that these earlier vital rates are not representative of those currently being experienced by the population. The lack of recent estimates of vital rates is a serious obstacle to the evaluation of alternative explanations for the continuing decline of the western stock of SSL.

The distribution of SSL at sea is not well understood, but such knowledge is critical to understanding the potential effects of fisheries and environmental change on the foraging ecology of this species. NFMS and ADF&G have made good progress in fitting SSL with satellite transmitters and data loggers that provide information on the movements and diving behavior of SSL at sea. However, despite the recognized importance of foraging distribution, there has been relatively little analysis of these new data. In our view, this represents a serious limitation of the analyses presented in the Nov2000BiOp (and, to a lesser extent, the Aug2001BiOp).

There has been considerable effort to increase the understanding of the diet of SSL through broad-scale collections of scats. Diet estimation in pinnipeds is fraught with difficulties, and SSL are no exception. While we applaud the research that has been done, the panel does not share the confidence expressed in the Nov2000BiOp that scats are a reliable tool for monitoring seasonal and temporal trends in SSL diets.

Task 2 - Design of Field Experiments

Experimental design to determine effectiveness of the Nov2000RPAs

During the time period of our review, the design of the experiment(s) to test the effect of fishing on SSL has been evolving and has therefore, from the standpoint of our review, constituted somewhat of a moving target. Apparently, the experimental design is constrained by the desire to ensure that jeopardy is alleviated for all management units. This presumably accounts for the somewhat surprising expectation that SSL populations in both the open and closed areas of the experiment would respond positively during the period of the experiment. In effect, the Nov2000RPA experimental design has two

treatments and no control. We are quite pessimistic about the likelihood of obtaining convincing results using the proposed design. Given the high degree of uncertainty that the proposed RPAs really will alleviate jeopardy, we think it is worthwhile to contemplate an experiment that has a true control, at least locally. Given that the present size of the SSL stock is over 30,000 animals and that the present rate of decline is small, there should be considerable scope for experimentation without undue risk.

An important component of the design of any experiement is the choice of response variables (i.e., attributes of SSL) used to determine how experimental treatments affect SSL. We evaluted a suite of morphometric/energetic, behavioural, ecological, and demographic variables that have been or might be considered informative in the interpretation of experiments. Based on our analysis, it seems clear that quite similar changes in SSL response variables are predicted under the fishery-, climate-, and fish-predator-effects hypotheses. Our conclusion is that, without a distinct spatial pattern of treatment and control areas, it will not be possible to distinguish among the three food-driven hypotheses for the decline in SSL using only these response variables.

Finally, we note that good experiments can only be designed and undertaken if there are adequate quantitative observations from which to reasonably construct alternative models (i.e., explanations) and predictions. Given the current state of our observations with respect to SSL foraging behaviour and the effects of fishing on prey behaviour at fine to meso scales, it might be considered somewhat premature to undertake large-scale manipulative experiments, particularly given the difficulties associated with achieving convincing results. On the other hand, the importance of learning whether fishing really is having an impact on SSL may outweigh the desire to make additional preliminary studies as a prelude to designing the best possible large-scale experiment.

Task 3 - Responses of Other Pinnipeds

Case studies for other pinniped species in which the effect of local prey depletion on demography has been investigated, or in which changes in demography have been attributed to local prey depletion, can be divided into three categories: fisheries-induced changes, environmentally-induced changes, and predator-induced changes.

The team was unaware of direct evidence that prey depletion by fisheries has affected the demography of any seal population, whereas there are a number of cases in which seal populations have continued to increase exponentially following the collapse of an important prey species. There is clear evidence of negative effects of environmental change on the demography of pinnipeds.

Two lessons emerge from our review. First, that changes in seal demography in response to a reduction in prey abundance are either so dramatic that they can be detected even without scientific study (e.g., Cape fur seals in Namibia, harp seals in Norway) or are relatively subtle, requiring time series of monitoring data (e.g., North Sea grey seals, Antarctic fur seals, southern elephant seals). Second, a reduction in first-year survival was involved in all the examples we have identified.

Task 4 - Review of August 2001 Draft Biological Opinion

The Aug2001BiOp concludes that managing the fisheries under RPA 4 would neither jeopardize the continued existence or recovery of the stock, nor would it lead to adverse modification of critical habitat. The conclusion with respect to jeopardy is based on new biological research on SSL presented in the Aug2001BiOp, which is used in an analysis of the effects of RPA 4 on the population trends of SSL over the next 8 years. The conclusion with respect to adverse modification is based on a forage ratio analysis.

New biological information

The Aug2001BiOp presents new information on the diets and distribution of SSL. However, only the new analyses of the distribution of SSL at sea are used directly in support of the RPA analysis. These new analyses indicated that most SSL locations at sea, derived from satellite telemetry, occur within 10 nm of land. However, this conclusion is quite sensitive to how the location data are analyzed. Different assumptions result in strikingly different conclusions about the way in which SSL use the ocean. As such, we have little confidence that this analysis provides a sound basis for drawing conclusions about the effect of the RPA on the dynamics of SSL.

Analysis in support of Aug2001RPA alleviation of jeopardy

Based on the analysis of the satellite telemetry data, the Aug2001BiOp assumed that the most important critical habitat is within 10nm of a rookery or haul out, because this is where SSL spend at least 75% of their time. A corollary of this is that 75% of the effects of a fishery on a haul out or rookery would be removed by closing the area within a 10-nm radius of that site to fishing. With a few further assumptions, the RPA Committee was able to simulate the potential effects of different area closures on trends in the number of SSL in 13 management areas over the next 8 years.

The RPA Committee clearly recognized that influential assumptions were involved in this population analysis. These include assuming that the effects of fisheries closures are related to local trends in SSL numbers rather than population wide ones, and assuming that only 50% (rather than the original 75%) of the effect of a fishery is removed by closing an area 10 nm around a haul out or rookery and that increased fishing outside 20 nm would have no effect. Trials of the RPA's performance using a computer model indicated that it was robust to the first of these assumptions, but not to the second. The potential effects of the third assumption were not tested. Given our concerns about the validity of the 75% value, and the possible importance of foraging beyond 20 nm, this raises considerable doubts about the reliability of the entire procedure.

Finally, simulations carried out by the team indicate that, under all the RPAs, local populations at the extreme western and eastern ends of the distribution of the western

SSL stock are predicted to decline steadily over the next 20 years. The acceptability of such a situation, as a matter of policy, merits further discussion.

Avoiding adverse modification of critical habitat

To assess whether fishing might adversely modify critical habitat, the Aug2001BiOp presented calculations of the ratio of the estimated unfished biomass of pollock, Atka mackerel and Pacific cod in the Gulf of Alaska (GOA), Aleutian Islands, and Bering Sea system to the estimated food requirements of the historical population of 184,000 SSL in the western stock. They assumed that this was a minimum per capita requirement for a "healthy" stock of SSL. They then calculated the same ratio for the biomass of these three prey species in SSL critical habitat and the requirements of the current SSL population. All but one of these values was greater than that required for a "healthy" stock, and hence no adverse modification was predicted.

Clearly, this approach does not address the central issue: do the fisheries for these species cause **local** depletion of prey within SSL critical habitat? As a result, it cannot be used to evaluate whether or not specific management actions are more or less likely to result in adverse modification. These calculations (that there is more than enough biomass of these three prey species in critical habitat to sustain the current SSL population) are also inconsistent with NMFS' position that nutritional stress associated with local prey depletion is a likely cause of at least some portion of the recent decline in SSL numbers.

The team sees little merit in this approach to the assessment of adverse modification of critical habitat.

Research Priorities

One of the team's tasks was to recommend an appropriate experimental design to improve our understanding of the interactions between fisheries and SSL, and the efficacy of imposed management measures to promote recovery of the SSL population. This was, in part, because the original Nov2000BiOp RPA (Alternative 3) involved contrasting regulation of fisheries in adjacent management areas, with some areas being effectively closed to fishing while others were not. However, the preferred Aug2001BiOp RPA (Alternative 4) involves a wide range of area- and fishery-specific measures, which are predicted to have more subtle effects on local SSL population dynamics than Alternative 3. The panel feels that it is **unlikely** that simple monitoring of the response of these local populations under Alternative 4 will provide any insight into the interactions between SSL and fisheries.

However, even if Alternative 3 was to be implemented, we suspect that the responses of local populations would be difficult to interpret. Although we believe that large-scale experiments can reduce the long-term risks to the western stock of SSL, it is not practicable to design such experiments at present. We therefore recommend that research

should focus initially on an integrated program of modeling and smaller scale manipulative experiments (see below).

Many elements of the recent and current research plans are unlikely to contribute either to the jeopardy finding of the Nov2000BiOp or to the no-jeopardy finding that the Aug2001BiOp attaches to the preferred RPA. Much of the deficiency has to do with a focus on physiological or behavioural indices, which cannot be converted to demographic consequences. Some of the inherent ambiguities in interpreting these indices are set forth in our discussion of response variables. The bottom line is that for results to be useful in the jeopardy decision, the effects of any posited mechanisms need, ultimately, to be quantified in units of population change (i.e., mortality or reproduction).

The SSL program has undergone a rapid shift in circumstances from modest budget to very large budget (although the longevity of this increased level of funding is uncertain). Nevertheless, this means that some research activities that previously were perceived as important, but budget-limited, could be expanded considerably. We strongly urge that in the next round of funding the highest priority is given to proposals which will have a direct bearing on the jeopardy finding and the effectiveness of the RPAs.

We believe priority should be given to the assessment of population trends and vital rates, and on better understanding the mechanisms underlying the current decline in the western SSL population. The high priority research items (not in order of priority) are:

• monitoring trends in population size and distribution

The Aug2001BiOp indicates that cessation of the decline in SSL numbers is the criterion that will be used to evaluate the success or failure of the implemented RPA. Therefore, ongoing monitoring of pup and non-pup numbers on rookeries and haulouts throughout the year and the geographic range of the stock is crucial to determining population status.

• estimation of vital rates

It is generally believed that the SSL population decline is an expression of reduced per capita recruitment owing, proximately, to reduced post-weaning juvenile survival. But the demographic parameter estimates upon which this judgement is based are derived from data from a period when the population decline was considerably steeper than at present. There is a strong suspicion that the causes of the decline were different than they are now. Therefore, new measurements are needed to estimate current vital rates.

• spatial and temporal scales of foraging

An understanding of the spatial and temporal distribution of SSL at sea and the factors that affect this distribution will be needed to identify ecologically important habitats, and to assess the response of SSL to environmental change and human activities, including fishing, that affect the distribution, abundance and quality of available prey.

• diet

We recognize that estimating the diet of SSL is difficult. Nevertheless, the importance of these data warrant the effort. NMFS is to be commended on the substantial effort that has gone into the collection of scat samples throughout the western stock. However, the reliance on frequency of occurrence as the measure of the relative importance of prey species is fraught with problems, and more informative and reliable measures should be sought. Thus, we would also recommend that other techniques, which are not dependent on the recovery of prey hard parts (e.g., fatty acid signature analysis), be seriously investigated. In the longer-term, such methods are likely to provide a more reliable basis for testing hypothesis about the factors underlying temporal and spatial variation in the diet of SSL.

• modeling

We expect prey availability, predators, and disease to affect the dynamics of SSL. Further, we expect that the effects of these factors to vary in time and space. Thus, it seems to the team that it will be useful to develop a modeling framework that can be used to integrate information on the foraging and reproductive energetics of SSL within a spatially explicit demographic model. Within this framework it should be possible to identify the types of perturbations that are likely to pose a problem for SSL and the resulting demographic consequences.

• retrospective data analysis

The historical data on counts of SSL at rookeries and haulouts is of high spatial resolution and provides an opportunity, independent of any manipulation experiment, to examine the relationship between SSL demography and possible influencing factors, such as fisheries. Nonparametric regression models could be used to investigate the relationship between the rate of change of SSL numbers at these sites and contemporary high resolution, spatially-explicit data on catch and effort for pollock and Atka mackerel close to the rookery over that time period.

• local depletion of prey and its consequences for SSL

The conclusion that fisheries for pollock, Atka mackerel and Pacific cod jeopardize the survival and recovery of the western stock of SSL is based on the hypothesis of localised depletion of prey within critical habitat. However, there is no direct evidence to support or refute this hypothesis. An integrated research program to address this issue is urgently required.

Introduction

The November 30, 2000 Biological Opinion (Nov2000BiOp) prepared by the National Marine Fisheries Service (NMFS) pursuant to the Endangered Species Act, resulted in a finding of jeopardy to the Endangered western stock of Steller sea lions (SSL; *Eumetopias jubatus*) relative to three fisheries under management jurisdiction of the North Pacific Fisheries Management Council (Council). The Nov2000BiOp sets forth a set of management measures (termed reasonable and prudent alternatives or RPAs) intended to alleviate jeopardy if implemented in the 2001 fishing season. Those measures are being implemented by NMFS under emergency rulemaking authority. The RPAs carry considerable economic and social costs for the pollock (*Theragra chalcogramma*), Atka mackerel (*Pleurogrammus monpterygius*), and Pacific cod (*Gadus macrocephalus*) fisheries. There is scientific debate regarding the conclusions of the Nov2000BiOp, and its associated RPAs, owing to the nature of the evidence regarding food competition between SSL and these commercial fisheries, and other factors that might be limiting the recovery of SSL.

Statement of Task

The Council initially tasked this team to review the Nov2000BiOp and provide their overall assessment of that document and its underlying science, assumptions, and hypotheses. More specifically, the team was to focus on the following three tasks:

- 1) Determine the types of information that should be collected and the analyses necessary to demonstrate an unequivocal adverse affect of commercial groundfish fisheries on SSL mortality. Characterize the current availability of such information, the critical gaps and the impact of data limitations on the determination of fishery/SSL competitive interactions.
- 2) Recommend an appropriate experimental design to improve our understanding of the interactions between fisheries and Steller sea lions, and the efficacy of imposed management measures to promote recovery of the SSL population.
- 3) Review reports of stressed pinniped populations worldwide and compare and contrast characteristics of those populations with conditions observed for SSL.

In July 2001, the team also was asked to review the August 2001 Draft Biological Opinion (Aug2001BiOp) with particular attention to the new RPAs (Aug2001RPA) it proposed to remove jeopardy. In that Opinion, NMFS concluded, "given the new biological information on Steller sea lions, that there were other possible ways to avoid jeopardy and adverse modification of critical habitat". This new Biological Opinion concluded there would be no jeopardy to the western SSL stock resulting from prosecution of the covered fisheries if the new RPAs were implemented.

There was little time for the team to review the Aug2001BiOp if it was to meet its September deadline. Therefore we have commented on only three critical topics: 1) the

significance of the new biological information, 2) the population dynamics analysis which purports to provide a framework for comparing the effects of different RPAs, and 3) the use of the forage ratio method to assess the likelihood of modification of critical habitat. We refer to this final component as our Task 4.

We begin with an overall evaluation of the arguments put forward in the Nov2000BiOp concerning the likelihood that the commercial fisheries for pollock, Atka mackerel, and Pacific cod, if pursued as then proposed without implementation of RPAs, would adversely affect the western stock of SSL. Within this framework, we assess current understanding of the population dynamics and foraging ecology of SSL, and the evidence that fishing results in reduced foraging efficiency of SSL through its effects on local prey abundance and levels of prey aggregation. We briefly also consider alternative hypotheses that have been proposed for the decline in SSL numbers. We then discuss the kinds of data that ought to be collected, and the types of analyses that could be done, to provide insight into the factors affecting trends in SSL abundance.

Comparative studies are often useful in providing insight when data on a population of interest are not available. Therefore, we examine other situations where changes in the abundance of pinniped species have been attributed to local depletion of their prey. We review the evidence that has been used to infer this relationship and the way in which the pinniped population responded to changes in prey abundance. We extend this comparative review to include a range of case studies where pinnipeds have faced potential competition from commercial fisheries or have been negatively affected by other factors, such as large-scale environmental variability. We discuss the kinds of studies, monitoring, and management experiments that might be conducted to test hypotheses regarding the impacts of fisheries on SSL. Finally, we conclude with our limited analysis of the Aug2001BiOp, within the context explained above.

Task 1 - Review of the Nov2000BiOp

We have not provided a detailed (i.e., point by point) evaluation of the arguments put forth in the Nov2000BiOp. There are a number of statements in the Nov2000BiOp that we feel are not well supported by evidence. However, for the most part, correcting these matters of fact or interpretation of the evidence will not alter the overall conclusion of that document: there is great uncertainty about the effects of the groundfish fisheries on SSL, but it is possible that these effects could be negative. The evidence presented in the Nov2000BiOp is almost entirely circumstantial. With respect to many of the key hypotheses, there are essentially no direct data bearing on specific mechanisms of the effects of fishing on SSL. For the most part, the arguments in the Nov2000BiOp are constructed on the basis that such effects are possible, biologically imaginable, and are not contradicted by the available data. The weight that this argument of "plausibility" has carried in the decision process is a matter of legal and juridical interpretation of the Endangered Species Act.

Biology of Steller sea lions

a) Population dynamics

There is no question that the number of SSL in the western stock has declined dramatically since the 1970s. The broad geographic extent of the decline and its duration over several decades are clearly causes for concern. However, there has been a marked decrease in the overall rate of decline and in the rates of decline in different parts of the SSL range over the past decade. These changes, in conjunction with the changes in direct mortality, suggests that the factors that contributed most strongly to the more rapid declines in the several decades prior to the 1990s may not be the most significant factors operating today. In fact, it is believed that directed take and incidental entanglement in active fishing gear played a large role in the earlier period, and both these factors are thought to be very minor now. Although the Nov2000BiOp acknowledges the likely change in the nature of the causal factors, it does not develop this idea to help evaluate alternative hypotheses. We believe that more information could be extracted from the counts of SSL by developing spatially explicit models using both the pup and non-pup data at the level of individual rookeries or haulouts. Such models could help us understand how demography has changed in different areas over the course of the decline. This information could be used to evaluate, for example, hypotheses concerning which components of the population have recently been affected.

The current view that some aspect of food availability or quality may be responsible for the declines in SSL has gained popularity based largely on inferences drawn from a comparison of measurements from samples of SSL taken during the 1970s and another sample taken during the 1980s. These samples indicated, or in some cases simply suggested, a reduction in body growth rate, in late-term pregnancy rates, and in juvenile survival that were consistent with food limitation hypotheses. But these inferences are based on vital rates that applied more than 15 years ago (see York 1994), when the oceanographic regime, the fishery activities, and the rate of decline of the SSL population were quite different from now. There are good reasons for suspecting that these earlier vital rates are not representative of those currently being experienced by the population. The lack of current estimates of pregnancy rates and survival rates for the various segments of the population compromise the current population projections. The absence of recent data on vital rates also constitute a missed opportunity, since such data could be used to test alternative hypotheses about the factors responsible for the current trends in numbers. This sort of modeling would, of course, be much more revealing if it accounted explicitly for movement among rookeries and haulouts. Such data are largely lacking, but should accumulate rapidly over the next decade.

b) Foraging ecology

Apart from travelling from one haulout or rookery to another, it can be reasonably assumed that SSL go to sea primarily to forage. Currently, the distribution of SSL at sea is not well understood, but such knowledge is critical to understanding the potential effects of fisheries and environmental change on the foraging ecology of this species.

Understanding the 3-dimensional use of the sea by SSL is also fundamental in identifying important habitats and in designing experiments and other studies to test hypotheses about the effects of local prey depletion by fisheries on SSL numbers.

The data summaries from the satellite tagged animals given in the Nov2000BiOp do not permit critical evaluation of how the analyses were done, and thus the conclusions drawn from the analyses cannot be properly assessed. The last published analysis of ranging behavior (Merrick and Loughlin 1997) was based on data collected during the period 1990-1993 (also see New Biological Information, Task 4 below).

The Nov2000BiOp repeatedly confuses the concepts of foraging and diet. Although clearly related, they are not the same and careless use of these terms can be misleading. Foraging refers to behaviors used in searching for, selecting, capturing and handling prey, and the ecological and prey characteristics that influence the decision to include a prey item in the diet. Diet is simply what was eaten. An example of the misuse of these terms is found in Table 4.2 where we are directed to foraging studies of SSL, but are presented with summaries of what was found in SSL stomach contents, i.e., diet. Although the confusion of these concepts may not seem important, it can be. Studies of what was found in the stomachs or scats of SSL (i.e., diet) are clearly important, but they provide little indication of where SSL forage, how often they dive, how deeply they dive, what fraction of the time they spend foraging, or how the composition in the diet relates to the spectrum of available prey items where and when the feeding took place. Each of these aspects of an animal's behavior could be used to shed light on how SSL might be affected by fishing, and by environmental change affecting prey availability.

There has been considerable effort to increase the understanding of the diet of SSL through broad-scale collections of scats. Diet estimation in pinnipeds is fraught with difficulties, and SSL are no exception. Nevertheless, the Nov2000BiOp concludes that scats are a "reliable tool for monitoring seasonal and temporal trends in predator diets and eliminates the need to euthanize the animal." While the second point is true, the first is almost certainly not, in most situations. One of the many known problems with the use of scats is that one has little idea of the age or sex of the animals whose scats were collected. Thus, there is usually no way of knowing how representative the sample is with respect to different age and sex classes. The potential sources of bias in estimating species composition of the diet from scats are reasonably well understood in principle, although how they affect estimates of the diet of individual species is less well understood. NMFS and ADF&G scientists have used, in the past, the split-sample frequency of occurrence of different prey species (Olesiuk et al. 1990) in individual scats to characterize SSL diet, rather than other more sophisticated methods of diet reconstruction (e.g., Frost and Lowry 1980; Hall et al. 2000). This is understandable, since feeding studies of SSL have indicated that a high proportion of otoliths, which would normally be measured in order to reconstruct diet, are completely digested during their passage through the gut. However, it should be recognized that frequency of occurrence tends to over-emphasize the importance of rare prey species and is relatively insensitive to changes in the proportion of the most important prey species in the diet (Olesiuk et al. 1990). In addition, the statistical properties of split-sample frequency of occurrence estimates are not well understood, which makes it difficult to detect significant changes in diet.

Another source of bias in the use of scats relates to the duration of foraging trips. VHF and SDR data indicate that female trips are relatively short during the summer, but can differ widely from 7.5 h to 39.1 h among rookeries (Springer et al. 1999, p. 27). Scat samples collected from females (or other age and sex classes) undertaking short foraging trips likely represent the diet of these animals in so far as such data can, but SSL undertaking trips longer than 24 h likely defecate at sea and thus scats collected at land sites may be biased towards the diet from the return trip in the immediate vicinity of haulouts. Winter foraging behavior could exacerbate this bias. Merrick and Loughlin's (1997) analysis of data from 1990-93 indicates that average trip duration of 5 adult females in winter was on the order of 8.5 d. If these data are representative, then scats collected at rookeries and haulouts are unlikely to be representative of winter diet. These points further underscore the importance of understanding the spatial and temporal characteristics of SSL foraging behavior.

The Nov2000BiOp attempts an integration and synthesis of the current understanding of SSL foraging in section 4.8.6.6. This synthesis is summarized in seven points. Our comments on these points are as follows:

Point 1 - "Steller sea lions are land-based predators but their attachment to land and foraging patterns/distribution may vary ...;"

This is a reasonable statement, evidence for which comes not only from studies of SSL, but from many other pinniped species.

Point 2 - "foraging sites relatively close to rookeries may be particularly important during the reproductive season when lactating females are limited by the nutritional requirements of their pups; "

Foraging sites close to rookeries are clearly important for lactating females, but all evidence to date suggests that during the first two months of lactation female SSL are not experiencing food shortages. The extent to which female foraging may be limited by the nutritional requirements of their pups during mid to late lactation is not known, but certainly pup fasting ability will place an upper limit on the duration of female foraging trips.

Point 3 - "Steller sea lions appear to be relatively shallow divers but are capable of (and apparently do) exploit deeper waters (e.g., beyond the shelf break);"

This point clearly depends on what is considered "shallow". Shallow diving appears to mean < 200 m. By itself this statement is not terribly useful. Data on SSL dive depth would be more useful if they were linked to bathymetry such that one could then estimate the fraction of benthic habitat available to different age and sex-classes.

Point 4 - "at present, pollock, Atka mackerel appear to be their most common or dominant prey, but Steller sea lions consume a variety of demersal, semi-demersal, and pelagic prey;"

That pollock and Atka mackerel are common in the diet of SSL seems well supported by available information, subject to the caveats about the quality of frequency-of-occurrence data from scats (e.g., biases arising from differential or complete digestion of prey remains, and foraging range effects on prey remains) and the fact that variation of diet among age and sex classes is poorly known,

Point 5 - "the availability of prey to an individual sea lion is determined by a range of factors ...;"

This is a rather general statement that could be made about any pinniped species and therefore is not particularly useful with respect to SSL foraging,

Point 6 - "diet diversity may also be an important determinant of foraging success and growth of Steller sea lion populations; and"

Diversity may indeed be important. However, this point is based on an observed correlation between diet diversity and rate of decline in different parts of the SSL range (Merrick et al. 1997; also see Task 4). As noted in the Nov2000BiOp, observed differences in diet diversity may simply reflect regional differences in prey availability that may have no direct effect on SSL demography. Thus, a more specific formulation and test of this hypothesis is needed before much significance can be attached to the observation.

Point 7 - "the broad distribution of sea lions sighted in the POP database indicates that sea lions forage at sites distant from rookeries and haulouts; the availability of prey at these sites may be critical ...".

It is quite likely that more distant (i.e., beyond 20 nm) foraging is important. The lack of analysis of SSL movements from existing satellite data, and the paucity of such data in winter, represent significant gaps in knowledge. As a result, the arguments about food availability advanced in the Nov2000BiOp are largely speculation.

c) Physiology

Captive studies - "The Steller sea lion captive research program at the University of British Columbia uses a bioenergetic paradigm to empirically test hypotheses related to the population decline." This is an overstatement. However, it is true that this captive program has contributed to our understanding of the energetic requirements of SSL. These data will be useful both in designing studies to test hypotheses and in interpreting the results of such studies.

Free-ranging studies - Essentially these studies have failed to yield any insights into the causes of the decline in SSL numbers, a point acknowledged in the Nov2000BiOp. Studies of free-ranging SSL have focused on the first 30-60 d of lactation, when females and pups can readily be sampled. Studies during mid-late lactation, when the energetic demands of lactation are greater, or during the winter, when energetic demands for themoregulation may be more severe, might have shed more light on the causes of the decline. However, such studies would have been more difficult to undertake because of reduced access to lactating females once they leave the rookeries in mid summer.

Effects of fisheries on Steller sea lions

The Nov2000BiOp argument for the effects of fisheries on SSL demography is summarized below:

- 1. Fish abundance is finite. Fishery removals are substantial and spatially concentrated. The argument is that fishing can reduce, on a local scale and for short time periods, targeted fish biomass and thereby make it more difficult for SSL to forage.
- 2. The likelihood of depletion is higher for patchily distributed fish (e.g., pollock and Atka mackerel). This is because fishing may reduce both the number of fish aggregations within an area, making aggregations more difficult for SSL to locate, and the density of fish within an aggregation, making them less profitable to foraging SSL. The effect of this hypothesized depletion on SSL will depend on the species' foraging strategy. Although SSL are probably adapted to foraging on the unfished schools of pollock and Atka mackerel, we would point out that it is also conceivable that SSL may be able to exploit fragmented fish schools more effectively.
- 3. SSL foraging efficiency may have been compromised by fisheries conducted near SSL rookeries and haulouts. The proportion of effort by the commercial pollock fishery within known SSL foraging areas has increased substantially since the 1970's. Nevertheless, the effect of this trend on the number and density of pollock schools is unknown. Also the ability of SSL to change their diet, which might be expected to occur with depletion of pollock, might be hampered by competition with other fisheries that also locally deplete their target species.
- 4. These effects are more significant the longer they last (i.e., they are cumulative) and are most significant during the winter for juvenile and adult female SSL. There are three reasons for this:
 - i. during winter SSL females face both the energetic demand of providing milk to their growing pup and of providing for the developing fetus,
 - ii. winter is a time of harsh environmental conditions likely increasing daily energy requirements, particularly for small animals with thin blubber,
 - iii. pups weaned during the winter may be challenged energetically because pups have greater metabolic and growth requirements per unit body mass and more limited foraging skills than older SSL.

Despite the acknowledged importance of winter conditions, spring foraging conditions also are likely important to adult females because poor foraging conditions could reduce birth rate, and pup birth mass and subsequent survival.

- 1. SSL do not have large fat reserves compared with other pinnipeds and require continuous access to food. Thus, they are susceptible to local depletion of prey by fisheries and have shown the effect of food limitation through reduced growth and condition as well as declining numbers.
- 2. There may be interference competition between SSL and fisheries as well as resource competition. It is speculated that the presence of fishing vessels and gear can cause disruption of feeding and abandonment of fishing areas used by SSL.
- 3. Indirect effects of fishing may reduce carrying capacity and affect the critical habitat of SSL. In this context, critical habitat is defined as the geographic extent of environment needed for the recovery and conservation of a species, and carrying capacity is the maximum number of individuals that could be supported by available resources.

Next, we briefly review the evidence of the effects of fishing on SSL presented in the Nov2000BiOp.

a) Depletion of pollock and Atka mackerel

The depletion of pollock has been documented from three areas: Bogoslof Island (AI), the donut hole, and Shelikof Strait (Fritz et al. 1995). In Shelikof Strait, for example, the fishery in 1970's developed to 300,000 tonnes/yr. By 1993, the estimated size of the Gulf of Alaska (GOA) pollock stock was reduced from 3 million tonnes to 1 million tonnes. NRC (1997) noted that SSL counts on nearby rookeries declined dramatically during the same period and individuals showed signs of reduced growth (Calkins and Goodwin 1988, Lowry et al. 1989). Uncertainties in these studies include the fact that prey density was rarely known in areas used by foraging SSL. This is because harvest rate is not necessarily a good indicator of prey availability. Using survey biomass estimates for a large region as an index of availability to SSL assumes a uniform distribution of prey in the area (an unlikely assumption). In addition, the correlation between fish distribution and catch distribution is often poor (Fritz 1993).

The depletion of Atka mackerel has been shown to occur through sharp declines in CPUE during repeated experimental trawling over relatively short periods (3 d to 17 wk; L. Fritz unpublished). Fritz estimated that harvest rates ranged between 55% and 91%, suggesting that there was substantial local depletion of the exploitable biomass. However, Atka mackerel do not have a swim bladder and therefore are not easily targeted by acoustics. Thus, there was no easy way to ascertain whether the number of shoals, size of shoals or density of shoals were reduced. Therefore, it is difficult to assess how such reductions in CPUE might affect SSL foraging success. Furthermore, it is unclear whether the shoals

disrupted by fishing reaggregate and how fast they might do so, or whether they remain more dispersed. Finally, it is unclear whether disaggregation, if it occurred, would benefit or hinder SSL foraging success.

b) Potential competition between fisheries and SSL

There are two lines of evidence here, 1) competition for prey of similar size and 2) competition for prey at similar depths. There is likely overlap in the size of fish taken in the pollock fishery and that consumed by adult SSL, but evidence for such an overlap in prey size for juvenile SSL is weak. Recent data on SSL diet, so far, have provided little information on the size of prey eaten. There also may be overlap in the depths used by foraging SSL and that trawled by fisheries. Some fish prey exhibit diel vertical migration such that competition by depth between SSL and fisheries could occur at some times of the day, but not others. However, we still have a rather poor understanding of the foraging depths used by SSL of various age and sex classes at different times of the year. It is also important to emphasize that overlap in prey size or depth distribution does not provide sufficient evidence to conclude that there is competition between SSL and fisheries.

c) Competition during winter

Again, there are two lines of evidence bearing on this possibility. First, captive SSL increase their level of food intake in fall and early winter (Kastelein et al. 1990). Second, although spawning aggregations of fish in late winter may provide a higher energy and more reliable food source for SSL, the fishery, by trawling these aggregations, may reduce their availability. Neither of these arguments directly addresses whether or not competition occurs, only that it is possible.

d) Interference competition

The POP observation and observer program databases are equivocal on this issue. There are few observations of SSL from fishing ships in comparison to the amount of fishing activity. This could be because SSL are disturbed and avoid the vessels or because they are tolerant of fishing operations and just rarely sighted. However, the by-catch of SSL in the 1970's and 1980's implies that some SSL were tolerant of fishing activity in that era.

e) Nutrient limitation in SSL

There are several lines of evidence that point to the effects of food limitation on the western stock of SSL. York's (1994) analysis of the age structures of SSL collected in 1975-1978 and 1985-1986 by Calkins and Goodwin (1988) showed or suggested:

- smaller animals in 1985,
- later maturity in 1985,

- lower birth rate in 1985,
- females with pups were older in 1985, and
- SSL pups in 1985 were reported with signs of anemia. However, reported values were within the normal range for pups 2-3 weeks of age (NRC 1997).

In addition, juvenile survival apparently declined in eastern AI (Ugamak Island, Merrick et al. 1987) and in the GOA (Marmot Island, Chumbley et al. 1999). Pitcher et al. (1998) found an increased proportion of abortions and poorer condition in pregnant females collected during late gestation in 1985-86 compared with those collected in 1975-78 on rookeries, haulouts and coastal waters of the GOA. Successful gestation was directly proportion to condition (mass index).

On the other hand, more recent studies that have compared SSL at rookeries in declining (western) and stable or increasing (eastern) populations have found little evidence of food stress:

- Rea et al. (1998) sampled 238 free-ranging pups < 1 month old during June and July 1990-1996 in the GOA, AI, and Southeast Alaska. They found no indication of nutritional stress in the declining populations,
- Castellini (unpublished data, Williams et al. 1999) measured girth, length, and blood chemistry parameters of lactating female SSL between 1993 and 1997 from both increasing and declining populations. The results showed that individuals in the western population were rounder, longer and heavier compared with those from the eastern population, and
- energy intake of 40 pups at 5 rookeries in declining and stable populations sampled between 1993 and 1997 did not differ significantly (unpublished data, Williams et al. 1999).

Finally, the Nov2000BiOp states that "The question of whether competition exists between the Steller sea lion and BSAL and GOA groundfish fisheries is a question of sea lion foraging success." This is a necessary but not sufficient basis upon which to draw conclusions. Poor foraging success may also be the result of environmental change. Without additional information, it is not possible to determine whether fishing, the environment, or a combination of the two is the causal factor. Furthermore, as the evidence above clearly reveals, support for the Nov2000BiOp argument is indirect.

The Nov2000BiOp concludes that the groundfish fishery, as previously conducted, poses jeopardy for the western stock of SSL. The basis of that decision rests on two unquestioned facts, one argument of plausibility of causation, and one argument of absence of conclusive evidence that alternative causes are wholly responsible. The two unquestioned facts are that the SSL stock has continued its decline (though at a slower rate) over the past decade, and that a massive groundfish fishery is being conducted more or less coincident in space and time with activities of the SSL. The argument of plausibility of causation is that there are imaginable, but unconfirmed, mechanisms whereby the fishery could cause the decline in SSL numbers. Alternative hypotheses for the cause of the decline are also plausible, but there is insufficient evidence for a strong inference that, singly or in combination, these mechanisms on their own could reasonably

account for the decline. In fact, there is strong evidence of major changes in the marine community in the GOA coincident with, or subsequent to, the oceanographic regime shift in the 1970s. Superficially, some of these changes are of a magnitude as great or greater than the effect of the fishery on its target stocks. Realistically, then, the question for a jeopardy evaluation should be whether the effect of the fishery, *in concert with the effect of environmental change*, is adversely affecting SSL numbers. The available data are not adequate for such an evaluation.

Task 2 - Design of Field Experiments

In the Nov2000BiOp, NMFS proposed to establish a "well-designed monitoring program that would be used to ascertain the extent to which the implemented measures [to] promote the recovery of sea lions."

Experimental design to determine effectiveness of the Nov2000RPAs

During the time period of our review, the design of the experiment(s) to test the effect of fishing on SSL has been evolving and has therefore, from the standpoint of our review, constituted somewhat of a moving target. Apparently, the design is constrained by a number of considerations, which are not conducive to obtaining clear results. Among the apparent constraints is the desire to ensure that the design "alleviate jeopardy", as judged by the Nov2000BiOp for all management units. This presumably accounts for the somewhat surprising expectation, expressed at the top of page 295 (Nov2000BiOp) that SSL populations in both the open and closed areas will respond positively during the period of the experiment. Certainly if fishing is a significant factor affecting SSL numbers then we would expect a non-zero, positive response in the areas closed to fishing. However, the planned experiment was designed so that conditions for SSL in the areas open to fishing are also predicted to improve. In effect, the Nov2000RPA experimental design has two treatments and no control. Given the high degree of uncertainty that the proposed RPAs really will alleviate jeopardy, we think it is worthwhile to contemplate an experiment that has a true control, at least locally. Given that the present size of the SSL stock is over 30,000 animals and that the present rate of decline is small, there should be considerable scope for experimentation without undue risk.

The Nov2000BiOp also states that both the RPA experiment and other studies will be used to assess the efficacy of management measures, but there is no indication of the types of studies anticipated. Certainly telemetry studies will be needed to determine to what extent the closed areas are actually used by foraging SSL. For example, if only 50% of animals use the treatment area intensively, the population response will only be about half that expected and one might incorrectly conclude that fishing was not a significant factor.

Design principles for ecological field experiments

Although the specific designs of the proposed field experiments have yet to be determined, there are certain principles that should apply rather generally to any such experiment. We briefly discuss some of these below to help focus the discussion about the merits of field experiments.

All experiments are based on the following logical model:

Observations \rightarrow Models \rightarrow Hypotheses (Predictions) \rightarrow Alternative or Null hypotheses \rightarrow Experiments \rightarrow Interpretation of results.

This framework (Underwood 1997) emphasizes that good experiments can only be designed and undertaken if there are adequate quantitative observations from which to reasonably construct alternative models (i.e., explanations) and predictions. Given the current state of our observations with respect to SSL foraging behaviour and the effects of fishing on prey behaviour at fine to meso scales, it might be considered somewhat premature to undertake large-scale manipulative experiments, particularly given the difficulties associated with achieving convincing results (Raffaelli and Moller 2000). On the other hand, the importance of finding out whether fishing really is having an impact on SSL may outweigh the desire to make additional preliminary studies as a prelude to desiging the best possible large-scale experiment.

Nevertheless, it cannot be overemphasized how difficult it will be to conduct large-scale field experiments to test hypotheses about the effects of fishing on SSL. To our knowledge, experiments in the open ocean at this spatial scale have not been previously attempted. But, on the positive side, if the enormous fishing power of the groundfish fisheries really were at the disposal of the experiment (unconstrained by the pressures that molded the Nov2000RPA), this too would be unprecedented.

Some of the issues that need to be resolved include:

- 1) number of replicates of the treatment and the control,
- 2) size of the experimental unit (individual rookeries, clusters of rookeries),
- 3) demographic response variable(s) to measure (pups, non-pups, both, others) and what level of change should we expect to be able to detect,
- 4) duration of the experiment (there will be lags in the response variable),
- 5) how is the treatment to be measured (fishing days, biomass removed, number of tows, others?),
- 6) other response variables to measure (diet, foraging trip duration, birth mass, pup growth rate, others), and
- 7) what are the alternative hypotheses (e.g., climate effects, predation) and how will they be evaluated (i.e., does the experiment make unique predictions about the effects of fishing?).

Response variables

The choice of response variables will play an important role in the design, implementation, analysis and interpretation of field experiements. Researchers conducting field studies on SSL previously have used a number of response variables and both the first "Is It Food Workshop" (Alaska Sea Grant 1993) and the NRC review of the Bering Sea ecosystem (NRC 1997) attempted to predict the likely response of a number of variables under the range of hypotheses that have been advanced to account for the decline of SSL.

In Table 1, we list a number of morphometric/energetic, behavioural, ecological, and demographic variables that have been or might be considered informative in the interpretation of both experimental and observational data. We do this because these variables, used either singly or in combinations, will be measured, and it is important to understand how each variable might be interpreted with respect to discriminating among competing hypotheses. For some response variables, the direction of change under specific hypotheses is debatable. For other response variables, it is not clear to us how, or even if, the variable would change under some of the hypotheses. Changes in the response variables in Table 1 are often equivocal because they may respond in different ways, under the same hypothesis, depending on whether the effects are size selective, local or operate at a larger scale, and result in reduced performance rather than mortality. Also, the magnitude of the change may vary depending on the intensity of the effect. Thus, using the response variables as evidence for a particular hypothesis can be misleading unless additional information is available concerning the underlying mechanisms. Nevertheless, simultaneous changes in several response variables may allow us to build up a balance of evidence to distinguish among the hypotheses even though no one change is conclusive in itself. Finally, the entries in Table 1 are what we consider to be the most likely responses, based on current information. They are not predictions of what will happen.

Most response variables can be measured using both longitudinal and cross-sectional sampling. The first method repeatedly samples marked (i.e., identified) individuals over time, whereas the second takes a 'random sample' of the population at each sampling period. The method used to measure the response variable is important because the two methods can yield different results when used in the same study (Lunn et al. 1994). This has been shown clearly in the case of pup growth rate and weaning mass. The longitudinal method is preferable, provided that a representative sample is initially selected (and controls are maintained), because it is less affected by selective mortality which can significantly bias estimates obtained through cross-sectional sampling. Although longitudinal methods are often preferred, they are operationally more difficult to use under many field conditions, because of the need to keep track of individual animals over a long period of time.

a) Morphometric/energetic response variables

Birth mass - This is often used as a response variable because, in principle, it should reflect conditions experienced by the female during gestation. Females on a high plane of

nutrition should give birth to larger offspring than those that are undernurished. However, birth mass can be difficult to interpret in practice because it can also be influenced by maternal phenotypic traits such as age, body size and birth date (e.g., Ellis et al. 2000). The use of such covariates will considerably strengthen conclusions based on birth mass.

Under the fishery effects, climate effects, and fish predator effects hypotheses, we would expect females in poor condition to give birth to smaller pups. No change in birth mass might be observed if females in the poorest condition simply do not give birth. However, the response of females to reduced food will likely be non-linear, as females will have some ability to modify their behavior to buffer the fetus from the effects of reduced maternal food intake. Under the killer whale and shark predation hypothesis, we can imagine situations where birth mass might decline, increase, or not change. If the effects of incidental take and subsistence harvest hypotheses are selective on females of a certain body size then birth mass could increase or decrease. However, we do not expect size- or age-dependent selection on adult females. Furthermore, levels of harvest are not likely to be large enough to cause any detectable change in mean birth mass, except perhaps at a very local level. If pollution and disease lead to morbidity, then we might expect the same response in birth mass under these hypotheses as under the three food limitation hypotheses (fishery, climate and fish predator effects). If disease and pollution result in mortality of females, then we would expect to see no change in birth mass. Finally, under the entanglement hypothesis, any change in birth mass will depend on whether the entanglement is size selective and whether it leads to death. If females are entangled but not killed, birth mass might be lower because of the increased energy expenditure of females. If entanglement results in mortality the remaining animals could benefit from reduced competition resulting in increased birth mass. However, we do not expect entagnglement mortality to be size selective, and unless the proportion of females entangled at a rookery is large, we do not expect the effect to be large enough to effect average birth mass.

Pup growth rate - Like birth mass, pup growth rate (typically measured as gain in mass) is a useful response variable because it depends to a considerable degree on female condition which in turn depends on foraging success. This is particularly true in the case of otariid females, like SSL, in which most of the energy used to support milk production comes from food aquired during brief foraging trips to sea. As such, pup growth rate is likely more responsive to variation in prey abundance than birth mass. Nevertheless, pup growth rate also may be affected by maternal age, body size, and birth date. Accounting for these covariates will be important in the use of this variable. As with birth mass, it is important to be aware of the potential for bias in cross-sectional estimates of pup growth rate. Where possible, longitudinal estimates are preferred.

Under the fishery, climate and fish predator effects hypotheses, females that are not able to satisfy the energetic requirements of their offspring should have slower-growing pups. Given the limited foraging range of lactating females, at least during early lactation in summer, such effects will generally be a reflection of local depletion of prey rather than reduced prey abundance at larger scales. Under the predation hypotheses we would expect no change in pup growth rate, unless predation was size selective on pre-weaned pups. However, these effects are likely to be difficult to detect on a rookery scale. For the remaining hypotheses, we would expect pup growth rate to respond in a similar way as birth mass.

Weaning mass - This is determined by birth mass plus the mass gained during lactation. As such it represents the energy investment of a female in her offspring. Evidence from a growing number of pinniped species indicates that larger offspring at weaning have a greater probability of surviving (e.g., Baker and Fowler 1992; Hall et al. 2001). Thus as a response variable, weaning mass provides a link between physiological/energetic and demographic processes affecting populations. However, like birth mass and growth rate, weaning mass can be strongly influenced by maternal traits (e.g., Pomeroy et al. 1999; Bowen et al. 2001) and thus accounting for covariates is critical to its use. We note that it is difficult to determine when weaning has occurred in SSL and thus, using weaning mass as a response variable in this species will be problematic.

Nevertheless, given that weaning mass provides a measure of a female's total energy investment in her offspring, it is expected that weaning mass would respond in a similar way to both birth mass and growth rate under each of the hypotheses in Table 1.

Body condition - There are a number of indices of body condition, but all are attempts to characterize the physical state of an individual relative to some norm. Animals judged to be in good condition are expected to reproduce and survive better than those that are in poor condition. As a measure of the physical state of an individual, condition can be affected by a number of factors including food intake, diet, disease, and pollution.

Thus, it is expected that under the fishery, climate and fish predator effects hypotheses, sea lions would have reduced body condition. Although in severe conditions males and females of all age classes ought to be affected, in less severe conditions some groups, such as newly weaned pups, and perhaps adult males, might suffer more than other members of the population. One difficulty in using body condition as a response variable is that under severe environmental conditions, animals in the worst condition may be more or less available to be sampled depending on the behavioral reaction of the animal to nutritional stress. That is, animals spending more time at sea searching for food may be less detectable by a monitoring system based on haulout and rookery sites, whereas animals that are so debilitated that they cannot forage may be more detectable. Failure to account for such differences could lead to biased estimates. We would expect no change in body condition under the predation, incidental take, subsistent harvest, and entanglement hypotheses and no change or perhaps reduced condition would be expected under the disease and pollution hypotheses.

Milk output - For most of lactation, milk is the only form of nutrient intake for young SSL. As offspring growth and survival are dependent on the adequate production and transfer of milk, the measurement of milk output should provide a sensitive measure of female foraging success, which in turn ought to reflect food availability. Nevertheless, milk production suffers as a response variable because it is rather difficult to measure in

large number of animals. Milk output is particularly difficult to measure in SSL beyond the first several months of lactation. However, this is the period when lactation may be most compromised by poor female foraging success.

Under the fishery, climate, and fish predator effects hypotheses, females experiencing nutritional stress should have reduced milk output. We would expect no change in milk output under the predation, incidental take, subsistent harvest, and entanglement hypotheses. However, depending on the type of disease or pollution affecting a female, milk output could be unaffected or could be reduced.

b) Behavioral response variables

Lactating female foraging trip duration - SSL and other otariid females alternate periods of suckling their young on land with foraging trips to sea. Except for the first few days of a long lactation period, when females use body stores to produce milk, females rely on successful foraging to ensure adequate milk production. The duration of these foraging trips is a reflection of both prey abundance and the distance between the foraging location and the rookery. Females undertake longer trips either because they have to travel a greater distance to forage or because they require more time to acquire the food needed to support both their own metabolic requirements and those of their offspring.

Thus under the fishery, climate, and fish predator effects hypotheses, an increased distance to prey, reduced prey abundance, or more dispersed prey should require more foraging time and thus foraging trips of increased duration. The fasting ability of pups may place an upper limit on the duration of female foraging trips. Beyond this limit there may be no change in foraging trip duration. In addition, comparisons of trip duration among females at different rookeries may not be informative because of differences in the characteristics of available prey near these rookeries. Foraging trip duration may also vary over the course of the lactation period and with female age and body size. Thus, these covariates will need to be considered when using trip duration under the predation hypothesis unless females spend less time foraging in an attempt to reduce the risk of predation. Similarly, we would expect no change under the predation, incidental take, subsistent harvest, and entanglement hypotheses, although entangled females might have longer trips due to increased energetic cost of transport. We are unsure how disease would affect female foraging trip duration.

Foraging effort - Although trip duration is relatively easy to measure, it is only one aspect of foraging behavior. More direct measures of the diving effort spent by females during a foraging trip, such as the number of dives, the time spent diving or the vertical distance traveled during diving also may be informative.

Under the fishery, climate, and fish predator effects hypotheses, reduced prey abundance or less concentrated patches of prey would result in more time searching, whereas an increased distance to prey could result in more foraging effort to pay for increased travel costs. In both cases, we might expect foraging effort to increase. However, if females choose to reduce the allocation of energy to their young in the face of reduced availability of prey, foraging effort may show no change. We expect foraging effort to respond in the same way as trip duration under the other hypotheses.

Pup/juvenile ranging behavior - Young pinnipeds must search their environment in order to find food. Both the distribution and abundance of food may affect the way animals search and this will be reflected in ranging behavior (i.e., the spatial extent of movements).

Under the fishery effects hypothesis, a local reduction in the availability of prey should result in an increase in the time spent searching and this could result in an increase in ranging behavior. Under the climate and fish predator effects hypotheses, ranging behavior could increase or decrease depending on whether the effect on prey is local or at a larger scale. We would expect no change under the incidental take, subsistent harvest, and entanglement hypotheses. We would also expect no change under the predation hypothesis, unless juveniles reduced foraging to avoid predation risks. Under the disease hypothesis, ranging behavior might be reduced because of impairment, but the observed response will depend on nature of the disease.

c) Ecological response variables

Diet Composition - The prey species eaten by a pinniped will depend on a number of factors. These could including the age, sex, and reproductive status of the predator and the characteristics of the prey, such as the relative abundance and distribution of each prey species, their anti-predator behaviours, and their profitability (i.e., the net energy return per unit prey handling time). We are just beginning to understand how these factors may affect diet choice in pinnipeds. There are several difficulties in using diet composition as a response variable. First, many factors can affect diet composition, so changes are always expected, but they are likely to be difficult to interpret without careful consideration of covariates. Second, without an understanding of the spatial scale used during foraging, it is difficult to distinguish between local and more widespread factors affecting diet choice. Third, changes in diet are difficult to interpret without information about the suite of prey species available to the foraging animals.

Nevertheless, there is considerable evidence that changes in the distribution and abundance of prey are associated with changes in diets of pinnipeds. Therefore under the fishery, climate, and fish predator effects hypotheses, we would expect diet to change, although predicting how it should change will be difficult given our current understanding of diet choice. Under the remaining hypotheses we would not expect the diet to change above what might be considered background variation. It is conceivable that strong predation pressure or chronic disease could alter feeding behavior and thus diet, but this would be difficult to investigate.

Diet Diversity - Pinnipeds typically consume a wide variety of prey species, but often relatively few species contribute most of the energy in the diet. Diversity indices provide

an informative way to represent both the number of species eaten and their relative contribution to the diet.

Under the fishery effects hypothesis, the abundance of dominant prey species in a particular region might be reduced by fishing, thereby resulting in an increase in the evenness of the prey field included in the diet and hence a increase in diversity. Under the climate and fish predator effects hypotheses, the direction of a change in diversity will depend upon which prey species are affected by the environmental change and on the diets of the competitors. As in the case of diet composition, we would not expect diversity to change above some background variation under the predation, incidental take, subsistent harvest, and entanglement hypotheses and we are unable to predict the likely response under the disease and pollution hypotheses.

d) Demographic response variables

Percentage of 1-year old and older young nursing - The duration of the lactation period is imprecisely known in SSL, but there is increasing evidence that most pups are weaned just prior to the birth of a female's subsequent offspring (i.e., after about 11 months). However, some SSL females nurse offspring beyond this period, in some cases for as long as several years. Although the duration of lactation may be difficult to estimate, the percentage of yearlings and older juveniles that are nursing might reflect the ability of females to deliver food to their young. Nutritionally stressed females may increase the duration of lactation to compensate for a lower rate of energy delivery to offspring.

Thus under the fishery, climate, and fish predator effects hypotheses, we might expect an increase in the lactation period and hence to see a greater percentage of older offspring nursing. However, the response of females to reduced food may depend on the severity of the shortage and under extreme shortage females may wean offspring earlier because their own survival is threatened, in which case the percentage of older offspring nursing might go down. Conversely, a female in good condition, and for some reason not pregnant, might extend lactation without substantial energetic cost. Under the predation, incidental take, subsistent harvest, and entanglement hypotheses, we would expect to observe no change in this variable, unless predation was selective for lactating females or older nursing pups, in which case the percentage of older offspring nursing might be reduced. The response of this percentage under the pollution hypothesis will depend on the effect of the pollutant on females and pups, which is difficult to predict.

Birth rate - Female seals that are nutritionally stressed may abort their fetus rather than invest heavily in lactation, since this might effect their subsequent fecundity and survival. Thus, we would expect a reduced birth rate under the fishery, climate, and fish predator effects hypotheses, but no change under predation, incidental take, subsistent harvest, and entanglement – unless mortality associated with these hypotheses is so large that it results in increased food availability for the survivors. Some diseases, such as the morbilliviruses, can cause spontaneous abortions, and some pollutants, such as organochlorines, can cause infertility or even sterility. We might therefore, in some circumstances, expect a reduction in birth rate under disease and pollution hypotheses.

Age at first birth - Pinnipeds need to be a minimum size before they can breed because they use their body reserves to provide the energy required for at least part of lactation. We would expect female growth rates to be reduced under the fishery, climate, and fish predator effects hypotheses, and possibly under disease and pollution hypotheses. As a result, the average age at which females give birth to their first pup is expected to increase. No change is expected under predation, incidental take, subsistent harvest, and entanglement. It should be recognized that a reliable estimate of age at first birth can only be obtained through destructive sampling or by individually marking a large sample of female pups and subsequent close monitoring of rookeries.

Juvenile survival - As noted under pup growth rate, reduced weaning mass has been shown to affect post-weaning survival in a number of pinniped species. In addition, reduced availability of easily accessible prey may affect the survival of all juvenile animals, regardless of their condition. However, juvenile animals are also likely to be more vulnerable to predation, incidental take, entanglement and subsistence harvest. They are also more susceptible to disease and may acquire exceptionally large pollutant burdens during lactation. As a result, a reduction in juvenile survival is predicted under all hypotheses.

Adult survival - All of the mortality related hypotheses (predation, incidental take, subsistent harvest, entanglement, disease, and pollution) ultimately predict a reduction in adult survival. However, the first response of adult animals to a reduction in food availability (i.e., fishery, climate, and fish predator effects) is probably to reduce investment in reproduction, either through a decreased birth rate or changes in the duration of lactation. The immediate consequence of the latter is likely to be a reduction in juvenile survival (see above). As a result, changes in these demographic and energetic variables are predicted to occur before any reduction in adult survival. However, if food availability is reduced sufficiently during the course of lactation, some individuals may chose to continue lactating and this could prejudice their future survival.

e) Summary

Although some of the predicted effects in Table 1 are necessarily uncertain at this time, it seems clear that quite similar changes are predicted under the fishery, climate, and fish predator effects hypotheses. Our conclusion is that, without a distinct spatial pattern of treatment and control areas, it will not be possible to distinguish among the three food-

driven hypotheses for the decline in SSL based only on the global signature in these response variables. Additional information will be needed, and this might be provided by spatial variation in food availability. This should be investigated further, especially insofar as the design of regulations has the potential to impose a spatial signal in the intensity of fishing. The same arguments apply to the mortality-related hypotheses (predation, incidental take, subsistent harvest, and entanglement), which also have almost identical predicted effects on the response variables

Smaller Scale Experiments

We are pessimistic about the prospects for resolving the critical uncertainties about the SSL decline from simply monitoring the response variables described above following the implementation of the RPAs. For this reason, we believe that a series of smaller scale experiments specifically designed to answer questions about the hypothesized mechanisms of the interaction between the fisheries and the SSL is required.

These will entail detailed measurements of the effects of fishing activities on the prey field and on the behavior of individual SSL fitted with satellite and/or GPS tags and perhaps other data loggers (e.g., Andrews 2001). These experiments should focus on the seasons and locations thought to represent the greatest nutritional stress for juveniles and adult females. Similarly, the sample of instrumented animals should include the age classes thought to be most severely affected. Although these experiments are smaller in scale than treating the RPAs as one grand experiment, they are still very substantial undertakings that will require a massive commitment of resources. It is our scientific judgement that this investment would be warranted.

An example of the kind of experiment we think would be informative is the acoustic research being conducted near Kodiak Island by the MACE group during August 2000 and 2001 (Chris Wilson, NMFS, AFSC, Seattle, WA, personal communication). In that experiment, two gully areas were chosen, and repeated acoustic transects were sampled in both areas, before, during, and after fishing was open in one of the areas. Analysis of these data could shed light on the impact of fishing on the number, size, and density of prey aggregations. If fishing effects on prey were found, it would be informative to expand the research to include coincident studies of the foraging behavior of SSL in the fished and unfished areas. This expanded experiment should be conducted during both winter and spring when the energy demand of lactating female SSL and juveniles is high and the hypothesized effects of localized depletion would be most likely detected.

Task 3 - Responses of Other Pinnipeds

Comparisons with other species in the action area

In assessing the causes of continuing declines of the western stock of SSL, the Nov2000BiOp has made little use of data from other SSL populations, or from other pinniped species in the action area. Indeed, the Nov2000BiOp pays little attention to the continuing and consistent increase in numbers of SSL in Southeast Alaska (i.e., the eastern stock) or to changes in SSL numbers in the Russian territories. Many SSL foraging areas are also used by Northern fur seals (*Callorhinus ursinus*) at certain times of the year, and by harbour seals (*Phoca vitulina*) throughout the year. We believe that comparative data from other SSL stocks and other species could be used to help distinguish among alternative hypotheses, as we discuss below.

The Nov2000BiOp notes on page 102 that the SSL population in the Russian territories had also declined to about one-third of historic levels by the late 1980s. Counts conducted in 1989, 1994, and 1999 indicated differing trends in different areas, but some measures of pup production overall have increased at about 2.7% annually during the 1990s. The sum of counts has increased, "but counts at repeated sites have declined indicating the trends in Russian territories cannot yet be described with confidence." We are a little mystified by the final remark, but the important point is that demography in the Russian population apparently changed in the 1990s after a period of dramatic decline. This is more consistent with a large-scale environmental effect than with the effects of fishing, unless patterns of fishing within the Russian territories have changed or fishing effort was considerably reduced in the 1990s.

The dramatic decline in harbour seal numbers at Tugidak Island in the central GOA also seems to have halted during the 1990s and there is evidence of an increase in this population through 1999 (ADF&G personal comm.). There are population estimates of harbour seals elsewhere in the action area that could also be examined.

Fur seals use the action area only seasonally. Nevertheless, the number of pups born at St. Paul and St. George Islands has been rather more stable over the past decade, in contrast to earlier declines.

The point here is that by looking more broadly and considering the population trends, diet and foraging distribution of similar species in the action area, it may be possible to distinguish among competing hypotheses about the causes of decline in SSL.

Lessons from other seal populations

In this section we review some case studies for other pinniped species in which the effect of local prey depletion on demography has been investigated, or changes in demography have been attributed to local prey depletion. For convenience, we divide the causes of prey depletion into three categories: fisheries-induced changes, environmentally-induced changes, and predator-induced changes.

a) Fisheries-induced prey depletion

There is, as far as we know, no direct evidence that prey depletion by fisheries has affected the demography of any seal population, whereas there are a number of cases in which seal populations have continued to increase exponentially following the collapse of an important prey species (e.g., grey seals, *Halichoerus grypus*, and Atlantic cod, *Gadus morhua*, in the Northwest Atlantic; Mohn and Bowen 1996).

The only detailed study known to the team of the effect of local depletion concerns the North Sea "industrial" fishery for small pelagic species, which are used as animal feed or to produce fish meal and oil. This includes a fishery for sand lance (mainly the lesser sand lance. Ammodytes marinus). Sand lance catches rose sharply from 1960 onwards and have varied between 540,000 and 970,000 tonnes since 1984 (Pedersen et al. 1999); they now account for nearly 50% by weight of all fish landings from the North Sea. Sand lance are an important prey species for many predatory fish, seabirds, and marine mammals. The sheer scale of this fishery has led to concerns about its impact on the entire North Sea ecosystem (e.g., Aikman 1997). In particular, there is substantial spatial overlap between the fishery and foraging by seals and breeding seabirds on a series of major sandbanks off the Firth of Forth in Scotland. Sand lance fishing began in this area in 1990 and catches rose rapidly to more than 100,000 tonnes in 1993. They then fluctuated around 40,000 tonnes until the area was voluntarily closed to sand lance fishing in 1999. In most years, over 90% of the catch was taken in June, and most of that within a 10-day period. The effects of this local depletion on foraging and breeding performance of three seabird species (kittiwake Rissa tridactyla, shag Phalacrocorax aristotelis, and common murre Uria aalge) and grey seals was investigated during 1997 and 1998 (Harwood 2000).

The total biomass of sand lance in 1998 was 15% less than in 1997, and there was a marked change in the age distribution of sand lance between the two years. Acoustic surveys indicated that the biomass of 0-group sand lance in June 1998 was less than half that in 1997 and individual fish were smaller. Total removals were similar in both years (69,000 tonnes in 1997 and 65,000 tonnes in 1998). Fish were the most important natural predator in both years. The fishery was responsible for 68% of all removals in 1998, compared to 34% in 1997.

Sand lance (mainly 1-year-old and 3-year-old fish) made up nearly 50% of the diet of grey seals in 1997, but only around 10% in 1998 (and in that year they were mostly 2-year-old fish). More cod and whiting were consumed in 1998. The proportion of sand lance in the diet of murres declined by 70% in 1998, with the alternative prey being clupeids. The diet of shags and kittiwakes showed much less change and was dominated by sand lance in both years. Both murres and shags spent more time diving and proportionally less time at the surface in 1998. In contrast, the surface feeding kittiwakes did not, or could not, change their foraging behavior. Kittiwakes suffered an almost complete breeding failure in 1998, whereas the productivity of guillemots and shags was only slightly reduced.

The proportion of female grey seals not breeding at the nearest rookery, and the number of breeding failures amongst marked animals at that colony, was negatively correlated with sand lance CPUE in the southern North Sea over the period 1990 to 1997. Female body condition was positively correlated with CPUE for the North Sea and the local stock area. None of these relationships had a measurable effect on the total number of pups born at the colony, which increased steadily over the study period.

The conclusion from this study is that the impact of local depletion by fisheries depends intimately on the foraging strategy of the predators that may be affected. Grey seals, murres and shags were able to make behavioural changes to compensate for the rapid reduction in the biomass of 1+ sand lance by the commercial fishery in June 1999, whereas surface-feeding kittiwakes were not. As a result, the observed response of most predators was relatively subtle and had no immediate effect on their demography.

Similarly, the relationships between grey seal breeding parameters (female condition, missed pregnancies, failed breeding) and sand lance abundance (as measured by CPUE) were also rather subtle and were only detectable because longitudinal data were available from a sub-population of permanently marked females at the relevant rookery. It should be noted that the year-to-year variations in sand lance abundance appear to be primarily a result of fluctuations in recruitment and not of the action of the fishery itself.

b) Environmentally-induced depletion of prey

The effects of ENSO (El Niño Southern Oscillation) events on the demography of a range of fur seal, sea lion and seal populations along the western seaboard of South and North America are well known (Trillmich and Ono 1991). However, there have been similar events in other parts of the world. For example, the intrusion of warm, lowoxvgen content water into the northern Benguela system off the Atlantic coast of Namibia in late 1993 and early 1994 resulted in the virtual disappearance of many pelagic and epipelagic fish species from the continental shelf. This had a dramatic effect on Cape fur seals (Arctocephalus pusillus pusillus) at Namibian colonies during the 1993/94 breeding season, summarized in Anon (1998). The initial effect was seen in a reduced growth rate of pups at Cape Cross (the northernmost colony of the Cape fur seal). This was followed by a mass mortality of pups at Cape Cross in the austral summer of 1993/94, and colonies further south were affected after a short delay. From February/March 1994 onwards, all colonies north of Lüderitz (in southern Namibia) experienced the highest levels of pup mortality ever observed, due to abandonment and starvation. By the end of May approximately 120,000 pups, out of a normal production of around 300,000, had died. Beginning in June, and worsening through July, surviving females aborted their pups. It is estimated that 40,000 foetuses were aborted at Cape Cross alone. At the same time large numbers of emaciated adults of both sexes washed up along much of the Namibian coast. Pup production in 1994/95 was 50-70% lower than in 1992/93 and 1993/94. Mass of pups at birth and early pup survival in 1994/95 was the lowest ever recorded.

Capelin (*Mallotus villosus*) are normally the most important prey species for the harp seal (*Phoca groenlandica*) population which breeds in the White Sea and feeds in the Barents Sea, making up more than 90% of the diet in some years. The Barents Sea capelin stock

collapsed in 1985/87 and remained at very low levels until 1990. At about the same time, large numbers of harp seals began appearing off the northwest coast as Norway, and by 1987, they were reported as far south as the southern North Sea. Very large numbers of harp seals (up to 60,000 in 1987) were taken as bycatch in gillnets along the coast of Finnmark, Troms and Nordland during this period. These "invading" harp seals, particularly in the subadults, were reported to be thin and in very poor condition (Wiig 1988 in Haug & Nilssen 1995). These events must have resulted in large scale mortality of young animals because the 1986-1988 year classes are virtually absent from the age structure of Norwegian samples of molting harp seals taken since 1990 (Kjellqwist et al. 1995). Despite these dramatic changes, Haug and Nilssen (1995) are cautious about attributing the 1980s invasions of harp seals to local depletion of capelin in the Barents Sea, partly because the capelin stock collapsed again in 1992/93 but there was only a relatively small influx of harp seals into Norwegian waters at that time.

Antarctic fur seals (*Arctocephalus gazella*) breeding on the islands around South Georgia feed almost entirely on krill (*Euphasia supurba*). Breeding performance of fur seals and a number of seabird species, which also prey on krill, has been monitored annually on one of these islands (Bird Island) since 1980. Performance of all krill predators increased up to the late 1980s, but has declined steadily since then. Reid and Croxall (2001) interpret these changes as a response to decreasing availability of krill, possibly as a consequence of ocean warming and reduced sea-ice extent. The main responses by fur seals have been a decrease in the mean birth weight of pups and an increase in foraging trip duration (Boyd et al. 1994) during a year of particularly low krill abundance.

c) Predator-induced depletion of prey

The numbers of southern elephant seals (*Mirounga leonina*) breeding on Macquarie Island in the southern Indian Ocean have been declining steadily since the early 1970s. Hindell (1991) demonstrated that this was, at least in part, due to a dramatic decline in first-year survival from around 45% in the 1950s to less than 2% in the 1960s. He concluded that the population had temporarily exceeded the carrying capacity of the local environment and was demonstrating signs of delayed density-dependence. However, although first-year survival has now recovered to levels similar to, if not higher than, those observed in the 1950s, the population at Macquarie has continued to decline (McMahon et al. 1999) indicating that some demographic rate besides first year survival is also involved.

On the basis of changes in the size distribution krill caught off South Georgia during the 1990s, and estimates of local krill mortality that were 50% higher than those recorded elsewhere in the species' range, Reid and Croxall (2001) concluded that Antarctic fur seals and seabirds from South Georgia were now "operating close to the limit of krill availability". As a consequence, there has been an "increase in the frequency of years where the amount of krill is insufficient to support predator demand", and abundance of all krill predators on Bird Island has declined since 1990.

d) Lessons for SSL management

Two major lessons emerge from this brief review: 1) changes in seal demography in response to a reduction in prey abundance are either so dramatic that they can be detected even without scientific study (Cape fur seals in Namibia, harp seals in Norway) or relatively subtle, requiring time series of monitoring data (North Sea grey seals, Antarctic fur seals, southern elephant seals) and 2) a reduction in first-year survival was involved in all the examples listed above. A reduction in pup birth mass or growth rate or an increase in female foraging trip duration was also observed in some cases. The second point supports NMFS' contention that a reduction in juvenile survival is probably involved in the continuing decline of the western population of SSL. However, it should be recognized that a decline in SSL juvenile survival has not been adequately documented, it has only been inferred from York's (1994) analysis of age-structure data and on observations of low survival from a small sample of marked animals. The data upon which both inferences are based are now quite dated. The inference problem for the SSL is unusually complicated because the population decline has been underway for decades, but the mix of potential causal factors has been changing during this time. As a consequence, it is not clear what time period provides the appropriate "baseline" against which demographic data from the most recent decade should be compared.

Task 4 - Review of August 2001 Draft Biological Opinion

The Aug2001BiOp differs substantially from the Nov2000BiOp both in style and Stylistically, the Aug2001BiOp is a more coherent and closely reasoned content. document that provides a balanced treatment of rival hypotheses and clearly identifies the assumptions that have been made at every stage. In terms of content, it contains new information on SSL at-sea distribution and behavior, and on diet. These data are used to support the case made in the Nov2000BiOp that fisheries for pollock. Atka mackerel and Pacific cod could jeopardize the continued existence of the western stock of SSL as a result of local depletion of these prey species in SSL critical habitat. The Aug2001BiOp accepts as given the conclusions of the Nov2000BiOp of jeopardy through local depletion of prey, and that this jeopardy can be avoided by implementing the RPA proposed in that BiOp, referred to as the "Restricted and Closed Area Approach", or Alternative 3. The main purpose of the Aug2001BiOp is to evaluate the performance of alternative RPAs developed by the Council's RPA Committee, in particular Alternative 4: the "Area and Fishery Specific Approach", that have lower economic and social costs than Alternative 3. To do this, the RPA Committee developed a new approach for comparing the effects of different RPAs on the dynamics of the western stock of SSL. In addition, the Aug2001BiOp includes a discussion of whether these RPAs might lead to adverse modification of SSL critical habitat. The Aug2001BiOp concludes that managing the fisheries under Alternative 4 would neither jeopardize the continued existence or recovery of the stock, nor would it lead to adverse modification of critical habitat

In this section, we first critically examine the new data on at-sea distribution and diet, and evaluate their relevance to the different RPAs. We then consider the methods

developed in the Aug2001BiOp to evaluate the effects of the alternative RPAs on jeopardy and adverse modification. Finally, we recommend additional research that we believe should be given the highest priority to determine the efficacy of management measures and to improve current understanding of the interactions between fisheries and SSL.

New information from biological research on SSL

a) At-sea distribution of SSL

One of the two main reasons given for the re-initiation of consultation resulting in the Aug2001BiOp was a new analysis of the distribution of SSL that "revealed a possible greater dependence on near shore waters than previously understood". The new analyses concern the at-sea distribution of SSL based on locations derived from satellite-linked time-depth recorders (SDRs); they are reviewed in Small (2001). The analyses were conducted at the request of the RPA Committee, and "do not represent the analytical approaches NMML and ADF&G scientists are pursuing with the SSL telemetry data" (Small, pers. comm.). Results are summarized in Table 5.1 of the Aug2001BiOp. This table is based on data collected from NMML's deployments of SDRs on SSL pups and adult females at rookeries in the Aleutian Islands and GOA. It indicates that between 74% and 99% of all locations obtained from these deployments were within 10 nm of shore.

While the Aug2001BiOp acknowledges that the current analysis suffers from a number of problems, conclusions about the distribution of foraging are nonetheless an important component of the Aug2001RPA analysis to remove jeopardy. Thus, it is essential to determine how robust the conclusions about the spatial distribution of foraging by SSL are to limitations in existing data and to the methods of analysis.

Both NMFS and ADF&G must be commended for their efforts to fit large numbers of SSL with these tags, which provide information on the distribution of animals at sea. The panel recognizes that this has been a costly and logistically difficult undertaking, and the importance of the resulting data clearly warrants this effort. Having said this, there are limitations (clearly acknowledged by both agencies) to the current data, which suggest that conclusions drawn from these data may not be reliable. These limitations are noted in the Aug2001BiOp (p110) and discussed at length in Small (2001). They are:

- 1. The location can only be determined if an animal fitted with an SRD is at the surface when a satellite passes overhead and if the satellite receives multiple transmissions within the 10-min interval. SSL spend more time at the surface in inshore waters than when they are offshore, because this is where they rest, sleep and interact socially. As a result, the raw location data gives a biased measure of the amount of time spent inshore.
- 2. At-sea locations do not necessarily indicate where an animal is foraging.

- 3. The large majority of pups, and perhaps most juveniles, in the sample were probably still nursing, and thus not foraging independently.
- 4. SRDs have not been deployed on subadults or females without pups.

The first problem is exacerbated by the fact that SSL return to a particular rookery or haulout after each foraging trip. Thus many of the locations in inshore waters relate to animals that are in transit to and from these sites, rather than foraging. Support for this comes from Andrew's studies of adult female SSL fitted with stomach temperature data loggers (Andrews 2001), which can be used to determine when an animal has ingested a prey item. He found that, although animals began making relatively deep (>10m) dives soon after they departed from their rookeries, the first prey was not ingested until 1-5 hours after departure. There are insufficient location data to determine exactly where successful foraging first took place, but if these animals were swimming directly away from the rookery they would have been 3-25 nm offshore (Small 2001). To examine the possible effects of these biases, 90% of the locations recorded within 2 nm of shore were removed from the database (i.e., it was arbitrarily assumed that the probability of obtaining a location from an animal that was close inshore was nine times greater than when it was further offshore). The resulting estimates are summarized in Table 5.1b of the Aug2001BiOp. They are strikingly different from those based on the raw data. Only about 40% of the remaining female locations in winter and pup/juvenile locations in summer were within 10 nm of shore. This suggests that about 50% of the locations of pups and juveniles in summer, and about 20% and 50% of adult females in summer and winter, respectively, were beyond 20 nm (i.e., beyond critical habitat). A less arbitrary way of taking account of the known bias would be to calculate the average location of each animal on each day that location information was received, and to use these summary data in the calculations. It should also be recognized that the appropriate sampling unit in these studies is the individual. Pooling the location data, as was done in the calculations for Table 5.1, results in an overrepresentation of individuals that retained their transmitters for long periods. In addition, the information in Table 5.1 is derived only from the 72 animals of the western stock (23 pups/juveniles and 49 adult females) handled by NMML. There are equivalent data from a further 17 pups handled by ADF&G.

Although lactating females and dependent pups are important components of the population, and thus were rightly the focus of such studies, it has been difficult to obtain records longer than a few months from individual animals. This means, in the case of lactating females, that our understanding of their foraging distribution is limited mainly to the early part of lactation (i.e., summer) and may not be representative of foraging during later lactation (i.e., fall and winter) when females are likely faced with higher milk energy output costs. All of the available evidence suggests that neither female SSL nor their pups are nutritionally stressed during the early phases of lactation. In the case of pups and dependent juveniles, their distribution may reflect largely that of their mothers rather than that of independently foraging young SSL. Analysis of the dive patterns of these animals and the duration of their trips from rookeries and haul outs (Loughlin et al. 2001) suggests that they do not move independently of their mothers until they are 11-12 months of age (i.e., from June of their second year). Thus, the spatial distribution of

foraging adult SSL during winter, and of independent sub-adult animals throughout the year, remains largely unknown. Nevertheless, the few winter foraging records that are available suggest that larger areas and more distant sites may be regularly used by foraging SSL.

All of these considerations indicate to us that the conclusion by the RPA committee (repeated on p112 of the Aug2001BiOp) that "areas within 10 nm from shore were about 3 times as important as those areas beyond 10 nm ... and ... the areas beyond 10 nm were [a] less important factor in the current decline of the species, and would therefore be less likely to be adversely affected by competition with fisheries" is extremely sensitive to the assumptions made in analyzing the data. As such, we have little confidence that this analysis provides a sound basis for drawing conclusions about the effect of the RPAs on the dynamics of SSL.

a) Diets of SSL

The other new information that has become available since the Nov2000BiOp is an analysis of the hard parts of prey retrieved from nearly 4,000 SSL scats collected between 1990 and 1998 (Sinclair and Zeppelin submitted). The authors used Principal Components Analysis and cluster analysis to identify three major diet groups: one dominated by Atka mackerel and cephalopods; one by pollock, salmon and arrowtooth flounder; and a third which was intermediate between the other two, but which also included significant quantities of sand lance, herring and Pacific cod. Most of the scats from the Central Aleutian Islands fell into the first cluster, most from the Eastern and Central GOA fell into the second cluster, scats from the Eastern Aleutian Islands fell into the third cluster, and scats from the Western GOA fell into a number of different clusters.

These broad regional groupings of rookeries and haulouts are similar to those identified by York et al. (1996) in their analysis of trends in SSL numbers. Following on the work of Merrick et al. (1997). Sinclair and Zeppelin (submitted) use this similarity, and other arguments, to suggest that low prey diversity may be a factor in the continued decline of SSLs since 1990. We have several problems with this conclusion. First, the analysis is based on simple frequency of occurrence of species remains in scats, rather than the more sensitive split-sample frequency of occurrence (see above), thus the presence of one otolith of a small fish such as a sand lance in a scat receives the same score as the presence of many bones from large pollock. Second, the differences in diet diversity are small (1.5 vs 2.1 in summer, and 1.9 vs 2.1 in winter). And third, York et al. (1996) had difficulty finding periods of time for trends that resulted in neighboring rookeries being in the same cluster. When they used distance from Outer Island and the rates of decline for the time periods 1959-1975, 1976-1985, 1985-1989 and 1989-1994, they obtained non-contiguous clusters (i.e. regions far apart were more similar to each other than regions close together). Only by choosing the time periods 1959-1975, 1976-1985, 1985-1994, 1976-1994 and 1985-1994 did they get 'reasonable' clusters. They could not get contiguous clusters if they used the 1989-94 time series (the nearest comparison to the time period covered by Sinclair and Zeppelin's data). This is clearly allowing a prejudgement of what is "reasonable" to drive the analysis. We are not persuaded that the expectation of "reasonable" clustering is justified. For this reason, we have little confidence in the identity of their regions.

Sinclair and Zeppelin also conclude that SSL "target prey when they are densely schooled in spawning or migratory aggregations nearshore". However, the team believes that their data do not justify such a strong conclusion. All they have shown is that when SSL are feeding inshore their diet tends to reflect the known abundance of prey species in that area. This is because, as noted above, scat analysis provides information only on the prey species that an animal has eaten in the period immediately before it hauled out. They provide no information on how the animals obtained those prey (e.g., whether they are dependent on large local aggregations or target solitary individuals), or on whether prey captured inshore are more or less important than those captured offshore.

Analysis in support of Aug2001RPAs alleviation of jeopardy

The new draft Aug2001BiOp takes great pains to emphasize that the arguments presented there to justify the adequacy of the new RPA are "qualitative." On the face of it, we found this puzzling, because the RPA measures are characterized by quantities defining the conduct of fisheries and the hoped for response of the SSL population growth rate is also defined in terms of quantities. After discussion with NMFS' staff it became clear that this terminology was adopted because the procedure developed by the RPA Committee, in their view, is intended to compare the relative, not the absolute, performance of the alternative RPAs. Nevertheless, the judgment that an RPA is adequate to remove jeopardy is inherently an absolute standard of performance.

The basis of the quantitative component of the analysis done by the RPA Committee is described in detail in DeMaster (2001), it follows logically from the development of the RPA in the Nov2000BiOp. It is assumed that the only effect of the fisheries on SSL population dynamics is through localised depletion in SSL critical habitat. Further, it is assumed that this localised depletion reduces the potential rate of increase of a local SSL population by 4% (the average rate of decline of the western stock since 1991). Initially, we also found this to be confusing and contradictory, especially when considered in the context of the Marine Mammal Protection Act (MMPA). It implies that, in the absence of any effects of fishing, SSL numbers would, at best, be approximately constant and may continue to decline. Indeed, this is accepted in the Nov2001BiOp (see p139). If this is really the case, the western stock is well above its Maximum Net Productivity Level (as defined in the MMPA), and is in no need of protection! However, the RPAs are being developed under the Endangered Species Act, not the MMPA, and we recognise that this is the context in which they should be evaluated.

The Aug2001BiOp assumes, on the basis of the analysis of the SDR telemetry data, that the most important critical habitat is within 10nm of a rookery or haul out, because this is where SSL spend at least 75% of their time. A corollary of this is that 75% of the effects of a fishery on a haul out or rookery can be removed by closing the area within a 10-nm

radius of that site to fishing. With a few further assumptions, it was then possible for the RPA Committee to calculate the predicted effects of different area closures on the dynamics of SSL in 13 different management areas over the next 8 years. An RPA which was predicted to result in a total population as large as, or larger than, that predicted under Alternative 3 (the RPA from the Nov2000BiOp) was considered to result in no jeopardy to the western stock. In fact, the situation was a little more complicated than this.

Earlier simulations based on Alternative 3 assumed that restrictions on fishing activity in management areas that were still open to fishing would have no effect on SSL population dynamics (DeMaster 2001). The Aug2001BiOp presents an additional scenario where these restrictions increase the rate of increase of the local population by 2% per annum. Not surprisingly, this results in a population trajectory with a higher final population size than either the original Alternative 3 or Alternative 4. The criterion for no jeopardy now seems to be that the predicted population trajectory should lie between that for the original Alternative 3 and that for Alternative 3 with a 2% benefit in restricted areas.

The RPA Committee clearly recognizes that influential assumptions are involved in this procedure, and has carried out some analyses to test its robustness (see pp 135-6 of the Aug2001BiOp). These include assuming that the effects of fisheries closures are related to local trends in SSL numbers rather than population wide ones, and assuming that only 50% (rather than 75%) of the effect of a fishery is removed by closing an area 10 nm around a haul out or rookery and that increased fishing outside 20 nm would have no effect. Trials of the RPA's performance using a computer model indicated that it was robust to the first of these assumptions, but not to the second. The potential effects of the third assumption were not tested. Given our concerns about the validity of the 75% value (see **At-sea distribution**), compounded by the uncertainty of effects of increased fishing outside 20 nm, this raises considerable doubts in our minds about the reliability of the entire procedure.

This procedure could have been applied to the other RPAs initially considered by the RPA Committee, but this was not done. It is particularly interesting to apply it to Alternative 1 ("No change" from the pre-2000 fisheries management practices), because this is a trajectory that, according to the Nov2000BiOp, involves jeopardy. We carried out the necessary simulation and found that under this Alternative the population is predicted to decline by around 2% per year over the next 8 years, compared with an annual decline of 0.77% under the original Alternative 3 and 0.41% under Alternative 4 (see Table 5.6 of the Aug2001BiOp). The 4% decline observed from 1991 to 2000 does not continue indefinitely because the dynamics of the total population becomes dominated by those local populations that have been increasing since 1991.

Clearly the distinction between jeopardy and no jeopardy is a rather fine one. The definition of jeopardy adopted by NMFS ("..action that reasonably would be expected ... to reduce ... the likelihood of both the survival and recovery ...") is suitably precautionary, but this seems to set an almost impossibly high standard for the avoidance of jeopardy for a species such as the SSL, about whose dynamics there are so many

uncertainties. In this case, the conclusion that jeopardy is removed by RPA Alternatives 3 and 4 rests entirely on a particular model of the way in which the fisheries may have affected SSL population dynamics. If this model does not accurately represent the actual mechanism (for example, if the major effects of the fishery occur in areas more than 10 nm from haulouts or rookeries) the proposed RPAs could actually contribute to jeopardy rather than remove it.

Neither DeMaster (2001) nor the Aug2001BiOp provide any information on predicted population trajectories within individual management areas. Simulations carried out by the team indicate that, under all the RPAs, local populations at the extreme western and eastern ends of the distribution of the western stock (i.e., in the western Aleutian Islands and in the eastern GOA) are predicted to decline steadily over the next 20 years. The acceptability of such a situation, as a matter of policy, merits further discussion.

However, we would note that all of these predictions must be interpreted with great caution. The 13 management areas do not reflect any natural biological divisions of the western stock of SSL, rather they appear to have been chosen for administrative convenience, and there is no *a priori* reason to assume that observed trends will continue. Indeed, recent evidence on resighting of branded animals (Raum-Suryan et al. in press) suggests that there may be considerable redistribution of animals on scales similar to or greater than those of the 13 management areas.

Avoiding adverse modification of critical habitat

Angliss and DeMaster (2001) have proposed an approach to evaluating whether or not adverse modification of critical habitat for SSL may have occurred, and this approach is used in the Aug2001BiOp. They calculated the ratio of the estimated unfished biomass of pollock, Atka mackerel and Pacific cod in the GOA, Aleutian Islands, and Bering Sea system to the estimated food requirements of the historical population of 184,000 SSL in the western stock. They assume that this is a minimum per capita requirement for a "healthy" stock. They then calculate the same ratio for the biomass of these three prey species in SSL critical habitat and the requirements of the current SSL population. Values are calculated for the entire region and separately for the GOA, Aleutian Islands and Bering Sea, on an annual and monthly basis. All but one of these values is greater than that required for a "healthy" stock, and hence they conclude that there has been no adverse modification.

However, the authors clearly recognise that this approach does not address the central issue: do the fisheries for these species cause **local** depletion of prey within SSL critical habitat? As a result, it cannot be used to evaluate whether or not specific management actions are more or less likely to result in adverse modification. They also recognise that the implication of these calculations (that there is more than enough biomass of these three prey species in critical habitat to sustain the current SSL population) is inconsistent with NMFS' position that nutritional stress associated with local prey depletion is a likely cause of at least some portion of the recent decline in SSL numbers.

Research priorities

One of the team's tasks was to recommend an appropriate experimental design to improve our understanding of the interactions between fisheries and SSL, and the efficacy of imposed management measures to promote recovery of the SSL population. This was, in part, because the original Nov2000BiOp RPA (Alternative 3) involved contrasting regulation of fisheries in adjacent management areas, with some areas being effectively closed to fishing while others were not. However, the preferred Aug2001BiOp RPA (Alternative 4) involves a wide range of area- and fishery-specific measures, which are predicted to have more subtle effects on local SSL population dynamics than Alternative 3. The panel feels that it is **unlikely** that simple monitoring of the response of these local populations under Alternative 4 will provide any insight into the interactions between SSL and fisheries.

However, even if Alternative 3 was to be implemented we suspect that the responses of local populations would be difficult to interpret. Although we believe that large-scale experiments can reduce the long-term risks to the western stock of SSL, it is not practicable to design such experiments at present. We therefore recommend that research should focus initially on an integrated program of modeling and smaller scale manipulative experiments (see below).

We suggest it would be worthwhile for NMFS to devote some effort to developing policy guidance that allows for the option of responsible and effective experimentation as part of the program for removing jeopardy. This is particularly necessary in this situation, where it simply is not possible to identify reasonable management alternatives that have a high certainty of ensuring survival and recovery of the population without future adjustment. We note that jeopardy has both a short-term and a long-term component. By focussing on the short term, during which there is very little true jeopardy, NMFS have ruled out many of their options for reducing jeopardy over a biologically relevant time scale. We believe that larger scale manipulative experiments should be considered in future RPAs once the results of the smaller scale experiments/modeling work become available.

Many elements of the recent and current research plans are unlikely to contribute either to the jeopardy finding of the Nov2000BiOp or the no-jeopardy finding that the Aug2001BiOp attaches to the preferred RPA, or to provide insights into causes underlying the continued decline of SSL. Much of the deficiency has to do with focus on physiological or behavioural indices, which cannot be converted to demographic consequences. Some of the inherent ambiguities in interpreting these indices are set forth in Table 1 and our discussion of response variables. The bottom line is that for results to be useful in the jeopardy decision, the effects of any posited mechanisms need, ultimately, to be quantified in units of population change (i.e., mortality or reproduction). The SSL program has undergone a rapid shift in circumstances from modest budget to very large budget (although the longevity of this increased level of funding is uncertain). Nevertheless, this means that some research activities that previously were perceived as important, but budget-limited, could be expanded considerably. We strongly urge that in the next round of funding the highest priority be given to proposals which will have a direct bearing on the jeopardy finding and the effectiveness of the RPAs.

We believe priority should be given to the assessment of population trends and vital rates, and on better understanding the mechanisms underlying the current decline in the western SSL population. The high priority research items (not in order of priority) are:

• monitoring trends in population size and distribution

The Aug2001BiOp indicates that cessation of the decline in SSL numbers is the criterion that will be used to evaluate the success or failure of the implemented RPA. Therefore, ongoing monitoring of pup and non-pup numbers on rookeries and haulouts throughout the year and the geographic range of the stock is crucial to determining population status. The precision of the monitoring of population counts will affect the resolution with which changes in population size and trajectory can be detected, and the time required to detect those changes. The most obvious ways to increase precision are to increase the frequency of visits to the many sites, to ensure systematic coverage during all seasons, and to improve the quality and analysis of aerial photographs. Enhanced quality and coverage of aerial photographs also could provide additional demographic information, such as age-class structure (e.g., juvenile:adult ratios; Holmes and York submitted).

• estimation of vital rates

It is generally believed that the SSL population decline is an expression of reduced per capita recruitment owing, proximately, to reduced post-weaning juvenile survival. But the demographic parameter estimates upon which this judgement is based are derived from data from a period prior to the decade of the 1990s, which was a time when the population decline was considerably steeper than at present, and there is strong suspicion that the causes of the decline were different than they are now. Thus, we recommend the re-establishment of a long-term program to permanently and individually mark (e.g., brand) large numbers of SSL at a number of sites. We emphasise that a fundamental component of this research is the establishment of systematic sighting surveys over a number of years. In undertaking this program, it is also critically important to decide which vital rates are to estimated and with what precision, as answers to these questions will determine both the number and location of marking sites, the number of individuals that will need to be marked and the sighting effort required.

• spatial and temporal scales of foraging

An understanding of the spatial and temporal distribution of SSL at sea and the factors that affect this distribution will be needed to identify ecologically important habitats, and to assess the response of SSL to environmental change and human activities, including fishing, that affect the distribution, abundance and quality of available prey. Both NMFS and ADF&G have devoted considerable effort to fitting SSL with SDRs to study their atsea distribution. We strongly support this research and recommend that it be continued with a focus on filling the gaps (e.g., winter distribution) identified by both by NMFS and ADF&G. We appreciate that the analysis of these data poses a number of analytical challenges, but we cannot over-emphasis the importance of rapid progress. The methods used to analyze these location data must account for the biases noted above to provide a more reliable estimate of the at-sea distribution of SSL. Analytical procedures that take account of the way in which central place foraging determines the accessibility of different areas of the ocean to SSL from each land site (e.g., those developed by Matthiopoulos submitted) would provide a more reliable identification of the most important foraging areas for this species. Such analyses, coupled with further studies on the distribution of foraging success (e.g., stomach temperature telemetry), should provide the basis for reasonable inferences about the foraging behaviour of SSL.

• diet

We recognize that estimating the diet of SSL is difficult. Nevertheless, the importance of these data warrant the effort. NMFS is to be commended on the substantial effort that has gone into the collection of scat samples throughout the western stock. However, the reliance on frequency of occurrence as the measure of the relative importance of prev species is fraught with problems, and more informative and reliable measures should be sought. Although the number of otoliths recovered from SSL scats is too few to provide the basis for more quantitative representation of the diet, other prey structures can be used to identify prey species and size. We are aware that there is ongoing SSL research in this regard and encourage its development. However, we caution that it is doubtful that the recovery of prey structures from SSL scats will provide a reliable means of diet estimation in this species. Thus, we would also recommend that other techniques, which are not dependent on the recovery of prey hard parts (e.g., fatty acid signature analysis; e.g., Iverson et al. 1997; Iverson et al. in prep.), be seriously investigated. In the longerterm, such methods are likely to provide a more reliable basis for testing hypothesis about the factors underlying temporal and spatial variation in the diet of SSL. Finally, given the large number of sites, seasons and age/sex classes that could be sampled, careful thought should be given to restrict the number of questions to those that are most likely to be informative with respect to food-related hypotheses and then to design an appropriate sampling scheme.

• modeling

We expect prey availability, predators, and disease to affect the dynamics of SSL. Further, we expect the effects of these factors to vary in time and space. Thus, it seems to the team that it will be useful to develop a modeling framework that can be used to integrate information on the foraging and reproductive energetics of SSL within a spatially explicit demographic model. That is, we need an analytical tool that can be used to assess the behavioral, energetic, and demographic consequences, for example, of changes in prey availability at different temporal and spatial scales. Differences in body size and energy expenditure among age and sex classes mean that individuals in the population will differ in their ability to tolerate reductions in prey availability. Thus, it should be possible to identify the types of perturbations that are likely to pose a problem for SSL and the resulting demographic consequences

• retrospective data analysis

The historical data on counts of SSL at rookeries and haulouts is of high spatial resolution and provides an opportunity, independent of any manipulation experiment, to examine the relationship between SSL demography and possible influencing factors, such Nonparametric regression models could be used to investigate the as fisheries. relationship between the rate of change of SSL numbers at these sites and contemporary high resolution, spatially-explicit data on catch and effort for pollock and Atka mackerel close to the rookery over that time period. Other potential factors, such as catch of other species (e.g., herring), geographic location of the rookery, and maximum historical SSL population at that site could also be used as covariates. This type of analysis can be done on groups of sites over any time period for which high resolution fisheries data are available. The advantages of this approach over analysis of larger areas are that the sample size is increased and there is more flexibility in the choice of spatial resolution and thus a greater chance of identifying signals in the data provided they were measured with high enough precision at this restricted spatial scale. However, this could be a problem at smaller spatial scales because the coefficient of variation for SSL counts tends to increase for smaller counts.

• local depletion of prey and its consequences for SSL

The conclusion that fisheries for pollock, Atka mackerel and Pacific cod jeopardize the survival and recovery of the western stock of SSL is based on the hypothesis of localised depletion of prey within critical habitat. However, there is no direct evidence to support or refute this hypothesis. An integrated research program to address this issue is urgently required. It should combine modelling of the foraging behaviour of lactating and juvenile SSL with studies of the fine-scale movements and foraging behaviour of individuals. An individual-based modeling framework will allow simulation of the behaviors of tagged individuals as well as including behavioral variability within and between individuals. The work already conducted by Andrews (2001) indicates that such studies are feasible, although the development of suitable GPS receivers would considerably enhance the resolution of data on SSL movements in relation to covariates (e.g., fishing activities, oceanographic features, prey). This research should be integrated with investigations of the impact of trawl fisheries on school size, school distribution and the density of fish within schools. The pilot study conducted near Kodiak Island (A. Hollowed and C. Wilson, NMFS, AFSC, pers. comm.) provides a useful example of how such research could be pursued. A longer-term goal of this research would be to link foraging success of young SSL to subsequent survival.

References

- Aikman, P. 1997. Industrial 'Hoover' Fishing: A Policy Vacuum. Greenpeace International, Amsterdam.
- Alaska Sea Grant. 1993. "Is it food?" Alaska Sea Grant Report, 93-1. Alaska Sea Grant Program, University of Alaska Fairbanks, Fairbanks, AK.
- Andrews, R.D. 2001. Foraging behavior and energetics of adult female Steller sea lions. Abstract presented at "Is It Food? II Workshop", Alaska Sea Life Center, Seward, AK.
- Angliss, R. and DeMaster, D.M. 2001. Evaluating the use of forage ratio analysis to assess availability of forage for Steller sea lions in critical habitat. National Marine Fisheries Service white paper. 13 pp.
- Anon. 1998. Proceedings of the International Workshop on Research and Management of Cape Fur Seals in Namibia. Ministry of Fisheries and Marine Resources, Swakopmund, South Africa.
- Baker, J.D. and Fowler, C.W. 1992. Pup weight and survival of northern fur seals *Callorhinus ursinus*. Journal of Zoology, Lond. **227:** 231-238.
- Bowen, W.D., Ellis, S.L., Iverson, S.J., and Boness, D.J. 2001. Maternal effects on offspring growth rate and weaning mass in harbour seals. Canadian Journal of Zoology 79: 1088-1101.
- Boyd, I.L., Arnould, J.P.Y., Barton, T., and Croxall, J.P. 1994. Foraging behavior of Antarctic fur seals during periods of contrasting prey abundance. Journal of Animal Ecology 63: 703-713.
- Calkins, D.G. and Goodwin, E. 1988. Investigation of the declining sea lion population in the Gulf of Alaska. Alaska Department of fish and Game, 333 Raspberry Road, Anchorage, AK.
- DeMaster, D.P. 2001. Evaluating the impact of Reasonable and Prudent Alternatives for the management of the BSAI and GOA groundfish fisheries on the western stock of Steller sea lion. National Marine Fisheries Service white paper. 13 pp.
- Ellis, S.L., Bowen, W.D., Boness, D.J., and Iverson, S.J. 2000. Maternal effects on offspring mass and stage of development at birth in the harbour seal, *Phoca vitulina*. Journal of Mammalogy **81:** 1143-1156.
- Fritz, L. 1993. Trawl locations of walleye pollock and Atka mackerel fisheries in the Bering Sea, Aleutian Islands, and Gulf of Alaska. AFSC Proc. Rep. 93-08.
- Fritz, L.W., Ferrero, R.C., and Berg, R.J. 1995. The threatened status of Steller sea lions, *Eumetopias jubatus*, under the Endangered Species Act: Effects on Alaska

Groundfish Fisheries Management. Mar. Fish. Rev. 57: 14-27.

- Frost, K.J. and Lowry, L.F. 1980. Feeding of ribbon seal (*Phoca fasciata*) in the Bering Sea in spring. Canadian Journal of Zoology **58:** 1601-1607.
- Hall, A., McConnell, B., and Barker, R. 2001. Factors affecting first-year survival in grey seals and their implications for life history. Journal of Animal Ecology 70: 138-149.
- Hall, A., McConnell, B., Pomeroy, P., Duck, C., Fedak, M., Matthiopoulos, J., and Walton, M. 2000. Variation in the diet, distribution, consumption and breeding population parameters of grey seals. Harwood, J. (ed.) *In* Effects of Large-scale Industrial Fisheries on Non Target Species. Report on Contract 95/78 to DGXIV, Directorate General Fisheries of the European Commission.
- Harwood, J. 2000. Effects of Large-scale Industrial Fisheries on Non Target Species. Report on contract 95/78 to DGXIV, Directorate General Fisheries of the European Commission.
- Haug, T. and Nilssen, K. 1995. Ecological implications of harp seal *Phoca groenlandica* invasions in northern Norway. p. 545-556. Blix, A., Walloe, L., and Ulltang, O. (eds.) *In* Whales, seals, fish and man. Amsterdam, Elsevier.
- Hindell, M.A. 1991. Some life-history parameters of a declining population of southern elephant seals, *Mirounga leonina*. Journal of Animal Ecology **60**: 119-134.
- Holmes, E.E. and York, A.E. 2001. Using age structure to detect impacts on threatened populations: a case study using Steller sea lions. unpublished.
- Iverson, S.J., Field, C., Bowen, W.D., and Blanchard, W. 2002. Quantitative fatty acid signature analysis: a new method of estimating predator diets. In preparation.
- Iverson, S.J., Frost, K.J., and Lowry, L.F. 1997. Fatty acid signatures reveal fine scale structure of foraging distribution of harbor seals and their prey in Prince William Sound. Marine Ecology Progress Series 151: 255-271.
- Kastelein, R.A., N. Vaughan, and P.R. Wiepkema. 1990. The food consumption of Steller sea lions (*Eumetopas jubatus*). Aquatic Mammals 15:13.
- Kjellqwist, S.A., Haug, T., and Oritsland, T. 1995. Trends in age-composition, growth and reproductive parameters of Barents Sea harp seals, *Phoca groenlandica*. ICES Journal of Marine Science 52: 197-208.
- Loughlin, T., Sterling, J., Merrick, R., and Sease, J. 2001. Immature Steller sea lion foraging behavior. National Marine Fisheries Service white paper. 39pp.

- Lowry, L.F., Frost, K.J., and Loughlin, T.R. 1989. Importance of walleye pollock in the diets of marine mammals in the Gulf of Alaska and Bering Sea, and implications for fishery management. Proc. Int. Symp. Biol. Walleye Pollock 1: 701-725.
- Lunn, N.J., Boyd, I.L., and Croxall, J.P. 1994. Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. Journal of Animal Ecology **63:** 827-840.
- Matthiopoulos, J. Animal movement in heterogeneous environments and the estimation of spatial usage. American Naturalist. Submitted.
- McMahon, C., Burton, H., and Bester, M. 1999. First-year survival of southern elephant seals, *Mirounga leonina*, at sub-Antarctic Macquarie Island. Polar Biology **21**: 279-284.
- Merrick, R.L., Chumbley, M.K., and Byrd, G.V. 1997. Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: a potential relationship. Canadian Journal of Fisheries and Aquatic Science **54**: 1342-1348.
- Merrick, R.L. and Loughlin, T.R. 1997. Foraging behavior of adult females and youngof-year Steller sea lions (*Eumetopias jubatus*) in Alaskan waters. Canadian Journal of Zoology **75:** 776-786.
- Mohn, R. and Bowen, W.D. 1996. Grey seal predation on the eastern Scotian Shelf: modeling the impact on Atlantic cod. Canadian Journal of Fisheries and Aquatic Science 53: 2722-2738.
- NRC 1996. The Bering Sea Ecosystem. National Research Council, Washington, D.C.
- Olesiuk, P.F., Bigg, M.A., Ellis, G.M., Crockford, S.J., and Wigen, R.J. 1990. An assessment of the feeding habits of harbour seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia, based on scat analysis. Can. Tech. Rep. Fish. Aquat. Sci. No. 1730 135 pp.
- Pedersen, S.A., Lewy, P., and Wright, P. 1999. Assessment of the lesser sandeel (*Ammodytes marinus*) in the North Sea based on revised stock divisions. Fisheries Research **41**: 221-241.
- Pitcher, K.W., Calkins, D.G., and Pendleton, G.W. 1998. Reproductive performance of female Steller sea lions from the Gulf of Alaska: Indications of nutritional stress? Canadian Journal of Zoology 76: 2075-2083.
- Pomeroy, P.P., Fedak, M.A., Rothery, P., and Anderson, S. 1999. Consequences of maternal size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland. Journal of Animal Ecology 68: 235-253.

Raffaelli, D. and Moller, H. 2000. Manipulative field experiments in animal ecology: Do

they promise more than they can deliver? Advances in Ecological Research **30**: 299-338.

- Raum-Suryan, K.L., Pitcher, K.W., Sease, J.L., Loughlin, T.R., and Calkins, D.G. Insights into dispersal, rookery fidelity, and metapopulation structure of Steller sea lions (*Eumatopias jubatus*) in an increasing and declining population in Alaska. Marine Mammal Science. In press.
- Rea, L.D., Castellini, M.A., Fadely, B.S., and Loughlin, T.R. 1998. Health status of young Alaska Steller sea lion pups (*Eumetopias jubatus*) as indicated by blood chemistry and hematology. Comparative Biochemistry and Physiology, Part A 120: 617-623.
- Reid, K. and Croxall, J. 2001. Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. Proceedings of the Royal Society, London Series B 268: 377-384.
- Ryg, M., Lydersen, C., Markussen, N. H., Smith, T. G., and Øritsland N A. 1990. Estimating the blubber content of phocid seals. Canadian Journal of Fisheries and Aquatic Science 47: 1223-1227.
- Sinclair, E. and Zeppelin, T. Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumatopias jubatus*). Journal of Mammalogy Submitted.
- Small, R. 2001. Satellite telemetry and Steller sea lion research. Alaska Department of Fish and Game and National Marine Fisheries Service white paper. 48pp.
- Springer, A., Baily, K., Bowen, W. D., Boyd, I., Estes, J., Iverson, S. J., and Piatt, J. 1999. Steller sea lion Feeding Ecology Workshop Review. Seattle, WA, Feb. 1999: 40 pp.
- Trillmich, F. and Ono, K.A. 1991. Pinnipeds and El Niño: Responses to Environmental Stress. Springer-Verlag, Berlin Heidelberg.
- Underwood, A.J. 1997. Experiments in Ecology: Their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge, U.K.
- Williams, T. M., Boness, D. J., Bowen, W. D., Boyd, I., Croll, D., Horning, M., Iverson, S. J., Calkins, D. and Didier, A. 1999. Steller sea lion Physiology Workshop Review. Seattle, WA, Feb. 1999: 34 pp.
- York, A.E. 1994. The population dynamics of Northern sea lions, 1975-1985. Marine Mammal Science 10: 38-51.
- York, A. E., Merrick, R. L., and Loughlin, T. R. An analysis of the Steller sea lion metapopulation in Alaska. p. 259-292. McCullough, D. R. (ed.) *In* Metapopulation and wildlife conservation. 1996. Washington, D.C., Island Press.

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Table 1. Like	the western stock o

				F	Hypothesis				
Response variable	FE	CE	FPE	PRED	IT	HS	D	PO	EN
Birth mass	R	R	R	U	NC	NC	R	R	NC
Pup growth rate	R	R	R	NC	NC	NC	NC/R	NC/R	NC
Weaning mass	R	R	R	NC	NC	NC	NC/R	NC/R	NC
Body condition	R	R	R	NC	NC	NC	NC/R	NC/R	NC
Lactating female foraging	Ι	Ι	Ι	NC/R	NC	NC	N	NC	NC
trip duration									
Foraging effort	Ι	I	Ι	NC/R	NC	NC	Ŋ	NC	NC
Milk output	R	R	R	NC	NC	NC	NC/R	NC/R	NC
Percentage of 1-year old	Ι	I	Ι	NC/R	NC	NC	Ŋ	U	NC
and older young nursing									
Pup/juvenile ranging	Ι	Ŋ	Ŋ	NC	NC	NC	R/U	NC	NC
behavior									
Diet composition (scats)	C	C	C	NC	NC	NC	Ŋ	NC	NC
Diet diversity	Ι	N	Ŋ	NC	NC	NC	Ŋ	Ŋ	NC
Birth rate	R	R	R	NC	NC	NC	NC/R	NC/R	NC
Age at first birth	I	I	Ι	NC	NC	NC	NC/I	NC/I	NC
Juvenile survival	R	R	R	R	R	R	R	R	Я
Adult survival	R/NC	R/NC	R/NC	R	R	R	R	R	Я

CE- Climate/Kegime Shift Effects on Food PRED- Killer whale and shark predation SH - Subsistence Harvest PO - Pollution FE - FISHERY Effects on Food FPE - Fish Predator Effects (competition) IT - Incidental Take D - Disease

EN - Entanglement in Fishing Gear

R = reduced, I = increased, NC = no change, C = change, U = uncertain