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The method of multiple hypotheses and the decline of Steller sea lions in western Alaska

N. WOLF, J. MELBOURNE AND M. MANGEL

In recent years, enormous effort has been expended to explain the cause of the precipitous decline of the western population of Steller sea lions (*Eumatopias jubatus*) since the late 1970s; however, despite these efforts and the proposal of a wide variety of hypotheses, the decline has proven to be very difficult to explain. The authors of a recent comprehensive review of the problem emphasized repeatedly that the system is in dire need of a modelling approach that takes advantage of the data available at small spatial scales (at the level of the rookery). We view this as an opportunity for ecological detection, a process in which multiple hypotheses simultaneously compete and their success is arbitrated by the relevant data. We describe ten hypotheses for which there are sufficient data to allow investigation, a method that allows one to link various sources of data to the hypotheses and the conclusions from this approach.

The decline of the western Alaska population of Steller sea lions has proven to be very difficult to explain, in part because most aspects of the population and the environmental variables proposed to explain its decline involve a combination of high spatial and temporal variability, and limited data. Consequently, most researchers pooled data across rookeries or across time, obscuring spatial and/or temporal patterns (Fig. 19.1). Some of these previous studies are described below.

(1) Construction of a Leslie matrix model for a stable population, followed by perturbation of various transition rates to find the most parsimonious way to produce a trajectory matching the observed decline. York (1994) determined that the initial decline could be
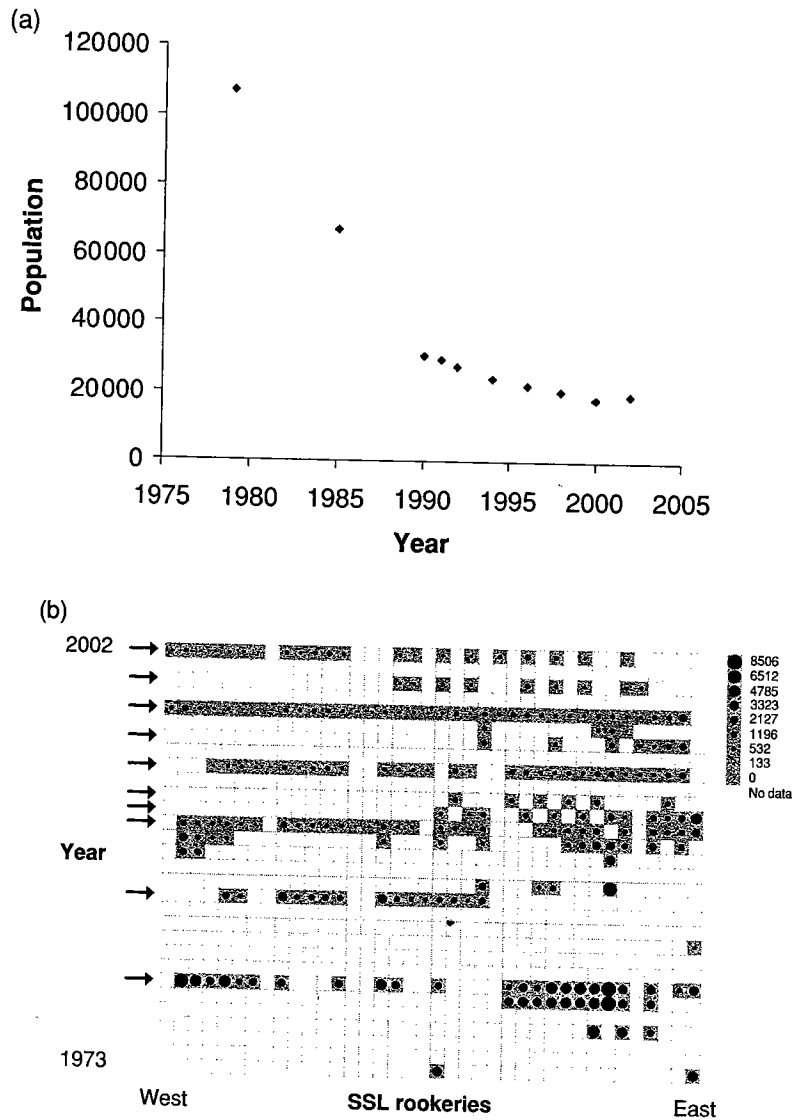
Fig. 19.1   (a) Composite time series of the Steller sea lion (SSL) population in western Alaska. (b) Space–time plot of the counts of non-pups at 38 individual rookeries from 1973 to 2002. The abscissa indicates rookeries from west to east, with each column representing a different rookery. The ordinate indicates time, with each row representing a single year. The area of each circle indicates the observed number of sea lions at that rookery in that year. The arrows indicate years in which a 'synoptic' survey of the entire population was taken. Notice, however, that the dataset is much richer than the synoptic survey (panel a, with 10 points total) would suggest.

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explained most easily by a 10% to 20% decrease in juvenile survival. Pascual and Adkison (1994) estimated the effective mortality and fecundity rates for six individual rookeries. Adkison *et al.* (1993) and Pascual and Adkison (1994) also modified the matrix model by allowing vital rates to vary according to alternative hypotheses.

(2) Assumption of a fixed set of underlying vital rates and calculation of the number of animals that would have to be removed in order to match the observed census data (e.g. Blackburn 1990 (cited in Castellini 1993), Loughlin & York 2002, NRC 2003.

(3) Construction of a simulation model that includes the hypothesized effect (e.g. Barrett-Lennard *et al.* 1995, NRC 2003).

(4) Analysis of trends across space rather than across time. Merrick *et al.* (1997) observed a correlation between population growth rate and diet diversity among different rookeries.

None of these studies made use of both spatial and temporal variation in sea lion counts and environmental data. Researchers either pooled data across space, combining all rookery censuses within each year and performing their analyses using a composite time series representing the entire western population (Fig. 19.1); or else pooled data across time, treating only the overall trend of the census at each rookery. A recent review of the problem (NRC 2003) emphasized that the system requires a modelling approach that takes advantage of the data available at small spatial scales. Here we give a précis of the results of such a study (Wolf & Mangel 2004)

POPULATION BIOLOGY OF THE STELLER SEA LION

Genetic (Bickham *et al.* 1998) and behavioural (Raum-Suryan *et al.* 2002) evidence suggest that 144° W longitude separates distinct populations and that the rookeries within each region qualify as a meta-populations (York *et al.* 1996). The eastern population is estimated to have been growing slowly since survey methods were standardized in the 1970s, but the western population declined by more than 80% (Fig. 19.1). The decline appears to have begun in the eastern Aleutians and spread from there, with associated changes in size-at-age and condition (Castellini 1993, Calkins *et al.* 1998, Sease & Loughlin 1999, Andrews *et al.* 2002). The western stock was listed as 'Endangered' in 1997.

Steller sea lions are largely opportunistic foragers. Walleye pollock (*Theragra chalcogramma*) are currently the principal diet component; they have also been the most abundant prey species since the mid 1970s,
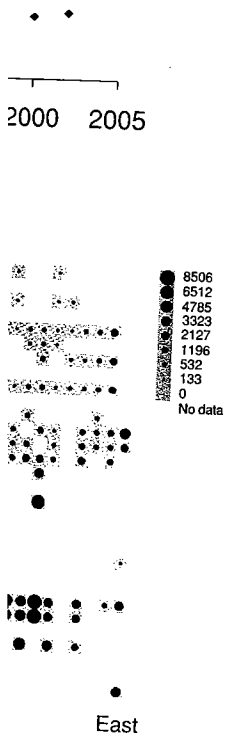
when the North Pacific climate switched to a warm regime favouring pollock (Alverson 1992, Anderson & Blackburn 2002). Other important prey species include Atka mackerel (*Pleurogrammus monopterygius*), Pacific cod (*Gadus macrocephalus*) and Pacific herring (*Clupea pallasi*).

RELEVANT FISHERIES

Walleye pollock, Atka mackerel and Pacific cod are harvested primarily using groundfish trawling gear. The largest groundfish harvests in the area occur in the Bering Sea. The peak catch occurred in 1972, followed by a decline in the late 1970s and a recovery in the mid 1980s. Pollock comprise over 76% of the groundfish caught in the Bering Sea (NRC 2003). In the Gulf of Alaska, the pollock catch peaked between 1976 and 1985. A fishery for groundfish developed in the Aleutian Islands in the late 1970s.

OTHER MARINE MAMMALS

The decline of the Steller sea lion was preceded by declines in populations of northern fur seal (*Callorhinus ursinus*) and Pacific harbour seal (*Phoca vitulina*) occupying the same region. The causes of these declines remain similarly unexplained (Merrick 1997, Springer *et al.* 2003). The range of the western population is also home to a large population of killer whales (*Orcinus orca*); some of these are 'transients', whose diet is thought to consist mainly of marine mammals, including Steller sea lions (Barrett-Lennard *et al.* 1995, Matkin *et al.* 2002). Unfortunately, very little is known about the spatial or temporal distribution of these whales. Steller sea lions may comprise 5% to 20% of their diet (Matkin *et al.* 2002). The stomach of one killer whale that washed up on a beach in British Columbia contained flipper tags from 14 different Steller sea lion pups, all of which had been tagged at the Marmot Island rookery 3 to 4 years before (Saulitis *et al.* 2000).

COMPETING HYPOTHESES

Competing hypotheses have been proposed to explain the decline of the western population. Sufficient data exist to explore ten hypotheses with alternative models and rank them according to their explanatory power (Hilborn & Mangel 1997).

H1 to H3: food limitation hypotheses

We assume that fecundity (H1), pup recruitment (H2) or non-pup survival probability (H3) is a positive function of the local encounter rate with

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groundfish prey. Specifically, starvation (H2, H3) or termination of pregnancy (H1) occur if an animal experiences a long series of unsuccessful foraging attempts. Under poor foraging conditions, animals may lose condition because they consume less prey, spend more time and energy hunting, or both. Body condition, in turn, is a significant determinant of the probability that a pregnant female actually completes her pregnancy and produces a pup (Pitcher et al. 1998). Poor foraging conditions also increase the probability of starvation and expose the animals to additional predation risk during any extra time spent foraging, leading to elevated mortality rates. The probability of pup recruitment may be linked indirectly to prey availability if mothers are more likely to abandon pups under poor foraging conditions, or directly when the inexperienced pups begin foraging for themselves near the end of their first year.

H4 to H6: 'Junk-food' hypotheses

We assume that fecundity (H4), pup recruitment (H5) or non-pup survival probability (H6) is a positive function of the local encounter rate with groundfish prey other than walleye pollock. Specifically, starvation (H5, H6) or termination of pregnancy (H4) occur with higher probability when alternative prey are scarce. The fact that a pollock-intensive diet might lead to poor body condition and depressed vital rates was first proposed by Alverson (1992), and was supported by evidence from captive sea lions that lost weight on a diet of pollock alone (Rosen & Trites 2000) and from correlative studies of diet diversity and population decline (Merrick et al. 1997). Pups, with limited dive depth, may be especially sensitive to the species composition of the prey base because some prey types are probably inaccessible to them.

H7 and H8: fishery-related mortality hypotheses

We assume that survival probability of pups (H7) or non-pups (H8) is a declining function of the local encounter rate with groundfish trawling operations. Incidental mortality, usually entanglement of sea lions in fishing gear, is now estimated to be killing less than 100 animals per year (Perez & Loughlin 1991, Loughlin & York 2002), but in the past it was much higher (NRC 2003). It was legal to shoot sea lions in defence of gear until 1990, and there are anecdotal reports suggesting that shooting (even unrelated to defence of gear) may still occur (NRC 2003). It may be very difficult to determine whether incidental or deliberate mortality is the problem, since both might scale with fishing effort. However, it seems likely that entanglement

would be a bigger problem for naïve pups (Loughlin *et al.* 1983), whereas adults are more likely to be targeted by shooters.

H9 and H10: predation–mortality hypotheses

Transient killer whales are predicted to prey upon sea lions or their pups when the whales' preferred prey, harbour seals, are scarce (Springer *et al.* 2003, Mangel & Wolf in press). Therefore, survival probability of sea lion pups (H9) or non-pups (H10) is predicted to decline if local harbour seal density falls below a threshold value.

THE APPROACH

The hypotheses and data were linked by the following procedure (all the details can be found in Wolf and Mangel (2004)).

(1) We formulated the alternative hypotheses as one-parameter scaling functions that modify vital rates according to local conditions.
(2) We sorted the data concerning 'local conditions' by rookery and year.
(3) We formulated a suitable population model, with appropriate process uncertainty and observation error (described below).
(4) We calculated the likelihood for all possible values of all parameters (one per hypothesis) simultaneously.
(5) We ranked the effects in terms of statistical support and strength of the effect.

In contrast to all previous modelling approaches, this procedure does not require a complete dataset, and makes use of variation both between rookeries and across time.

In the population model (step 3), we assume two age classes: pups and non-pups. The population dynamics (Box 19.1) can then be characterized by the survival and fecundity of non-pups and the survival of pups to the non-pup stage (recruitment). There are thus three parameters that characterize how population size changes from one year to the next. Because each of these parameters must be between 0 and 1, process uncertainty (*sensu* Hilborn and Mangel (1997)) is captured using binominal transitions. In particular, three binomial distributions represent all possible transitions in the model: recruitment (the number of pups that survive from the previous year, with rate parameter ρ), survival (the number of non-pups that survive, with rate parameter σ) and fecundity (the number of non-pups that give birth to new pups, with rate parameter ϕ). The probability distributions

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> **Box 19.1 The population model**
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> The population model uses two age classes: pups and non-pups. The number of pups in a particular year at a particular rookery, $J(i, t)$, is determined by the per-capita probability of reproduction by female non-pups, $N(i, t)$, in that year at the same rookery. The number of non-pups in a particular year is determined by the survival of non-pups from the previous year and the recruitment (survival to age 1) of pups produced in the previous year. These transitions capture process uncertainty through a set of nested binomial distributions. Although the true number of pups can be estimated by aerial survey, the observed number of non-pups, $N_{obs}(i, t)$, is smaller than the true number – so a beta-binomial model is used to account for observation error (see Fig. 19.2).

for the numbers of non-pups (N) and pups (J) at time t, given the numbers at time $t - 1$, are computed directly from the associated binomial distributions.

Although pups can be accurately counted during aerial surveys, some fraction of the non-pups are likely to be at sea foraging during the surveys. Thus, the observed number of non-pups is smaller than the true number of non-pups. We characterize this observation uncertainty using a beta-binomial distribution (Martz & Waller 1982, Evans et al. 2000, Wolf & Mangel 2004).

We set fixed background values for the life-history parameters (denoted by ρ_0, σ_0 and ϕ_0) that are modified by local conditions to reflect a particular hypothesis. We chose background values from observed values measured on the Marmot Island rookery by Calkins and Pitcher (1982) and used by York (1994), and Pascual and Adkison (1994). The annual growth rate of a population using these values is 0.4% (Pascual & Adkison 1994). Fecundity estimates also account for only about 50% of the pups being female (York 1994, NRC 2003) and for about 50% of the non-pup population being juvenile (Holmes & York 2003).

The background values for life-history parameters are then modified to take account of local conditions. For the case of food limitation (H1 to H3), the modification is that low abundance of groundfish and other prey causes local fecundity (hypothesis 1), pup recruitment (hypothesis 2), or non-pup survival probability (hypothesis 3) to be diminished. These are
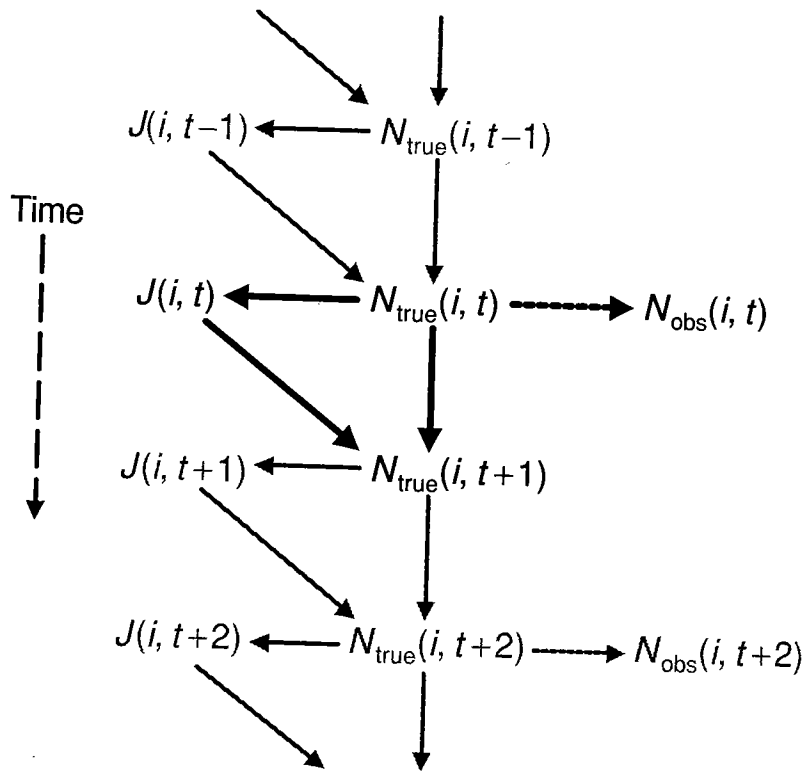
Fig. 19.2

characterized by a Holling Type III functional response (Holling 1959; Box 19.2). The choice of a sigmoid function implies that sea lions are unlikely to find enough to eat when prey are scarce, and unlikely *not* to find enough to eat when prey are abundant.

For the case of the junk-food hypotheses (H4 to H6), the modification of the background life-history parameters is that a high proportion of walleye pollock among the available prey causes local fecundity (hypothesis 4), pup recruitment (hypothesis 5), or non-pup survival probability (hypothesis 6) to be diminished. We model this as the fraction of non-pollock food raised to an unknown power (Box 19.2).

For the case of fishery-related mortality (H7 and H8), we assume that the survival probability of pups (hypothesis 7) or non-pups (hypothesis 8) is diminished in areas where there is more commercial fishery activity (Box 19.2 and Fig. 19.3c).

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Box 19.2   Hypotheses to explain the decline

We formulated ten different hypotheses as functions relating life-history parameters of Steller sea lions to local conditions. Function i ($i = 1, 2, 3, \ldots, 10$) is parameterized with a single unknown constant, c_i, in such a way that a zero value for the constant indicates no effect for hypothesis i. Hypotheses 1 to 3 are related to food; specifically, they propose that low prey abundance leads to diminished fecundity, pup recruitment or non-pup survival rates. These are captured as separate Holling Type III functional-response curves, with the half-saturation values denoted by c_1, c_2 and c_3 respectively. Hypotheses 4 to 6 propose that an elevated fraction of pollock among available prey in the environment leads to diminished fecundity, pup recruitment or non-pup survival, respectively, for the sea lions. These effects are captured by raising the fraction of non-pollock in the environment to the power c_i ($i = 4, 5, 6$), where $c_i \geq 0$. Hypotheses 7 and 8 describe the possibility that increased fishing activity near a rookery leads to diminished pup recruitment (hypothesis 7) or non-pup survival (hypothesis 8). We assume that this is characterized by a negative exponential distribution with parameter $c_i \geq 0$. Hypotheses 9 and 10 are related to predation pressure by killer whales. They are investigated by using optimal diet theory (Mangel & Wolf in press) in which it is assumed that predators consume sea lions (depressing recruitment or survival rates) when the density of the more profitable prey (harbour seals) falls below a critical value. The survival rate is depressed by c_i ($i = 9, 10$) (see Fig. 19.3).

Finally, for the case of the predation-mortality hypotheses (H9 and H10), we assume that killer whales broaden their diet to include Steller sea lions when harbour seals are scarce, so that the survival probability of sea lion pups (hypothesis 9) or non-pups (hypothesis 10) decline when local harbour seal populations fall below a critical value (Mangel & Wolf, in press). In particular, we set the critical harbour seal density by comparing the densities of harbour seals around sea lion rookeries with rising and falling populations, and choosing a point between these distributions. (If killer whale predation is a significant source of mortality for Steller sea lions, then the densities of harbour seals around sea lion rookeries with
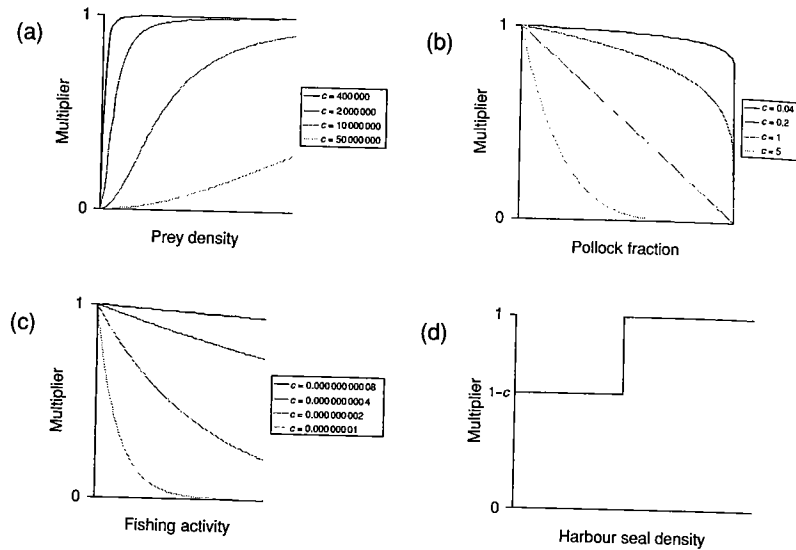
Fig. 19.3

rising and falling populations should tend to be above and below the critical value respectively.)

Thus, the local value of each vital rate is calculated by multiplying the background rate by all the relevant scaling factors. Note that there are ten unknown parameters, one per hypothesis. In each case, a parameter value of zero indicates that the corresponding hypothesis has no effect.

SOURCES OF DATA

In order to test the various hypotheses using the model, we acquired data on relevant prey species from triennial groundfish survey results collected by the National Marine Fisheries Service/Alaska Fisheries Science Center (NMFS/AFSC) in the Gulf of Alaska/Aleutian Islands (http://www.afsc.noaa.gov/race/groundfish/default_gf.htm). We calculated estimates of fishing activity in minutes per year from the NMFS groundfish fishery observer database. This database covers foreign and joint-venture groundfish fisheries from 1973 to 1991 and domestic fisheries from 1986 to 2001.

Estimates of harbour seal density came from online NMFS/AFSC marine mammal stock assessments and reports (Withrow *et al.* 2000, 2001, 2002, Angliss & Lodge 2002), a Marine Mammal Commission report (Hoover-Miller 1994), and eight journal articles (Bailey & Faust

1980, Everitt & Braham 1980, Pitcher 1990, Frost *et al.* 1999, Mathews & Pendleton 2000, Jemison & Kelly 2001, Boveng *et al.* 2003, Small *et al.* 2003). The Steller sea lion counts were from the NMFS/AFSC/National Marine Mammal Laboratory (NMML) online database (http://nmml. afsc.noaa.gov/AlaskaEcosystems/sslhome/stellerhome.html). We limited our consideration to year–rookery combinations in which counts from June or July were available for both pups and non-pups, and to rookeries for which such censuses from at least two different years were available. When more than one count was available for a particular rookery in a single year, we took the average. Several sets of adjacent rookeries were censused as one large rookery early in the dataset and as separate rookeries in later years. In some of these cases, we combined the counts from the separate rookeries in later years in order to extend the time series for the 'joint' rookery. When prey abundance or harbour seal density estimates were missing for certain area–year combinations, we used linear interpolation to estimate the missing value from reported values in earlier and later years for the same area. Further details about the acquisition and treatment of data are found in Wolf and Mangel (2004).

RESULTS

We estimated the unknown parameters by comparing the predictions of the stochastic population model with the observed counts. To do this we started with the beta-binomial observation error distribution and a two-life-stage stochastic population model employing the local vital rates, and calculated the probability of observing the sequence of reported pup and non-pup counts at a particular rookery, given: (a) relevant local conditions and (b) a particular set of parameter values in the hypothesized equations. We then computed the maximum-likelihood estimate (MLE) of each parameter and constructed ten one-dimensional profile likelihoods (Hilborn & Mangel 1997) so that we could examine the support for each parameter, holding the others at their MLEs. For each parameter, we computed a profile-likelihood interval by finding the area under the curve that contains 95% of the total area.

The result of these computations is shown in Fig. 19.4. Each column represents one class of hypothesized impacts (overall abundance of food, fraction of food that is pollock, fishing activity or predation) and the rows represent the hypothesized effects on fecundity, recruitment or survival. Each plot shows the profile likelihood for the relevant parameter in the functional form. A peak at a non-zero value indicates support for the
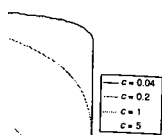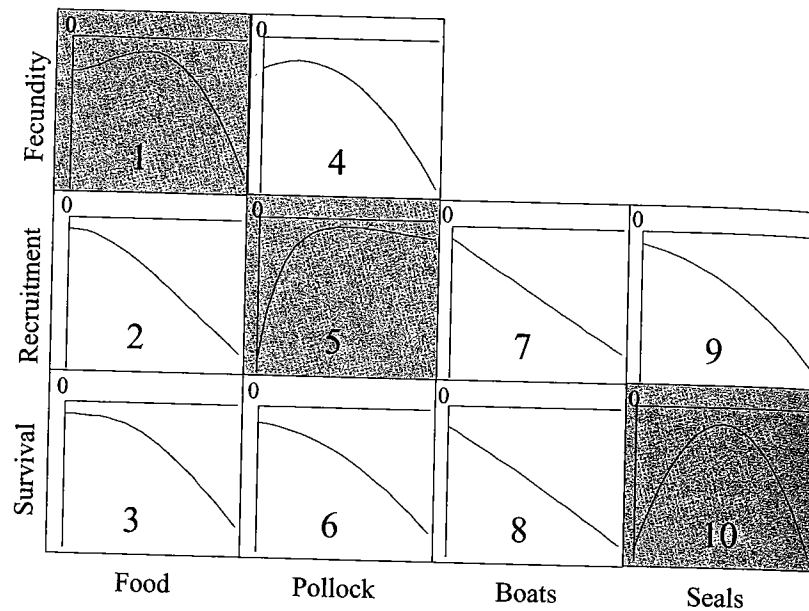
Fig. 19.4   Likelihood profiles for the parameters associated with the functional forms for the four classes of hypotheses and their effects on the relevant life-history parameters. See text for further details.

corresponding effect. We therefore find: strong support for hypotheses 1, 5 and 10; weak support for hypothesis 4; and no support for the other six hypotheses.

We also computed Aikaike's information criterion (AIC) weights (Burnham & Anderson 1998) from the likelihood information. Hypotheses 1, 4, 5 and 10 account for >99% of the AIC weight (and hypothesis 4 only provides 5% of that total). In Fig. 19.5, we show the functional forms associated with the different hypotheses, evaluated at the MLE values of the parameters, and in Fig. 19.6 we show the lost production of Steller sea lions due to the effects in hypotheses 1, 4, 5 and 10.

DISCUSSION

The strong message of ecology is that the world changes and that the reasons for change are manifold. Thus, rather than trying to 'prove' one mechanism, we should recognize that multiple mechanisms will almost always be at work, and we should ask how to weigh the importance of different mechanisms. It is this approach that we have taken in understanding the decline
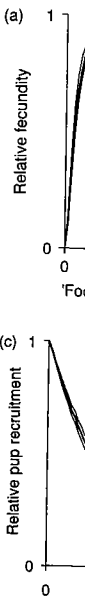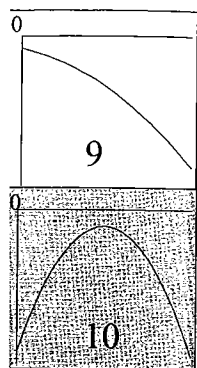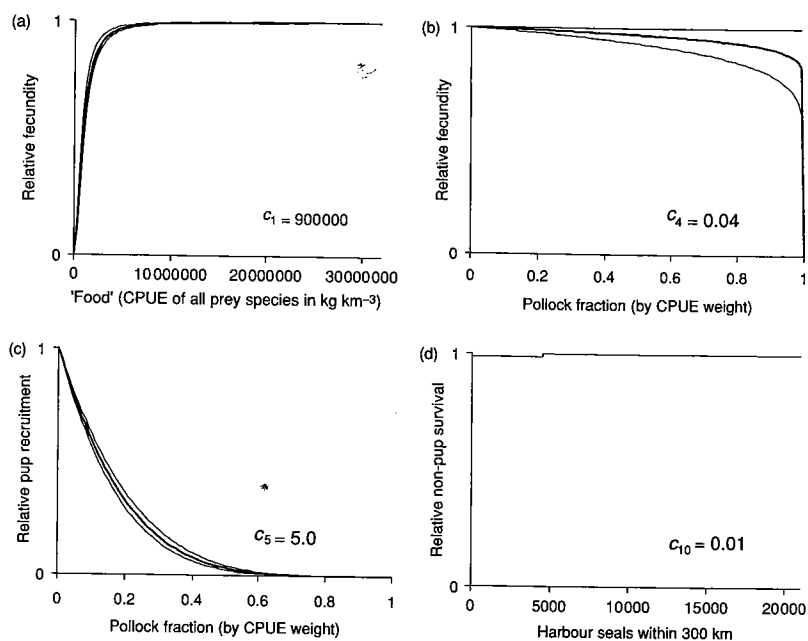
Fig. 19.5 Vital rate functions corresponding to MLE parameter values. (a) Hypothesis 1: food availability affects fecundity (magnitude of effect: medium). (b) Hypothesis 4: pollock fraction affects fecundity (magnitude of effect: weak at best). (c) Hypothesis 5: pollock fraction affects pup recruitment (magnitude of effect: very strong). (d) Hypothesis 10: harbour seals (via predation) affect non-pup survival (magnitude of effect: weak but persistent).

of the western population of Steller sea lions. There is good evidence for two strong effects: H1, total prey availability affects fecundity; H5, pollock fraction in the environment affects pup recruitment. One moderate effect was found: H10, harbour seal density (predation) affects non-pup survival. There was also marginal evidence for one weak effect: H4, pollock fraction in the environment affects fecundity. No evidence was found for any of the other hypotheses. What our work has done is to guide the weight of the evidence, when all plausible hypotheses are competing, towards those that win the competition.

Although we used the word mechanism, we recognize that a study such as this one cannot demonstrate causality. It would seem that H1 is a relatively clear and simple mechanism: lower abundance of all prey types leads to lower fecundity through the direct effect of reduced resource accumulation by adults and thus reduced storage for reproduction. H10 also has

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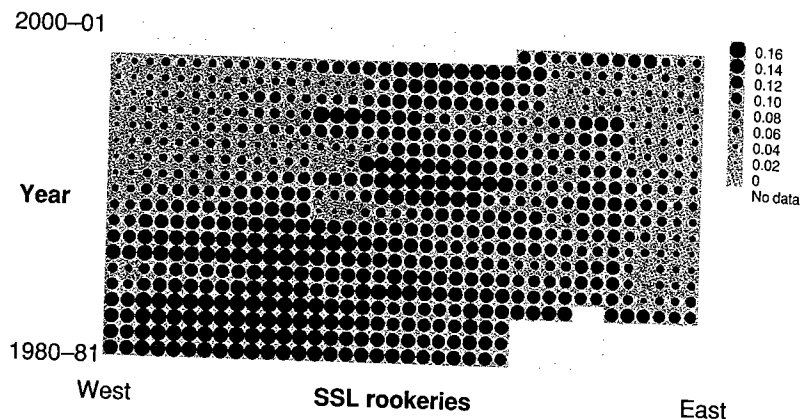West   **SSL rookeries**   East

Fig. 19.6   Lost production of the Steller sea lion population due to hypotheses 1, 4, 5 and 10. The diameter of each circle represents the fraction of potential production lost.

a clear mechanism, but note that its MLE is about 0.01, so that the effect of changes in the breadth of the diet of killer whales leads to only a 1% reduction in non-pup survival, and then only in cases where harbour seal numbers are sufficiently low.

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

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

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

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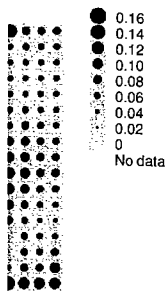
- rookeries around which fishing is reduced or prohibited if the total prey biomass in the pre-season zone is below a critical threshold (determined by c_1).
- rookeries around which a directed pollock fishery occurs if the pre-season survey suggests pollock fraction is above a critical threshold (determined by c_5).

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

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

The question 'Is it food?' has been asked a number of times in the context of the decline of Steller sea lions. As with most questions in biology, we shall never be able to 'prove' that it is lack of food. However, we conclude that the weight of the current evidence is that it is indeed food – and both the quantity and quality of the food matters. The more recent question 'Is it killer whale predation?' can be answered too: sometimes, if harbour seal populations are sufficiently low; however, the predation does not cause a large reduction in survival, but has a persistent annual effect.

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