

Ecosystem models show combined effects of fishing, predation, competition, and ocean productivity on Steller sea lions (*Eumetopias jubatus*) in Alaska

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Abstract: Steller sea lions (*Eumetopias jubatus*) increased in the eastern portion of their range while declining in the Gulf of Alaska and Aleutian Islands from the late 1970s to late 1990s. We constructed ecosystem models of the central and western Aleutians and of southeast Alaska to simultaneously evaluate four hypotheses explaining sea lion dynamics: killer whale (*Orcinus orca*) predation, ocean productivity, fisheries, and competition with other species. Comparisons of model predictions with historical time series data indicate that all four factors likely contributed to the trends observed in sea lion numbers in both ecosystems. Changes in ocean productivity conveyed by the Pacific Decadal Oscillation influenced the abundance trajectory of several species. Fishing could have affected the ecosystem structure by influencing the abundance of Atka mackerel (*Pleurogrammus monopterygius*) in the Aleutians and Pacific herring (*Clupea pallasii*) in southeast Alaska. Pacific halibut (*Hippoglossus stenolepis*) in the Aleutians and arrowtooth flounder (*Atheresthes stomias*) in southeast Alaska appear to impede sea lion population growth through competitive interactions. Predation by killer whales was important when sea lions were less abundant in the 1990s in the Aleutians and in the 1960s in Southeast Alaska, but appear to have little effect when sea lion numbers were high.

Résumé : La population d'otaries de Steller (*Eumetopias jubatus*) a augmenté dans le sud-est de l'Alaska tandis qu'elle a décliné de façon dramatique dans le Golfe de l'Alaska et les îles Aléoutiennes, de la fin des années 1970 jusqu'à la fin des années 1990. Nous avons construit des modèles d'écosystème des îles Aléoutiennes (centre et ouest) et du sud-est de l'Alaska pour examiner simultanément quatre hypothèses: la prédation par les orques (*Orcinus orca*), la productivité océanique, la pêche, et la compétition avec d'autres espèces. La comparaison des prédictions du modèle et des séries temporelles indique que ces quatre facteurs ont vraisemblablement contribué aux variations d'abondance des otaries dans les deux écosystèmes. Les changements de productivité océanique, représentés par l'oscillation pacifique décennale, ont influencé l'abondance de plusieurs espèces. La pêche semble avoir affecté l'écosystème en influençant l'abondance du maquereau d'Atka (*Pleurogrammus monopterygius*) dans les Aléoutiennes et du hareng du Pacifique (*Clupea pallasii*) dans le sud-est de l'Alaska. La compétition avec le flétan du Pacifique (*Hippoglossus stenolepis*) dans les Aléoutiennes et la plie à grande bouche (*Atheresthes stomias*) dans le sud-est ont contribué au ralentissement de la croissance de la population d'otaries. La prédation par les orques s'est avérée être un facteur important lors des faibles abondances des populations d'otaries, soit dans les années 1990 dans les Aléoutiennes et dans les années 1960 dans le sud-est. La prédation a par contre peu d'effet lorsque les otaries sont abondantes.

Introduction

Steller sea lions (*Eumetopias jubatus*) declined by more than 80% in the western Gulf of Alaska (GOA) from the late 1970s to the late 1990s (Merrick et al. 1987; Trites and Larkin 1996; Calkins et al. 1999). In contrast, the population in southeast Alaska (SE Alaska) and British Columbia (B.C.) have increased during the same period (Calkins et al. 1999).

Various hypotheses have been formulated to explain the decline (DeMaster and Atkinson 2002; National Research Council 2003), but none have been put forward to explain the increase of sea lions in SE Alaska.

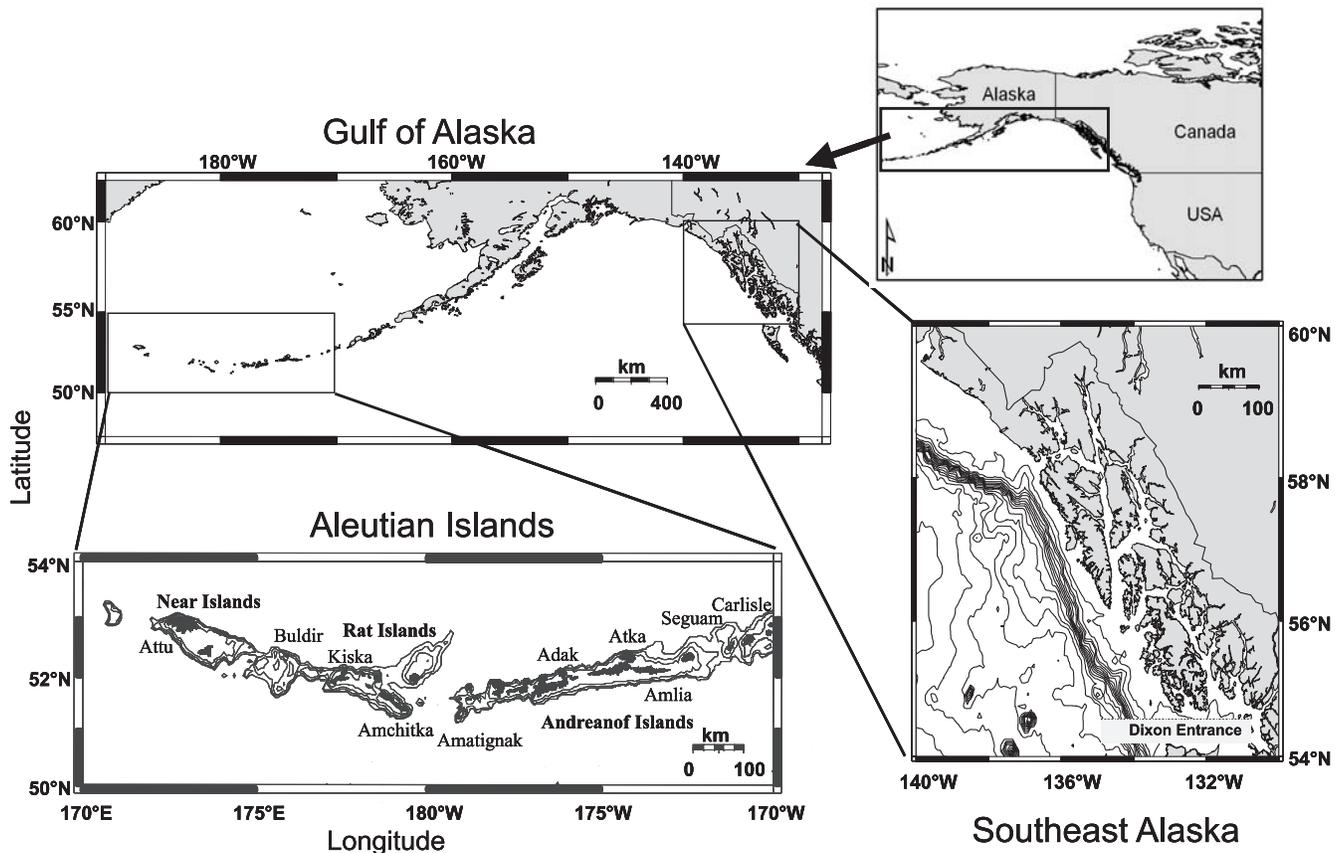
Three of the leading hypotheses to explain the decline in the western GOA are predation, change in oceans productivity, and fishing. The first of these proposes that the decline may be related to predation by transient killer whales (*Orcinus orca*) in the western GOA (Heise et al. 2003; Springer et al. 2003; Williams et al. 2004). The second hypothesis is that the carrying capacity for sea lions was reduced by a decrease in primary production in the western GOA because of a shift in ocean climate that occurred in 1977, altering the quantity and (or) the quality of the food web (Merrick et al. 1997; Anderson and Piatt 1999; Trites et al. 2006c). The third hypothesis is that the large-scale fisheries in the GOA modified the ecosystem structure and function to the detriment of sea lions (Alverson 1992; Hansen 1996; Trites and Donnelly

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Fig. 1. Location of the two study areas, Southeast Alaska and the central and western Aleutian Islands.



2003). Another possible explanation is that sea lions are unsuccessfully competing with other species (Trites et al. 1999; Aydin 2002). Most of the research conducted to date into the reasons for the decline of the western population of Steller sea lions has attempted to test only one hypothesis at a time.

The objective of our study was to examine the combined effects of fishing, predation, competition, and ocean productivity on Steller sea lions in the western GOA using ecosystem modelling. We employed a widely used ecosystem modelling approach, Ecopath with Ecosim (EwE, www.ecopath.org; Christensen and Walters 2004). We also sought to gain insights in the population decline in the Aleutian Islands by examining reasons why the SE Alaska population might have increased. We therefore compared two contrasting study areas that differed by the trends of their respective sea lion populations, their fishing histories, and the characteristics of their ecosystems: the western and central Aleutian Islands (henceforth simply referred to as the Aleutian Islands) and SE Alaska (Fig. 1). We modelled the period 1963–2002, which encompasses the ocean regime shift, the development of the major fisheries, and the major changes in Steller sea lion abundances.

Materials and methods

Study area

The Aleutian Islands of our study are contained within 170°E and 170°W, to the 500 m depth contour, for a total

area of 56 936 km² (Fig. 1). The eastern cutoff point was Carlisle Island, which meant that the region did not include Unimak Pass, a known aggregation area for marine mammals. The SE Alaska study area consisted of the continental shelf east of 140°W to 1000 m depth and included the eastern part of the Yakutat region (140°W–137°W) and the coastal region east of 137°W. The southern limit was the border between B.C. and Alaska (Dixon Entrance).

The Aleutian Islands are characterized by a narrow shelf and very few rivers able to sustain salmon species (*Oncorhynchus* spp.). The area is currently characterized by a large biomass of Atka mackerel (*Pleurogrammus monopterygius*) that is commercially fished. In contrast, SE Alaska is characterized by a large number of rivers that are important for salmon species, as well as for its large population of Pacific herring (*Clupea pallasii*) and many species of rockfish (*Sebastes* spp.). The most important species for evaluating the hypotheses are transient killer whales, Steller sea lions, Atka mackerel, salmon, Pacific herring, arrowtooth flounder (*Atheresthes stomias*), and Pacific halibut (*Hippoglossus stenolepis*). Parameters for these species are described in detail below.

The model

Ecosystem models account for the biomass (t·km⁻²) of each functional group (composed of a single species or a group of species), their diet composition, consumption per unit of biomass, natural and fishing mortality, accumulation of biomass, and net migration. The principle behind this

ecosystem modelling approach is that biomass and energy are conserved on a yearly basis (Walters et al. 1997). Ecosim is a tool for dynamic simulations based on the Ecopath model, an instantaneous image of the ecosystem in time. Ecosim uses a system of differential equations to describe the changes in biomass and flow within the system over time by accounting for change in predation, consumption rate, and fishing (Walters et al. 1997; Christensen et al. 2005). Thus, the rate of change of biomass of group i (B_i) is described by

$$(1) \quad \frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (m_i + F_i + e_i)B_i$$

where g_i is the net growth efficiency; Q_{ji} and Q_{ij} are the consumption rate of group j by group i and the consumption of group i by group j , respectively; I_i is the immigration flow in $t \cdot km^{-2}$; m_i is non-predation mortality; F_i is fishing mortality; and e_i is emigration rate (Christensen and Walters 2004).

EwE allows the fitting of time series of abundance and thus a comparison of how the model replicates observed behaviour through time. Ecosim is also able to incorporate multiple stanzas representing life history stages for species with complex life histories (sea lions and walleye pollock (*Theragra chalcogramma*) in these models). The stanzas are linked and their respective production per unit of biomass (P/B per year), consumption per unit of biomass (Q/B per year), and growth are calculated from a baseline estimate for a leading group (the adults in our case). Growth for each stanza is calculated following the von Bertalanffy growth curve and assuming stable survivorship through ages (Christensen et al. 2005).

The functional predator–prey relationship is based on the foraging arena theory, dividing the prey biomass into vulnerable and invulnerable pools (Walters and Kitchell 2001). The transfer rate between these two pools (also called vulnerability) can range from 0 to ∞ , with higher rates implying that the behaviour of both the prey and the predator have weaker effects on limiting predation rates. A large vulnerability value also means that the predator initial biomass is low compared with its carrying capacity and that a change in its biomass will cause a corresponding change in the mortality rate of its prey. The system will thus be more stable when a predator is close to its carrying capacity and more variable when far from it. Vulnerability values can be specified for each predator–prey pair. Owing to uncertainties in how this parameter might change among prey species and notably to reduce the number of parameters that needs to be estimated, we chose to assume that the vulnerability setting is the same for all species of prey that a given predator consumes.

This functional predator–prey response equation predicts changes in diet composition due to changes in relative availability of prey and alternative prey, but it does not allow switching of the diet to new prey that were not consumed initially. In Ecosim, the predator can follow a type II functional response (Holling 1959), in which a prey consumption increases with prey abundance until an asymptote is reached. A type II functional relationship supposes that killer whales are able to maintain their rate of predation on sea lions as abundance declines by using other mammals as well. A type III functional relationship is due to the predator changing prey types as its preferred prey reaches a low level. In

Ecosim, the addition of the foraging arena model can also produce a type III functional response, because at low density the prey will change its behavior and be less accessible to predation.

In addition to vulnerability, consumption is governed by limitations placed on predator consumption rates by foraging time adjustments, maximum relative feeding time, and handling time effects (Walters and Martell 2004; Christensen et al. 2005). The time that a predator spends foraging increases as relative prey availability diminishes. This in turn results in greater exposure and greater risk of the predator itself being eaten. The feeding time adjustment factor determines how fast individuals adjust their feeding times. A value of 0 causes feeding time to remain constant, with all changes in relative food availability being channelled to changes in growth rate. A value of 1 results in a fast time response, less predation risks, and a lesser growth rate. In our models, the feeding adjustment time was set to 0.5 for marine mammals, except for sea lion pups and embryos, and was 0 for other species (assuming that large predators are more likely to vary their feeding search time as food availability changes). As a rule, the maximum relative feeding time was not allowed to increase more than twofold (Christensen et al. 2005). Killer whales have no predators and were allowed to increase their maximum feeding time to 10 instead of 2 times the initial value, and the fraction of total mortality sensitive to predation mortality was set at 0.2. The handling time parameter was left at default values, assuming that the limitations imposed by the vulnerability values were sufficient. The relative foraging time factors were evaluated iteratively at each monthly time step (Walters and Martell 2004, p. 242).

Model fitting was achieved by evaluating vulnerabilities that minimized the sum of squares of differences between model predictions and the catch and biomass time series data. In addition, indices of climate changes were added to modify primary production.

We forced the model to fit the catches for groups without reliable biomass or fishing mortality series (toothed whales, mammal-eating sharks, salmon, large demersal, sablefish (*Anoplopoma fimbria*), and Pacific halibut in the Aleutians; toothed whales, small mammals, sea otters (*Enhydra lutris*), sharks, slope rockfish, walleye pollock, and flatfish in SE Alaska). Using a stock reduction analysis (Kimura 1985), historical catches were treated as fixed, known quantities and were subtracted from simulated stock size over time so as to aid in estimating how large (and (or) productive) the stock must have been to sustain those catches. Given the production of the stock and the catch time series, the model estimated the minimum biomass necessary for fisheries and predators' needs. Catches were sometimes forced for only part of the time series, typically for the beginning of the time series.

Data

The ecosystem models were initialized in 1963 and comprised 39 functional groups, with 9 groups of marine mammals and 21 groups of fish (Table 1). Commercially important species were considered separately in the models to ensure that fisheries were accounted for adequately. The structure of the models reflected the goals of our study. Thus we explicitly considered Steller sea lions, their predators,

Table 1. Functional groups description and parameters used for the balanced and fitted Aleutian Islands and Southeast Alaska models.

Group	Species	Aleutians						Southeast Alaska					
		Biomass (t·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE (year ⁻¹)	BA (year ⁻¹)	Vuln. ^c	Biomass (t·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE (year ⁻¹)	BA (year ⁻¹)	Vuln. ^c
Transient killer whales	Mammal-eating <i>Orcinus orca</i>	0.0006	0.025	10.8	0	—	>100	0.0007	0.02	11	0	—	>100
	<i>Physeter catodon</i> and fish-eating <i>Orcinus orca</i> and beaked whales in the Aleutians	0.013	0.036	11.1	0.95	-0.03	1	0.0175	0.03	11.5	0.05	-0.03	1.03
Baleen whales	<i>Balaenoptera physalus</i> ,	0.145	0.099	7	0.31	-0.02	>100	0.0361	0.099	10.9	0.12	-0.05	1.8
	<i>Balaenoptera borealis</i> , <i>Megaptera novaeangliae</i> , <i>Balaenoptera acutorostrata</i> and <i>Eschrichtius robustus</i> and <i>Balaenoptera musculus</i> in the Aleutians												
Steller sea lion	<i>Eumetopias jubatus</i>	0.0001	0.02	220.8	0	—	—	2.39×10 ⁻⁶	0.02	227.9	0	—	—
	Embryo	0.00202	0.521	83.4	0.68	—	—	0.0001	0.59	86.4	0.82	—	—
Pup	Juvenile	0.0301	0.241	39.6	0.52	—	5	0.00144	0.19	40.5	0.75	—	1
	Adult	0.148	0.174	25.6	0.11	—	25	0.013	0.11	25.5	0.7	—	1
Small mammals	Mainly <i>Phocoena vitulina</i> in Southeast Alaska and <i>Phocoenoides dalli</i> in the Aleutians	0.022	0.2	22.7	0.29	-0.01	3.85	0.041	0.21	28.85	0.8	—	1
	Sea otter	0.004	0.117	86.4	0.44	—	—	0.00003	0.21	85	0.95	0.2	65
Birds	All marine pelagic and coastal marine birds listed in Hunt et al. 2000	0.00177	0.113	65.4	0.95	—	—	0.006	0.38	68	0.39	—	—
	Mammal-eating sharks	0.05	0.125	0.6	0.43	—	1	0.01	0.13	1.3	0.07	—	—
Sharks and skates	<i>Carcharodon carcharias</i> , and <i>Hexanchus griseus</i>	2.6	0.159	0.8	0.15	—	2.57	0.25	0.12	1.2	0.71	—	—
	Mainly <i>Lamna ditropis</i> , <i>Squalus acanthias</i> , <i>Raja binoculata</i>	1.162	1.168	4.3	0.5	—	1	1.11	2.1	10.5	0.35	—	1.1
Pelagic, large	<i>Onchorhynchus gorbuscha</i> , <i>Onchorhynchus kisutch</i> , <i>Onchorhynchus keta</i> , <i>Onchorhynchus tshawytscha</i> , <i>Onchorhynchus nerka</i>	0.004	0.22	1.5	0.95	—	—	0.034	0.22	1.1	0.95	—	—
	Includes <i>Mola mola</i> , <i>Trachipterus altivelis</i> , <i>Merluccius productus</i>												

Table 1 (continued).

Group	Species	Aleutians					Southeast Alaska					
		Biomass (t·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE (year ⁻¹)	BA (year ⁻¹)	Vuln. ^c	Biomass (t·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE (year ⁻¹)	BA (year ⁻¹)
Pelagic, small	<i>Mallotus villosus</i> , Osmeridae, <i>Engraulis mordax</i> , <i>Scomber japonicus</i>	2.723	0.8	3.6	0.95	—	—	0.89	4.45	0.95	—	—
Atka mackerel ^a	<i>Pleurogrammus monopterygius</i>	13.5	0.34	1.7	0.99	—	1.1	—	—	—	—	—
Sand lance	<i>Ammodytes hexapterus</i>	0.779	0.8	3.6	0.95	—	—	1.15	5.75	0.58	—	—
Pacific herring	<i>Clupea pallasii</i>	2.771	0.16	1	0.95	—	1.21	1.27	6.35	0.83	-0.15	25
Walleye pollock	<i>Theragra chalcogramma</i>	0.67	1.2	4.7	0.78	—	—	1.2	5.9	0.88	—	—
Juvenile		6.08	0.304	2	0.99	—	1	0.3	1.5	0.87	0.02	>100
Adult		1.1	0.068	0.7	0.94	—	5	0.07	0.35	0.78	—	1.31
Pacific ocean perch	<i>Sebastes alutus</i>	1.23	0.1	1	0.95	—	1	0.11	0.54	0.95	—	—
Rockfish, slope	Mainly <i>Sebastes aleutianus</i> , <i>Sebastes borealis</i> , <i>Sebastes flavidus</i> , <i>Sebastes polyspinus</i> , <i>Sebastolobus</i> sp.	—	—	—	—	—	—	—	—	—	—	—
Rockfish, shelf ^b	Mainly <i>Sebastes ruberrimus</i>	—	—	—	—	—	—	0.02	0.11	0.95	—	—
Sablefish	<i>Anoplopoma fimbria</i>	1.8	0.106	1	0.49	-0.02	>100	0.13	0.65	0.67	0.03	1.24
Pacific cod	<i>Gadus macrocephalus</i>	2.4	0.37	2.3	0.55	0.03	1.1	0.28	1.85	0.91	0.02	2
Pacific halibut	<i>Hippoglossus stenolepis</i>	0.4	0.19	1.3	0.9	0.03	25	0.28	1.8	0.91	—	1
Arrowtooth flounder	<i>Atheresthes stomias</i>	0.5	0.3	2	0.6	—	1	0.5	1	0.98	0.03	>100
Demersal, large	Species from 20 to 240 cm, including <i>Myoxocephalus polyacanthocephalus</i> , <i>Hydrolagus collieti</i> , <i>Anarrhichthys ocellatus</i> , etc.	3.26	0.4	2	0.95	—	—	0.27	1.34	0.95	—	—
Flatfish	All soles and flounder	2.83	0.188	1.7	0.5	—	—	0.263	1.3	0.95	—	—
Demersal, small	Species smaller than 62 cm; Hexagrammids, Liparidae, Zoarcidae, Cottidae, Agonidae	5.1	0.6	3	0.95	—	—	1.07	4.3	0.95	—	—
Deepwater, large	Grenadiers, lancetfishes, rattails, eels	0.49	0.4	2	0.95	—	—	0.45	2.2	0.95	—	—
Deepwater, small	Myctophidae and Bathylagidae	7.6	0.8	3.6	0.95	—	—	1	4	0.5	—	—
Shrimps	Commercially and noncommercially exploited	3.22	2.04	10.2	0.95	—	—	2	13	0.95	—	—

Table 1 (concluded).

Group	Species	Aleutians					Southeast Alaska					
		Biomass (t·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE	BA (year ⁻¹)	Vuln. ^c	Biomass (t·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE	BA (year ⁻¹)
Benthic invertebrates	Ostracods, nematods, amphipods, coelenterates, noncarnivorous echinoderms	26.21	2.529	8.4	0.95	—	50	2	17	0.27	—	—
Epibenthic, carnivorous	Crabs, carnivorous echinoderms	8.12	1.283	5	0.95	—	2.88	1.3	8.7	0.95	—	—
Cephalopods	Octopuses and squids	2.09	2.94	7.2	0.95	—	0.22	2.55	10	0.95	—	—
Zooplankton, large	Mysids, chaetognaths, euphausiids, and jellyfishes	14.08	5.87	16	0.95	—	40	4.3	16.9	0.82	—	—
Zooplankton, small	Including calanoids	9.4	23.73	112.4	0.95	—	17.15	20	112	0.9	—	—
Phytoplankton		17.19	129.55	—	0.37	—	31.8	100	—	0.74	—	—
Marine plants	Macrophytes	12.9	8.12	—	0.1	—	23.23	4.4	—	0.88	—	—

Note: P/B, production per unit of biomass; Q/B, consumption per unit of biomass; EE, ecotrophic efficiency; BA, biomass accumulation rate; Vuln., vulnerability. Values estimated by Ecopath are in bold.

^aAleutians model only.

^bSoutheast Alaska model only.

^cLists vulnerability that were changed from the default value of 2.

and their principal prey species and only summarized the data that directly pertained to our objectives. Additional details about the models are given by Heymans (2005) and Guénette (2005).

Biomass estimates and time series generally came from stock assessment reports from the National Marine Fisheries Service (NMFS) and the Alaska Department of Fish and Game (ADF&G) or as estimates from survey data provided by NMFS. Catch series were assembled from stock assessment reports and from data provided by ADF&G and NMFS. Time series of fishing mortality estimates were obtained from stock assessment or calculated from the catch/biomass ratio. Catch, biomass, and fishing mortality for the period 1963–2000 were assembled from stock assessment reports and related publications.

In some cases, it was necessary to attempt population reconstruction to estimate biomass from 1963 to 1977. In these cases, we used a simple Schaefer model:

$$(2) \quad N_{t+1} = N_t + N_t r (1 - N_t/k) - C_t$$

where r is the intrinsic rate of growth, N_t is the abundance at time t , k is the carrying capacity, and C_t is the catch. The best solution, based on sum of squares, for k given a range of values of r and the initial abundance in the model time series (N_i) was found using the Solver routine in Microsoft Excel (Microsoft Corporation, Redmond, Washington).

For the Aleutians model, P/B and Q/B were generally obtained from a preliminary model developed at NMFS (Y. Ortiz, School of Aquatic and Fishery Sciences, University of Washington, 1122 NE Boat Street, Seattle, WA 98115, USA). However, they were corrected or complemented according to the following methods, which were also used to estimate parameters for the SE Alaska model (see Table 1 for results). Consumption rates for mammals were based on energy requirements found in Perez and McAlister (1993) using the empirical equation $E = aM^{0.75}$, where E is the energy requirement per day (kcal·day⁻¹; 1 calorie = 4.186 J), M is the mean body weight (kg), and a is a coefficient varying with the group of mammals ($a = 320$ for otariids, 200 for phocids, 192 for mysticetes, 317 for odontocetes, and 320 for sea otters). Direct ration estimates were used for sea lions (Winship and Trites 2003) and sea otters (Estes and Palmisano 1974). The average Q/B has been weighted by species biomass (see Table 1). Fish Q/B per year was typically calculated according to the empirical regression of Christensen and Pauly (1992):

$$(3) \quad Q/B = 10^{6.37} \times 0.0313^{Tk} W_{\infty}^{-0.168} 1.38^{Pf} 1.89^{Hd}$$

where W_{∞} is the asymptotic body weight in grams, Tk is the mean annual temperature expressed as $1000/(T (^{\circ}C) + 273.1)$, Pf equals 1 for predators and zooplankton feeders and 0 for all others, and Hd equals 1 for herbivores and 0 for carnivores. However, this method typically overestimated the consumption for long-lived fish (Guénette 2005), which was calculated instead using a production/consumption ratio of 0.2.

Fish natural mortality (M) was preferably taken from the literature (e.g., stock assessment reports) for commercial species. For other species, natural mortality was derived from the empirical model of Pauly (1980):

$$(4) \quad M = K^{0.65} L_{\infty}^{-0.279} T^{0.463}$$

where K (year^{-1}) and L_{∞} (cm) refer to the curvature and asymptotic length parameters, respectively, of the von Bertalanffy growth function, and T is the mean annual water temperature ($^{\circ}\text{C}$). Alternative estimates were taken from Hoenig's empirical equation (Hoenig 1983) for species that are not as well known:

$$(5) \quad \ln(M) = 1.44 - 0.982 \ln(\text{max age})$$

P/B values resulting for the sum of natural and fishing mortalities are listed in Table 1.

Fish diets obtained from NMFS for the Aleutian Islands were often specific for the area, while diet compositions for SE Alaska were generally taken from local or regional studies (for details see Gu nette 2005; Heymans 2005). When necessary, diet data for the SE Alaska model were adapted from studies made in the central GOA and studies from the Hecate Strait (B.C.). For example, the Pacific halibut diet taken from the central GOA included a lot of walleye pollock, a species that is relatively less abundant in SE Alaska. Walleye pollock was partially replaced by sablefish based on observations by Sigler et al. (2002) and by Pacific herring, arrowtooth flounder, rockfish, and flatfish, prey that were shown to be used by Pacific halibut in the Hecate Strait (I. Pearsall and J. Fargo, Fisheries and Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, BC V9R 5K6, personal communication). The resulting diet matrices represented the 1980s and the 1990s, when most studies were carried out, and were modified to account for the changes in relative biomass between 1963 and the 1990s. For example, the proportion of Pacific herring in diets of fish and mammals of SE Alaska had to be decreased because the biomass of herring was too low to support all these species in 1963. Dietary proportions were therefore decreased for all predators but even more so for the predators that were responsible for a larger fraction of herring predation mortality. Changes to the diet were made on the basis of preserving diet preferences, not adding any new food items to counterbalance the decrease in biomass of an important food item. In the Aleutians, it was not necessary to modify the diet of arrowtooth flounder and Pacific halibut as it was in the SE Alaska model (Table 2). In the Aleutians, sea lion diet was modified by decreasing the proportion of Pacific halibut and Pacific ocean perch because the biomass of these prey species was lower in the 1960s. In SE Alaska, Pacific herring was replaced in the sea lion diet with salmon, rockfish, Pacific ocean perch, and sand lance (*Ammodytes hexapterus*).

Transient killer whales

Diets for transient killer whales, the ecotype of killer whale that eats only marine mammals, were inferred from observations reported in the literature as well as from stomach contents and visual observations of hunting behaviour and killings (Ford et al. 1998; Ford and Ellis 1999; Heise et al. 2003). Admittedly, these estimates may be biased by the different probabilities of observing any of these events for each prey species. Transient killer whales are assumed to feed primarily on small marine mammals (harbour seals (*Phocoena vitulina*), harbour porpoises (*Phocoena phocoena*), etc.), sea lions, and baleen whales (Table 2). Sea otters (*Enhydra lutris*) were included in the killer whales diet in the Aleutians

based on recent observations (Estes et al. 1998; Doroff et al. 2003). To explore the possible impact of killer whales on Steller sea lions, we considered several scenarios about the proportion of sea lions consumed by killer whales in the Aleutians model.

Springer et al. (2003) assumed that 14 transient killer whales occur year-round in the western Aleutians ($0.0006 \text{ t}\cdot\text{km}^{-2}$). Alternatively, Fiscus et al. (1981) counted 63 killer whales in the central Aleutian Islands (from the Rat Islands to the Fox Islands). Assuming that 10% (six) of these 63 whales were transients (Waite et al. 2002) results in a total biomass of $0.0003 \text{ t}\cdot\text{km}^{-2}$.

Of the 219 transient killer whales catalogued so far from Washington to SE Alaska, 6% have only been seen in SE Alaska, 50% have been seen in SE Alaska and B.C., and 44% in B.C. and Washington (Ford and Ellis 1999). Between 1984 and 2002, there have been 703 sightings of 137 different whales in SE Alaska (Straley et al. 2003). Thus, 133 transients were assumed to be present in SE Alaska during the 1990s. As transients are constantly travelling and may cover large distances within a month (Ford and Ellis 1999), we assumed that they stayed in SE Alaska for 2–3 months, which amounted to 26 whales year-round ($0.0007 \text{ t}\cdot\text{km}^{-2}$).

Steller sea lions

Steller sea lions were separated into four age-classes: foetus (6 months), pups (1 year), juveniles (1–3 years), and adults (4+). The foetal stage existed only to bring the foetus from weight 0 to 21 kg, their average weight at birth, and was 2 months shorter than the actual gestation period, given the von Bertalanffy growth curve parameters: $K = 0.282 \text{ year}^{-1}$ and maximum weight = 569 kg (Winship et al. 2001). Inclusion of the foetal life stage in the model was necessary to compensate for the growth calculation in Ecosim that uses a default value of -0.1 for the von Bertalanffy growth curve parameter t_0 . When it comes to fish, t_0 is negligible given their weight at birth, whereas the bias becomes very important with mammals. The foetal stanza had no impact in the ecosystem model because foetuses incur a small mortality and feed on imported energy (i.e., via their mothers). Pups were differentiated from juveniles because they consume little if any prey and depend on their mother's milk for their first year of life (Trites et al. 2006b). Thus they also eat imports in the model. Although pups probably constitute easy prey for a large part of the year, their mortality is not dependent on the search for food, so the feeding adjustment of pups and embryo was set to zero in Ecosim. The ratio $W_{\text{mat}}/W_{\infty}$ used in Ecopath to increase fecundity as body weight increases is unnecessary for mammals and was set to a very small value instead of zero (C. Walters, The University of British Columbia, Fisheries Centre, 2202 Main Mall Vancouver, BC V6T 1Z4, Canada, personal communication). In the Aleutians, annual instantaneous mortality rates (M) were 0.17 for adults, 0.24 for juveniles, and 0.52 for pups. These values were calculated from the slope of the natural log of numbers at age, based on published life tables (Trites and Larkin 1992). In SE Alaska, recent estimates from mark-resighting data in SE Alaska yielded lower rates of total annual mortality, averaging 0.11 for adults, 0.19 for juveniles, and 0.59 for pups (Pendleton et al. 2004).

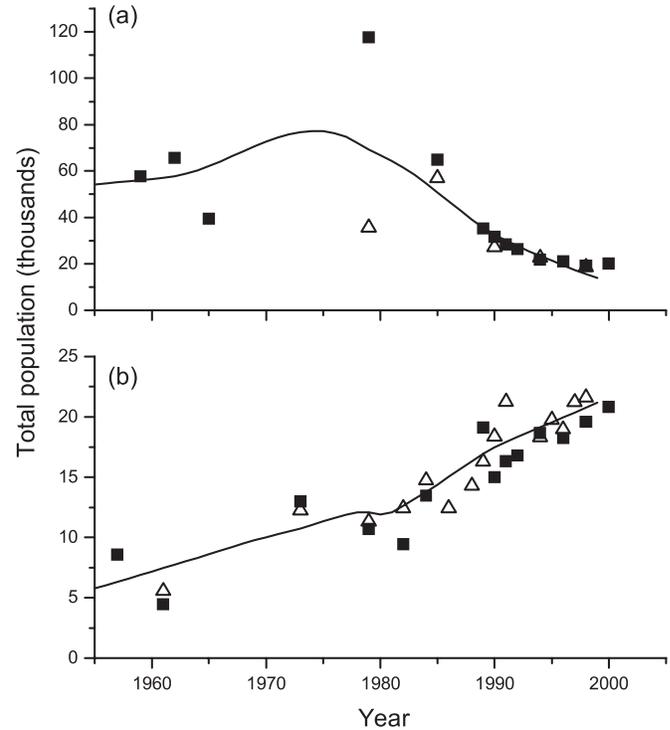
Table 2. Examples of modifications of diets from the 1990s to the 1960s for the Aleutian Islands and Southeast Alaska models.

Prey	Southeast Alaska															
	Aleutians						Southeast Alaska									
	Killer whale		Sea lion adult		Pacific halibut		Arrowtooth flounder		Killer whale		Sea lion adult		Pacific halibut		Arrowtooth flounder	
1990s	1963	1990s	1963	1990s	1963	1990s	1963	1990s	1963	1990s	1963	1990s	1963	1990s	1963	
Transient killer whales																
Toothed whales																
Baleen whales	1	1														
Steller sea lion																
Pup	1	10														
Juvenile	9	40														
Adult	6	30														
Small mammals	78	15														
Sea otter	4	3														
Birds	1	1														
Mammal-eating sharks																
Sharks and skates																
Salmon			0.7	0.7												
Pelagic, large			10.6	10.6												
Pelagic, small																
Atka mackerel			41.6	42.7												
Sand lance			0.5	0.5												
Pacific herring																
Walleye pollock																
Juvenile			0.7	0.7												
Adult			1	2.6												
Pacific ocean perch			0.02													
Rockfish, slope			1.5	1.6												
Rockfish, shelf																
Sablefish			0.1													
Pacific cod			6.3	6.3												
Pacific halibut			0.2													
Arrowtooth flounder			1.1													
Demersal, large			4.4	4.7												
Flatfish			2.7	2.7												
Demersal, small			16.2	16.2												
Deepwater, large																
Deepwater, small			1.6	1.6												
Shrimps																
Benthic invertebrates																
Epibenthic, carnivorous																
Cephalopods																
Zooplankton, large			8.1	8.1												
Zooplankton, small																

Table 2 (concluded).

	Aleutians				Southeast Alaska			
	Killer whale 1990s	Sea lion adult 1990s	Pacific halibut 1990s	Arrowtooth flounder 1990s	Killer whale 1990s	Sea lion adult 1990s	Pacific halibut 1990s	Arrowtooth flounder 1990s
Prey	1963	1963	1963	1963	1963	1960s	1963	1963
Phytoplankton								
Marine plants								
Detritus								
Imports								
			5.1	0.6	2		1.84	
								1.84

Fig. 2. Total population estimates obtained from Steller sea lion (*Eumetopias jubatus*) pups (open triangles) and non-pups (solid squares) and the estimated total population size (trend) obtained from a local regression model (Trites and Larkin 1996) for (a) the Aleutian Islands and (b) Southeast Alaska.



Steller sea lions abundance time series were obtained from a local regression model applied to counts of pups and non-pups made since 1956 (Trites and Larkin 1996). Sea lions were not counted continually over our study period (1963–2000). For example, counts in SE Alaska were only made once between 1961 and 1978, after which they were performed more regularly (Fig. 2). In the Aleutians, a number of rookeries were not counted during infrequent surveys, resulting in several years between 1963 and 1985 when counts were considered too partial to be included in the analysis. Thus in both areas, there was greater uncertainty in the population trajectory before the mid-1970s. Nevertheless, the results from these regressions represent the best estimate of abundance available. The proportion of juveniles and adults were calculated from a simple, age-structured population model and used as time series, while counts were used for pups. In the Aleutian Islands, the population totalled an estimated 57 653 animals in 1963, increasing to 72 113 in 1979, and declining to 13 852 in 2000 (Fig. 2). In SE Alaska, the number of sea lions increased from 8030 in 1963 to 21 175 animals in 1999.

Estimated number of Steller sea lions killed for subsistence, incidental harvest, shooting, and other sources of mortality were compiled from Wolfe et al. (2002), Perez (2003), Alverson (1992), and Trites and Larkin (1992) for the Aleutians. The hunting mortality for this area is rather small compared with that of the central GOA (see National Research Council 2003). No hunting was reported in SE Alaska.

Diets of Steller sea lions were estimated from the frequency of occurrence of prey remains found in scat samples

in SE Alaska in the 1990s (A.W. Trites, unpublished data) and were modified to account for lower relative biomass of Pacific herring, salmon, and walleye pollock present in the ecosystem in the early 1960s. Thus, sea lion diet was dominated by salmon (~21%), sand lance (~15%), Pacific herring (~15%), arrowtooth flounder (~7%), and small demersal fish (~10%). Diet compositions obtained from similar studies for sea lions in the Aleutians (Sinclair and Zeppelin 2002) were dominated by Atka mackerel (33% and 40% for juveniles and adults, respectively), salmon (~11%), and small demersal fish (25% and 16% for juveniles and adults, respectively).

Although killer whales were the main predator of Steller sea lions in both models, Pacific sleeper sharks (*Somniosus pacificus*) could also contribute to sea lion pup mortality, as sharks are known to prey on mammals in Greenland (Hulbert et al. 2002). In Alaska, although marine mammals (mainly cetaceans) have been found with a frequency of occurrence of 15% in shark stomachs, it is not certain at this stage if they were eaten alive or scavenged (Hulbert et al. 2003). Loughlin and York (2000) assumed that sleeper and salmon (*Lamna ditropis*) sharks accounted for 1% of predation of sea lions when they tried to account for all sources of sea lion mortality. In the Aleutians, sharks were assumed to obtain 0.2% of their diet from pups and 3.5% from juvenile sea lions. In the SE Alaska model, sea lion pups and juveniles only supplied 0.1% of the shark diet.

Atka mackerel

Atka mackerel occur along the Aleutian chain but are most abundant at the western end (Scheffer 1959) and are practically nonexistent in SE Alaska. Stock assessment for this species only began in 1977, while the fishery started in 1972, with 4907 t being caught by the former USSR (Forrester et al. 1983). The biomass of Atka mackerel was estimated at 6.2 t·km⁻² in 1979. In the absence of data, the 1963 biomass was estimated at 13.6 t·km⁻² by Ecopath. Natural and fishing mortalities were estimated at 0.34 year⁻¹ and 0, respectively, in 1963. Maximum F was 0.17 year⁻¹ in 1996.

Pacific herring

Pacific herring does not seem to be prevalent in the western and central Aleutian Islands, but was abundant in the 1930s in the eastern Aleutians around Unalaska and Dutch Harbour (Scheffer 1959). In addition, most of the herring food and bait fishery in the Aleutian Islands are part of the fishery on the Eastern Bering Sea herring stock (Duesterloh and Burkey 2003). There were no estimates for herring biomass in this area.

In SE Alaska, Pacific herring has been exploited since the 1880s and was heavily exploited between the 1920s and the late 1960s (Hebert and Pritchett 2003). Fishing was reduced in the 1970s and the population increased rapidly afterward. The spawning biomass (3+) of the five main spawning areas was obtained from age-structured models (methods described in Carlile et al. 1996) and the more recent population estimates provided for 1977–2002 (D. Carlile, ADF&G, Douglas Island Center Building, 802 3rd Street, P.O. Box 240020, Douglas, AK 99824-0020, USA, personal communication). The biomass trajectory for 1963–1976 was estimated using a stock reduction model (eq. 2) based on the 1977–2002 biomass and the 1900–2002 catch time series. The Schaefer biomass model was solved for k (assumed to be equal to bio-

mass in year 1900) using a series of initial values of r because the data were not informative enough to estimate both parameters at once. The penalized likelihood was calculated using F prior calculated as $(F_{\text{avg}} - 0.07)^2$, where F_{avg} is the average fishing mortality (i.e., ratio of observed catches to the predicted biomass) for the years 1990–2001 (S. Martell, The University of British Columbia, Fisheries Centre, 2202 Main Mall, Vancouver, BC V6T 1Z4, Canada, personal communication). For a set of r values ranging from 0.3 to 0.7, the reconstruction model yielded a 1963 population biomass of 48 787 – 24 007 t as the likelihood increased. Based on the maximum acceptable value of annual fishing mortality rate fixed at 0.9 and the comparison of predicted 1977–2003 biomass trajectory with that calculated by the age-structured model, the initial intrinsic growth rate of 0.5 year⁻¹ yielded a reasonable estimate of 32 000 t (0.89 t·km⁻²) in 1963.

Salmon

Five species of salmon are present in the GOA, each spending various amount of time in fresh water, coastal areas, and offshore in the North Pacific. Except for some populations of Chinook (*Oncorhynchus tshawytscha*) in SE Alaska, coastal waters are part of the migrating route, as smolts migrate towards the GOA and return as spawners towards fresh water, one or more years later. Given the geographical boundaries of the ecosystem models, it was not possible to account for the whole life history of salmon, so they were regrouped and only spawners were considered in the model. As a consequence, salmon ecotrophic efficiency in the model was expected to be low.

The salmon present in the Aleutian Islands area are mostly part of the western Alaska stock, of the Bering Sea from the Yukon River to Unimak Island (Rogers 1987). These stocks migrate through the Aleutians from the Bering Sea to the GOA as smolts and back into the Bering Sea as adults (Scheffer 1959). Salmon catches from 1911 to 1997 were reported by Byerly et al. (1999), and no salmon catches were made since 1994 in the western Aleutians. As no biomass estimate was available, we used the catch in the entire Aleutian Islands as a proxy for salmon biomass trends, assuming that catches are proportional to biomass. The annual P/B for 1963 (1.17) was estimated based on the natural mortalities of the various salmon stocks (see Heymans 2005).

In SE Alaska, salmon spend only a small period of their life in coastal marine waters of the study area, where they sustain a large fishery. The catches in number and the average body weight of the catches by species for years 1969–2002 were provided by M. Kallenberger (ADF&G, Douglas Island Center Building, 802 3rd Street, P.O. Box 240020, Douglas, AK 99824-0020, USA, personal communication). The natural mortality was taken from various sources (see Guénette 2005) and averaged at 1.44 year⁻¹. The fishing mortality time series was taken from stock assessments references for Chinook and coho (*Oncorhynchus kisutch*). For species more difficult to assess such as pink (*Oncorhynchus gorbuscha*), sockeye (*Oncorhynchus nerka*), and chum (*Oncorhynchus keta*), fishing mortality was based on recent estimates for each species, qualitative estimates of how the fishery evolved since 1963, and the catch times series (see Guénette 2005). Thus, fishing mortality in 1963 was assumed to be the same as it was in 1977 (0.67 year⁻¹), and the biomass was estimated at

1.11 t·km⁻². Although the biomass time series data are not very good, since we had to interpolate for several years for pink, chum, and sockeye, they conformed with the increase in abundance observed for several species (especially pink salmon, the most abundant species) in catch and abundance index since the 1970s (H. Geiger, ADF&G, Douglas Island Center Building, 802 3rd Street, P.O. Box 240020, Douglas, AK 99824-0020, USA, personal communication). To balance the model, salmon diet had to be modified to increase the imports from 75% to 93%, implying that a larger part of their life history and feeding behaviour takes place outside the study area.

Pacific halibut

The Pacific halibut survey estimates for the western Aleutians were obtained from Ronholt et al. (1994) for 1980–1986 and from Zenger (2002) for 1991–2002, giving estimates of 0.29 t·km⁻² for 1979 and 0.58 t·km⁻² for 1991. No estimates of biomass were available for 1963. *P/B* (0.19 year⁻¹) was based on a natural mortality estimated at 0.1 year⁻¹ (Pauly's empirical equation) and fishing mortality equal to that of 1991. Catches were taken from Forrester et al. (1978) for 1963–1970, from Forrester et al. (1983) for 1971–1973, from Clark and Hare (2003) for 1974–1980, and from the International Pacific Halibut Commission (IPHC) web site (<http://www.iphc.washington.edu/halcom>) for recent years. In absence of reliable estimates of *F*, halibut catches were forced in the model.

In SE Alaska, Pacific halibut biomass, effort, and fishing mortality (1974–2001) were all taken from assessment reports (Clark and Hare 2002) for IPHC Area 2C, which covers the area delimited by 137°W. Catch statistics for 1929–2002 were available from the IPHC web site. The biomass of legal size (larger than 80 cm, which corresponds to age 4–5 in the 1990s) was estimated at 0.64 t·km⁻² in 1999, and the biomass of small individuals was considered negligible. In 1977, the biomass amounted to 18 794 t or 0.26 t·km⁻². Natural mortality was estimated at 0.1 year⁻¹ (Pauly's empirical equation), and fishing mortality was estimated at 0.16 year⁻¹ and 0.1 year⁻¹ in 1999 and 1977, respectively. In 1963, the catches amounted to 6192 t, and the biomass was assumed to be similar to that of 1974, which seemed to be sufficient to balance the model and fit the time series.

Arrowtooth flounder

The biomass of arrowtooth flounder in the Bering Sea – Aleutian Islands was estimated at 284 965 t (0.52 t·km⁻²) in 1979 (Wilderbuer and Sample 2003). No biomass estimate was available for 1963. Catches for 1970–2002 were taken from the stock assessment report, which peaked around 6500 t in 1979 and again around 5000 t in 1991 (Wilderbuer and Sample 2003). After 1997, catches decreased because of fisheries restrictions and the phasing out of the foreign fishery. Arrowtooth flounder has a low commercial value and are mostly discarded in various trawl and longline target fisheries, with the largest discards being in the Pacific cod (*Gadus macrocephalus*) and flatfish fisheries (Wilderbuer and Sample 2003). Prior to 1970, catches of all flounders combined were given by Ronholt et al. (1994), which we prorated by the ratio of arrowtooth flounder to other flounder given by Anonymous (2001). In 1963, the natural mortality rate of 0.3 year⁻¹ (Wilderbuer and Sample 2003) was used as

an estimate of *P/B*, assuming that fishing mortality was negligible. The average annual *Q/B* (2.6) ratio for adult arrowtooth flounder was obtained from NFMS data.

In SE Alaska, biomass was calculated using the stock assessment for the whole Gulf, assuming that SE Alaska contained 13% of the GOA biomass (J. Turnock, Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration (NOAA), 7600 Sand Point Way NE, Building 4, Seattle, WA 98115, USA, personal communication) and that the same percentage was valid for the whole time series. Catches for the period 1991–2002 were taken from the NOAA database. Before that, arrowtooth flounder were mostly discarded and declared as part of the flatfish group. In the NMFS database, all flatfish were reported together in 1956–1970 and 1977–1990, so we assumed that two-thirds of the flatfish were arrowtooth flounder (J. Berger, Alaska Fisheries Science Center, NOAA, 7600 Sand Point Way NE, Building 4, Seattle, WA 98115, USA, personal communication). Catches were generally under 1000 t annually, except in the 1970s when it approached 5000 t. Fishing mortality was estimated at 0.0006 year⁻¹ in 1963. Natural mortality (0.2 year⁻¹) was taken from Turnock et al. (2002). A *Q/B* ratio of 1.05 year⁻¹ was calculated using a *P/Q* of 0.2.

Fitting the model

Time series of biomass, catches, and fishing mortalities were used to fit the models for the period 1963–2002. The models were driven with fishing mortality and fitted by trying to obtain predicted biomass and catches trajectories similar to those observed during the study period for marine mammals as well as for fish. The model was first fitted manually to identify possible solutions and the most sensitive parameters, modifying initial biomass, biomass accumulation, and predation vulnerability (Table 1). This resulted in making some manual modifications to the biomass accumulation rates (see Table 1). Other corrections to biomass accumulations were necessary because of the history of some fisheries, but we did not undertake to include them and explore their impact until we began fitting the time series. For example, the only way to fit the Pacific herring time series data was to include a negative biomass accumulation that acknowledges that the herring population was not stable when we started the model in 1963. It was also necessary to increase the initial biomass of sablefish in the SE Alaska to obtain predicted catches as high as those observed. For the Aleutians model, Pacific halibut was attributed a positive biomass accumulation because of the increase in population abundance observed between 1963 and 2002.

However, this method of adjusting the model is unlikely to produce an optimal solution in a timely manner, and therefore we preferred formal fitting to the time series by using a nonlinear search procedure, allowing vulnerabilities to be modified. We used the knowledge gained in the manual fitting to start the search procedure with different initial parameters to avoid being caught in local optimal solutions. The criterion was a weighted sum of squares of deviations (SS) between logarithms of observed and predicted biomasses and catches. Climate influences (e.g., Pacific Decadal Oscillation (PDO)) on the ecosystem productivity were also included in the model to improve the fit to time series. Although the search for an optimal solution does not result

Table 3. Biomass and prey of transient killer whales in the Southeast Alaska and four scenarios used for the Aleutians models.

	Aleutians				Southeast Alaska
	Scenario 1	Scenario 2	Scenario 3	Scenario 4	
Biomass (t·km⁻²)	0.0003	0.0006	0.0006	0.0003	0.0007
Prey (%)					
Baleen whales	1	5	1	1	6
Steller sea lion					
Pup	1	8	10	10	0.4
Juvenile	9	12	40	40	5
Adult	6	8	30	30	13
Small mammals	78	62	15	15	72.6
Sea otter	4	4	3	3	0
Birds	1	1	1	1	1
Imports	0	0	0	0	2

in a unique solution given that the data is generally imperfect, one should not presume that just any parameter modification would result in a good fit. The food web interactions and the numerous time series constitute strong constraints that reduce the range of possible solutions.

Recent work using Ecosim without time series data has been useful on theoretical grounds to explore the effect of model structure and complexity on the simulated responses to disturbances (e.g., Vasconcellos et al. 1997; Fulton et al. 2004; Pinnegar et al. 2005) and the impact of alternative trophic functional relationships on model behaviour (Mackinson et al. 2003). This modelling approach does not mean that all combinations of parameter values are equally possible and falls short when evaluating and comparing scenarios without the benefits of having time series data. It is particularly difficult to differentiate between high growth rate – low initial biomass and low growth rate – high initial biomass scenarios without time series data. Thus, the Ecosim approach that uses time series data is far superior to comparing characteristics of Ecopath models in spite of any apparent inaccuracies that this modelling method may have. For example, using models for recent years for which there is obviously more available data would not allow the role of change in ocean productivity to be evaluated nor to understand what happened during the 1970s.

The PDO was used to modify the productivity of primary producers and account for changes in oceanic regimes in the Pacific Ocean (Hare and Mantua 2000). Monthly values of PDO (<http://jisao.washington.edu/pdo/PDO.latest>) were transformed to obtain a range of 1 and were used directly in SE Alaska, which improved the fit to the time series. In the Aleutians, it was necessary to use the inverse PDO (Heymans et al. 2005). This is consistent with the fact that the PDO is inversely related to sea surface temperature in the Aleutians and positively correlated in SE Alaska (Mantua et al. 1997). Similarly, during positive PDO years (1977 and onwards), annual discharge in the Skeena River, at the southern limit of SE Alaska, averaged 8% lower than that in the negative PDO years (before 1977) (Mantua et al. 1997). In contrast, discharge in the Kenai River in the central GOA in positive

PDO years averaged 18% higher than that during the negative years.

Simulations

Given the uncertainty about killer whale parameters, we evaluated the impact of the initial killer whale abundance and their diet by comparing the results of four scenarios using the Aleutian Islands model. Scenario 1 started with a low biomass of killer whales (0.0003 t·km⁻²) and assumed that Steller sea lions constituted only 16% of the killer whale diet (Table 3). The second scenario used a higher estimate of killer whale biomass (0.0006 t·km⁻²) and assumed that sea lions provided 28% of killer whale nutritional needs. At high killer whale biomass, small mammals were not abundant enough to provide 78% of killer whales needs, which were therefore reduced to 62% (Table 3). Scenario 3 also used the higher estimate of killer whale biomass and assumed that sea lions were the main prey for killer whales, for a total of 80%. Scenario 4 featured a low killer whale biomass, with sea lions being a preferred prey for killer whales, constituting 80% of their dietary needs.

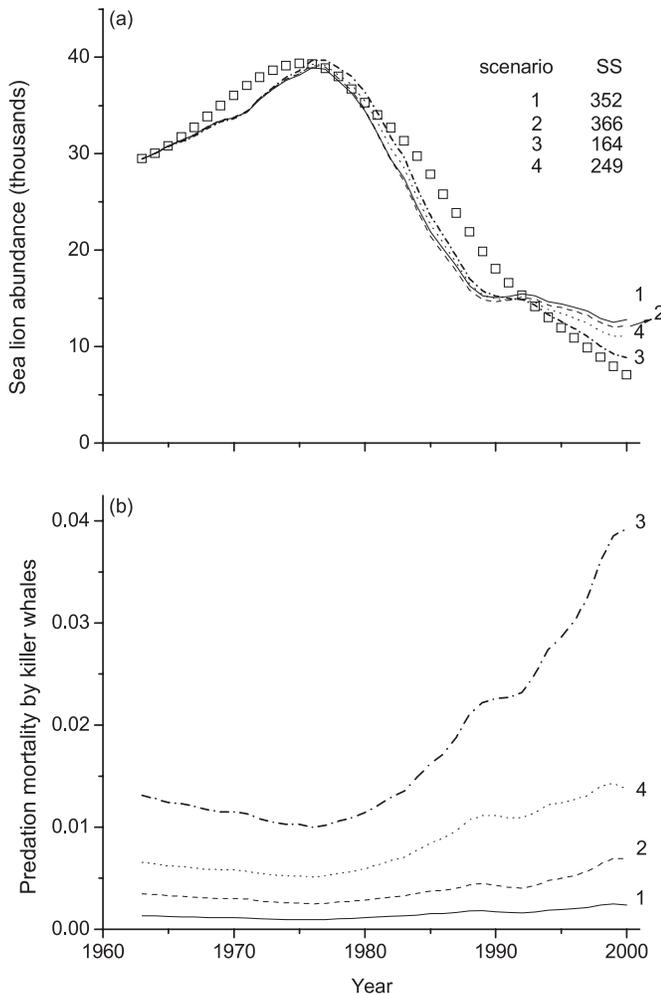
The predicted trajectory of Steller sea lions was likely due to a combination of several factors. After identifying the most likely sources of influence on the sea lion abundance trajectory, we examined their respective influence by removing them one at a time. Simulation results for each scenario were compared based on the shape of sea lion abundance trajectories and the sum of squares between the observed and predicted times series of adult sea lion abundance. For convenience, the sums of squares were divided by 10⁶. We chose to compare scenarios showing total adult sea lion abundance trajectories given that the abundances of the three modelled stanzas were correlated.

Results

Aleutian Islands

Ecosim predicted an initial increase in the Steller sea lion population in the Aleutians followed by a steep decline after 1975, which yielded a good fit to the reference time series

Fig. 3. (a) Trajectory of adult Steller sea lion (*Eumetopias jubatus*) abundance in the Aleutians under four scenarios: (1) low abundance of killer whales (*Orcinus orca*) and low predation on sea lions; (2) high abundance of killer whales and low predation on sea lions; (3) high killer whale abundance and high predation on sea lions; (4) low killer whale abundance and high predation on sea lions. The sums of squares (SS) for each scenario are provided. The reference abundance data is represented by squares. (b) Annual instantaneous predation mortality rate on adult sea lions under each scenario.



for all scenarios of killer whale abundance and diet allocations (Fig. 3a). The main difference between scenarios was the steepness of the sea lion decline in the 1990s. As killer whale predation on sea lions increased, the rate of decline in sea lions increased under all scenarios (Fig. 3a), regardless of how killer whale predation was distributed among age classes or stanzas (pups, juveniles, adults). The steep decline in the 1990s suggested by the reference data was more closely matched by scenario 3, which assumed a high killer whale biomass and a high proportion of sea lions in killer whale diet. The initial proportion of sea lion in the diet of killer whale had a dramatic effect on the instantaneous rate of mortality inflicted on sea lions. Under scenario 3, annual mortality of pups caused by killer whales increased from 0.32 in 1963 to 0.98 in 2002 (Fig. 3b). In comparison, when

a low rate of predation was inflicted by killer whales in scenario 1, the annual mortality remained about constant (0.03) throughout the study period. Adult sea lion mortality caused by killer whale predation, although smaller, followed the same trends. Note that in contrast with killer whale-induced mortality, the mortality caused by hunting and incidentals from conflict with fishing reached a maximum of 0.01 year⁻¹ in the 1980s for juvenile and adult sea lions.

The third scenario provided the best fit to the data and was therefore used as the baseline for further simulations. Model predictions from Ecosim corresponded fairly well with the abundance and catch data of commercial fish, sea lions, and other mammals (Fig. 4). Ecosim predicted that both small mammals and sea otters would have declined starting in the mid-1970s. However, predictions for small mammals are difficult to evaluate given the paucity of the data and a general lack of information. In the case of sea otters, the observed decline in recent years was not completely explained by the model, the slope of the decline not being steep enough to mimic the observed sea otter depletion.

Ecosim predictions for Atka mackerel matched the stock assessment trends, except for the 1970s and late 1990s. In addition, Ecosim predicted that the 1960s biomass would be similar to that of 1992 (~13 t·km⁻²). It should be mentioned here that the parameters used to fit Atka mackerel had a direct impact on the trajectory of sea lions after 1977. By assuming a vulnerability of about 2 for Atka mackerel, the declining slope shifted to the left starting in the 1980s, suggesting an earlier decline of sea lions, while a lower vulnerability (<1.5) resulted in a sea lion decline occurring closer to the reference data (Fig. 4). The lower vulnerability indicates that sea lions were eating Atka mackerel at close to the maximum rate limited by mackerel behaviour.

The 1963 walleye pollock biomass was estimated at ~6–8 t·km⁻², which was similar to that of the 1990s. According to data, Pacific halibut increased by about threefold between 1980 and 2002, and this was well reproduced by the model predictions. In addition, the model predicted a Pacific halibut biomass of 0.4 t·km⁻² in 1963 or twice as much as that of 1980 (0.17 t·km⁻²). The trends observed for the Pacific ocean perch were mainly dominated by the large overexploitation of the 1960s. However, it was impossible to recreate the high level of catches of the 1990s suggested by the data (Fig. 4). The trends for arrowtooth flounder, Pacific cod, and sablefish were only vaguely similar to the time series. As expected, Ecosim could not capture the dynamics of salmon because most aspects of the species' life histories occur outside of the study area. In the Aleutians, however, salmon is only a minor player (in the sense of being a minor prey for sea lions) and did not have much impact on the model outcome.

The simulations indicate that fishing, environmental variations, killer whale predation, and competition with Pacific halibut were all important factors in determining the Steller sea lion population trajectory. We therefore examined each of these factors individually in terms of their direct effect on sea lion numbers using the SS between the baseline sea lion trajectory and the abundance time series as a measure of fit. The SS of the best-fitting model (using all factors) was 164. Ecosim captured the increase of sea lion abundance that

Fig. 4. Comparison of the reference (a) biomass (t·km⁻²) and (b) catch (t·km⁻²·year⁻¹) times series data (squares) and Ecosim predictions (lines) for 12 functional groups in the Aleutians model. The dotted lines show the effect that increasing the vulnerability of Atka mackerel and Steller sea lions (*Eumetopias jubatus*). The thin line for sea otters (*Enhydra lutris*) in panel a shows the trajectory abundance in the absence of killer whales (*Orcinus orca*). Triangles indicate forced catches.

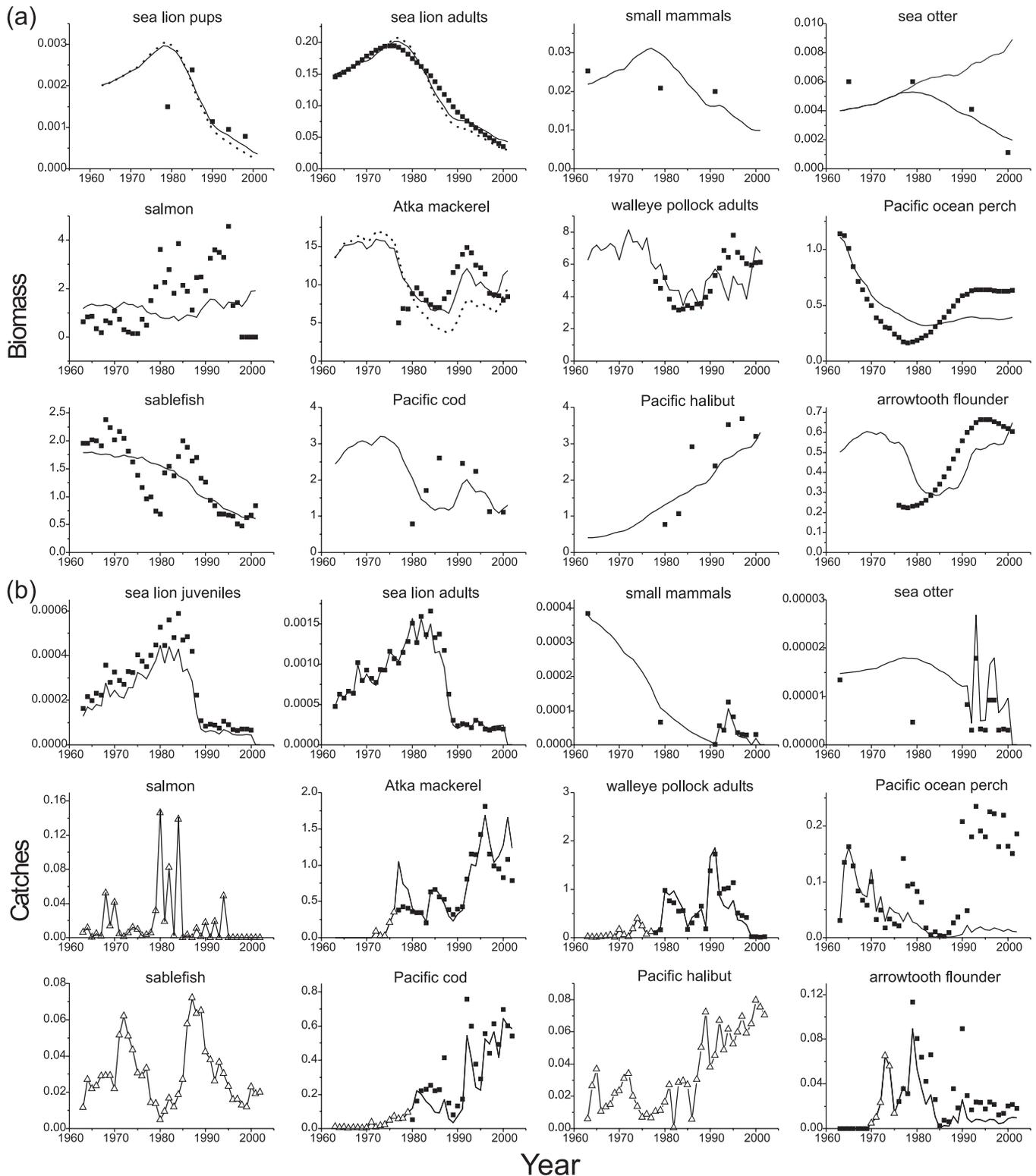
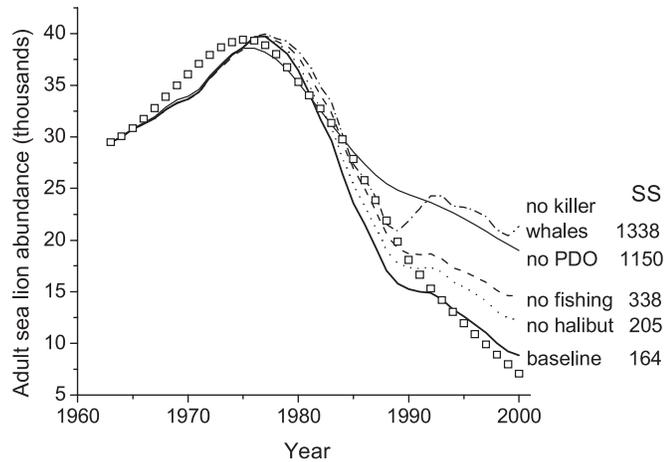


Fig. 5. Relative impact of removing (i) Pacific halibut (*Hippoglossus stenolepis*) and (ii) killer whales (*Orcinus orca*), (iii) banning fishing, and (iv) removing the Pacific Decadal Oscillation (PDO) from the model, starting in 1975. The reference time series is represented by squares, and the sums of squares (SS) are given for each scenario.



occurred in the 1960s because of the influence of the PDO, but when the effect of the PDO was removed starting in 1975, the model predicted that sea lions would have only declined by a small number from 1975 to 1998 (Fig. 5). The resulting SS was 1150.

Depleting killer whales starting in 1975 showed that Steller sea lion numbers would have still declined but that the decline would have been less extreme (SS = 1338). The model indicates that sea lions would have declined until 1989, then increased abruptly between 1989 and 1992, followed by a soft decline thereafter. The abrupt change in 1989 is linked to the increase of Atka mackerel biomass during this period (Figs. 4 and 5). In the absence of killer whales, the model predicted that sea lions would become more abundant and would have inflicted more predation mortality on Atka mackerel. This in turn would have caused sea lions to increase the time they spent feeding, as well as exposed them to higher predation risks.

A simulated ban on fishing starting in 1975 lessened the Steller sea lion decline compared with the baseline (Fig. 5). However, the impact was not as important as that of the other scenarios, increasing the SS to only 338. Atka mackerel, being the preferred prey and the principal fishing target, explained 63% of the effect of banning fishing.

In the absence of Pacific halibut, for which we simulated a depletion starting in 1975, Steller sea lions maintained a higher level of abundance than the best fit trajectory, for a total SS of 205 (Fig. 5). The impact from Pacific halibut depletion was the least important of the four factors considered. The competition between sea lions and halibut was mainly due to their common prey, Atka mackerel. As the predicted halibut biomass increased ninefold between 1963 and 2000 (Fig. 4), the predation mortality inflicted by halibut on Atka mackerel was predicted to rise from 0.005 to 0.04 year⁻¹.

It is noteworthy that the factors examined above have the same relative effect on the ecosystem overall as they do on Steller sea lions alone. Thus, the strongest effect on most ob-

served groups was climate, while the absence of killer whales had the second most important effect, followed by fishing and Pacific halibut competition. It is interesting that the model predicts an increase in the abundance of sea otters in the absence of killer whales (Fig. 4).

Southeast Alaska

For the SE Alaska model, Ecosim predicted that Steller sea lion abundance would generally increase between 1963 and 2002 (Fig. 6). However, Ecosim predicted that the abundance of sea lions decreased in the 1960s–1970s, reaching lower levels than what the reference time series suggested. In addition, it was impossible to emulate the continuous increase of the 1990s. The reasons for these discrepancies will be explored below.

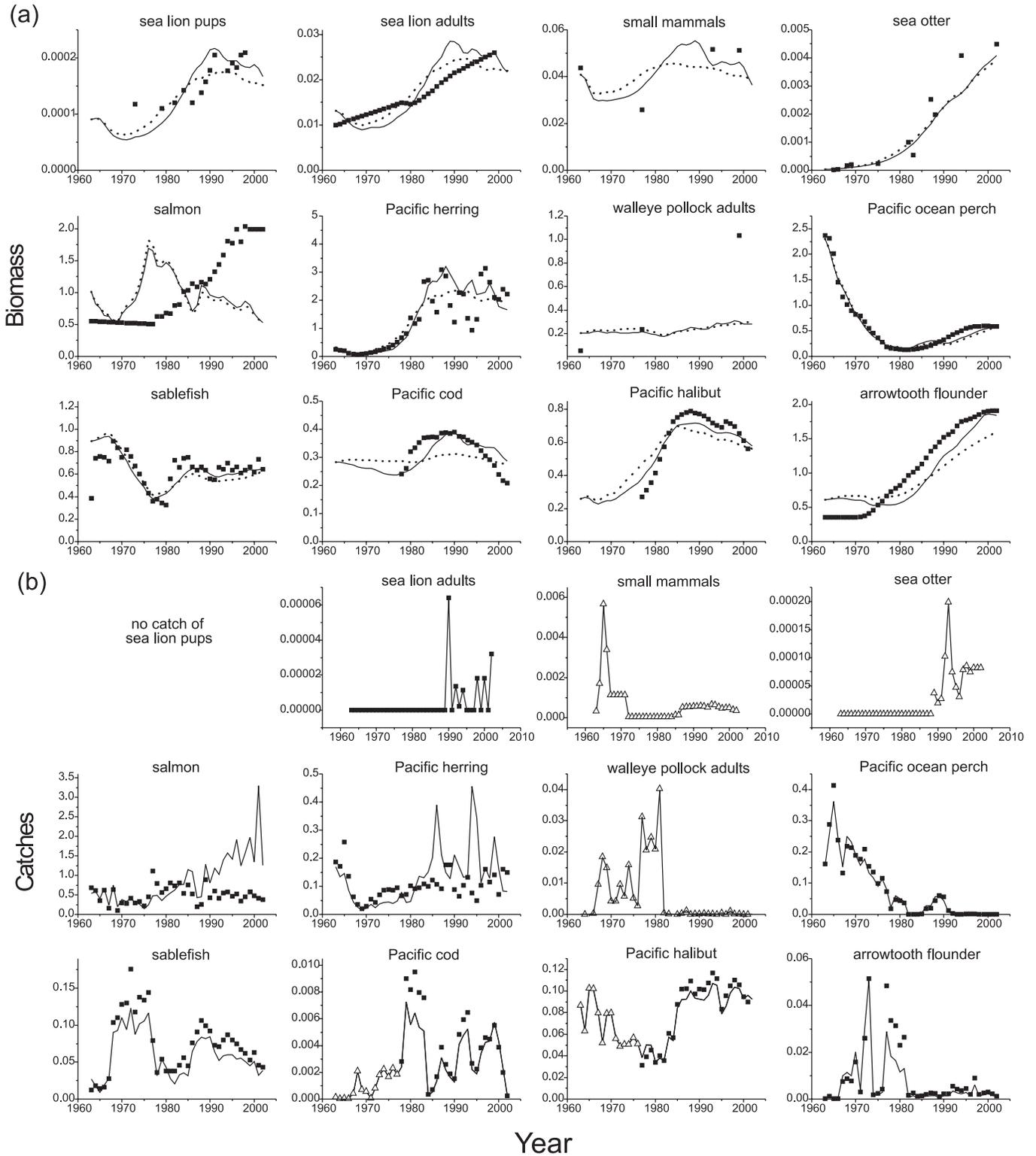
As for the preceding model, the SE Alaska model failed to capture the dynamics of salmon because most aspects of the species life histories occur outside of the study areas. However, Ecosim predictions were quite close to the observed biomass for Pacific herring, Pacific ocean perch, sablefish, Pacific cod, and arrowtooth flounder (Fig. 6). Pacific herring was predicted to increase at the end of the 1970s and stayed high in the following years. However, the highly variable herring recruitment was not captured by Ecosim. Annual mortality caused by killer whale predation on sea lion pups reached 0.34 in 1963, a value similar to that of the Aleutians. However, contrary to the Aleutians model, mortality decreased through time (to 0.26 year⁻¹ in 2002) as sea lion biomass increased. Sea otters only increased if the vulnerability parameter of otter prey was increased. Unfortunately, the data available and included in the model offered no further insights into sea otter dynamics (Gu nette 2005).

Simulations showed that Pacific herring and salmon biomass, environmental variations, competition with arrowtooth flounder, and killer whale predation were factors that could impact the Steller sea lion abundance trends. The SS between the baseline scenario and the reference time series reached 112. When ignoring the PDO, the biomass trajectory of Pacific halibut, Pacific cod, and especially Pacific herring was flattened considerably (Fig. 7a). The impact of the PDO was more obvious on Pacific herring for which the increase of the late 1970s was lessened to half of the observed peak biomass. As a consequence, Ecosim predicted that the sea lion trajectory would be flattened (Fig. 7a), decreasing less in the 1970s, and reaching lower levels in the 1990s; thus the SS increased to 119.

A simulated depletion of killer whales starting in 1963 resulted in a steady increase in Steller sea lion abundance for the whole study period and yielded the highest SS (203). Depleting arrowtooth flounder caused sea lion abundance to increase more steeply in the 1980s, but still caused sea lion numbers to flatten out in the 1990s. Under this scenario, the SS decreased to 77. It is worth noting that Pacific herring predation mortality caused by arrowtooth flounder increased over time (threefold) as arrowtooth flounder abundance increased (sevenfold). Depleting Pacific halibut did not have any substantial effect on sea lion abundance.

Simulating a ban on Pacific herring fishing starting in 1963 resulted in Steller sea lions increasing steadily and reaching a higher level of abundance than the baseline by the late 1960s. Sea lion numbers started to decline in the

Fig. 6. Comparison of the reference (a) biomass ($t \cdot km^{-2}$) and (b) catch ($t \cdot km^{-2} \cdot year^{-1}$) time series data (squares) and Ecosim predictions (lines) for 12 functional groups in the Southeast Alaska model. The dotted lines show the impact of ignoring the Pacific Decadal Oscillation in the Ecosim simulations for each functional group. Triangles indicate forced catches.

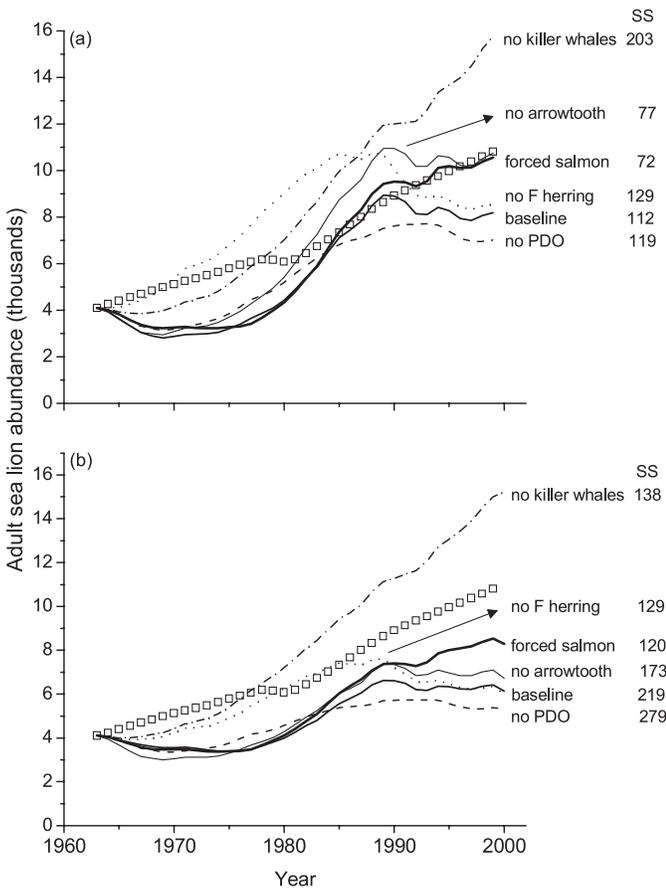


mid-1980s probably because of the failure of the model to account for increases in salmon (Fig. 7a). This scenario increased the SS to 129. Forcing the salmon biomass to match the times series, however imprecise it was, caused sea lion

abundance to continue increasing during the 1990s, following the data trend quite closely and reducing the SS to 72 (Fig. 7a).

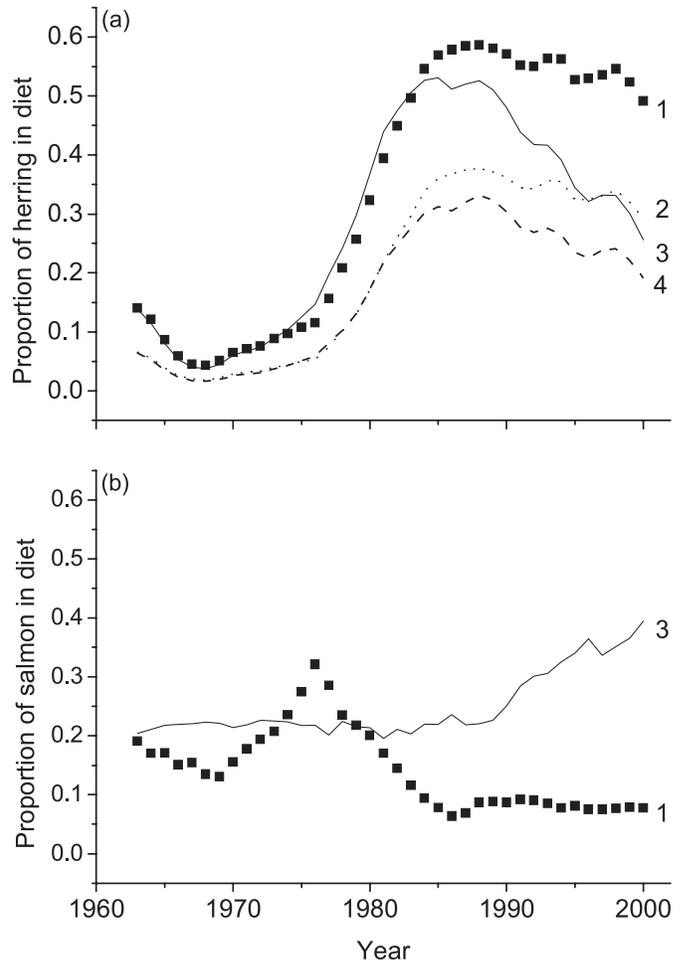
Based on the many studies that have either used Ecopath alone or have used Ecopath with Ecosim without time series

Fig. 7. (a) Relative impact of removing (i) killer whales (*Orcinus orca*) and (ii) arrowtooth flounder (*Atheresthes stomias*), (iii) banning Pacific herring (*Clupea pallasii*) fishing (no F herring), (iv) removing the Pacific Decadal Oscillation (PDO), and (v) forcing salmon biomass in the Southeast Alaska model. (b) Relative impact of the same scenarios when the proportion of herring in the initial Steller sea lion (*Eumetopias jubatus*) diet was reduced. The sums of squares (SS) for each scenario are provided.



data, it is common to assume that the initial diet is crucial to the outcome of simulations. To verify this, we used Steller sea lion predation on Pacific herring in the GOA as an example of how the initial parameters have a limited influence on model outcomes. If the proportion of herring in the initial sea lion diet had been reduced to 7% instead of 15% of the working model, sea lions would not have increased as much (Fig. 7b). The trajectories of sea lion abundance resulting from each scenario tell a similar story about the relative importance and relative effect of each scenario, except that a change herring abundance would have a lesser impact on sea lion abundance if herring was initially less important in the sea lion diet, as demonstrated by the relative SS (Fig. 7b). When salmon biomass was not forced, the trajectories of proportion of herring in the sea lion diet followed similar general patterns over time because of the increase in herring in the ecosystem (Fig. 8a). The proportion of herring in the sea lion diet in 1999 reached 52% for the initial herring scenarios and 32% for the reduced herring scenarios. Forcing salmon biomass resulted in Ecosim predicting that the proportion of herring in sea lion diet would decline starting in

Fig. 8. Trajectories of the proportion of (a) Pacific herring (*Clupea pallasii*) and (b) salmon (*Oncorhynchus* spp.) in the Steller sea lion (*Eumetopias jubatus*) diet in the Southeast Alaska model under four scenarios: (1) original sea lion diet; (2) sea lion diet reduced in herring; (3) original diet and forced salmon; (4) reduced diet and forced salmon.

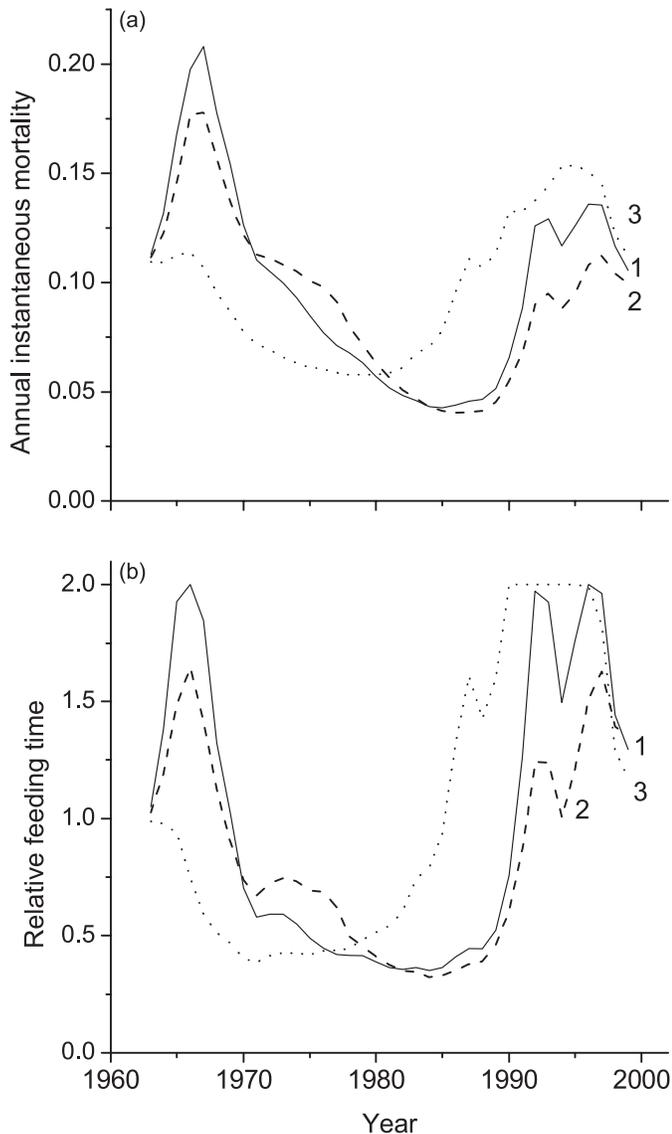


the late 1980s, reaching 30% in the original diet scenario and 22% in the reduced diet scenario in 1999. Thus, the dynamics of predation on herring resulted in a proportion of herring in sea lion diet that is comparable with that used in the original diet used in the balanced 1999 model (26%). In comparison, when the salmon was forced, its biomass increased in the 1980s–1990s, and thus, the proportion of salmon in the sea lion diet would increase (Fig. 8b).

Predation on Steller sea lions results from a combination of killer whale abundance, killer whale diet preference, and the risk that sea lions take to find their prey. Sea lion mortality and feeding time increased in the 1990s as salmon biomass plummeted in the baseline model. Forcing salmon biomass to increase in the 1990s resulted in less sea lion mortality (Fig. 9a) as their feeding time decreased (Fig. 9b). Similarly, in absence of fishing for Pacific herring, sea lions' feeding time and total mortality decreased in the 1960s–1970s (Fig. 9).

The present model did not capture the increase in walleye pollock biomass (Fig. 6) suggested by admittedly very sparse data (Alton 1981; M. Sigler, National Marine Fisheries Service, Auke Bay Laboratory, 11305 Glacier Highway, Juneau,

Fig. 9. Southeast Alaska adult Steller sea lions (*Eumetopias jubatus*) total annual instantaneous mortality (a) and relative feeding time (b) for three scenarios: (1) baseline, (2) forced salmon (*Oncorhynchus* spp.) biomass, (3) no fishing for Pacific herring (*Clupea pallasii*).



AK 99801, USA, personal communication). However, recent studies show that walleye pollock is consistently present in feeding areas such as Benjamin Island (SE Alaska) and constitute a reliable prey for Steller sea lions, being found in 86% of scats (Womble and Sigler 2006). In contrast, larger scale studies in SE Alaska show frequency of occurrences of about 50% (Trites et al. 2007). Given the small initial walleye pollock biomass in the model, their contribution to sea lion diet is quite small (around 5%). We wanted to verify the impact of walleye pollock on sea lion trajectories when (i) the initial biomass and the biomass accumulation were higher and (ii) walleye pollock contribution to sea lion diet was increased to 12%. However, none of these scenarios caused a major change in the sea lion trajectory.

Discussion

The choice of the model area delimitation corresponded to Steller sea lion population trends and perceived homogeneity of ecosystem features based on oceanography, fish composition, and geography. Our goal was to minimize the occurrence of contradictory sources of variation affecting the trend in sea lion abundance within a model area. We expected that a coastal model would be suited for sea lions as well as other coastal species. The downside of this approach is the lack of fit to the data for species that have a larger distribution area and depend less on the modelled area. For these species, the usual approach is to assume that the population of the modelled area is proportional to the biomass estimated by area, which in Alaska determines the level of catch allocated in each area. All of the population dynamics are then assumed to happen within the model area. This can be true and sufficient in some cases and can explain some discrepancies in other cases. The sablefish population is a good case at hand, as it is considered a single stock and yet shows substantial movement among the Bering Sea, the Aleutian Islands, and the GOA. Its preferred habitat is the eastern GOA, which may explain in part why the match to sablefish biomass time series data was better in SE Alaska than it was in the Aleutians model.

SE Alaska and the western Aleutian Islands are dynamic ecosystems influenced by a combination of factors that have to be considered simultaneously to explain the events of the past 40 years. In both case studies, the ecosystem models successfully reproduced the Steller sea lion abundance trends as well as those of other exploited groups of species. Admittedly, there is a lack of information for diets in the 1960s as well as abundance data for important species such as Atka mackerel, Pacific halibut, and walleye pollock. However, a number of our simulations confirmed that the initial dietary values were not as important as the rates of change of biomass through time. Simulations that used dramatically different initial biomass estimates of Atka mackerel showed that it is unlikely that the biomass trajectories between 1963 and 1980 could have differed much from our predictions and still yielded the reported fishing catches irrespectively of their importance to predator diets (S. Guénette, unpublished data). Data is admittedly missing on forage fish trends in this region and could modify the model behaviour if we could have included their dynamics. The biomass trajectory of walleye pollock in SE Alaska is largely unknown, although localized estimates suggest that walleye pollock abundance increased since the 1970s. Our simulations suggest that walleye pollock had a secondary role in determining sea lion abundance trajectories in both ecosystems during this study period. However, their role may change as walleye pollock and Pacific hake (*Merluccius productus*) increase in SE Alaska. Finally reducing the proportion of Pacific herring in the sea lion diet changed the absolute rate of increase of sea lions but did not appreciably change the relative importance of each of the important controlling factors in the SE Alaska model.

According to Ecosim predictions, change in ocean productivity and killer whale predation explain a large part of the Steller sea lion decline in the Aleutians, while fishing

and competition with Pacific halibut also played a role. Fishing was important mainly through its impact on Atka mackerel. In SE Alaska, Ecosim predictions did not follow the sea lion data as closely as it did in the Aleutians model. Simulations suggested that Pacific herring and salmon biomass, killer whale predation, competition from arrowtooth flounder, and the 1976–1977 change in ocean productivity could explain the continuous increase in sea lions between 1963 and 2002. The increase in abundance of sea lions in SE Alaska in the 1970s–1980s paralleled the increases in herring and salmon. The discrepancy between observations and model predictions in the 1960s–1970s reflected the depletion of herring by fishing, killer whale predation, and the PDO, while in the 1990s, the model did not capture the increase of salmon.

Loughlin and York (2000) noted that Steller sea lions in both regions of Alaska experienced similar sources of mortality (i.e., killer whale predation, the influence of PDO on fish trajectories, and the influence of fishing). One exception was that subsistence hunting only occurred in the Aleutians. The index of ocean productivity (the PDO) had inverse effects in the two ecosystems studied and caused downward trajectories in several species of fish in the Aleutians in contrast with the upward trends in SE Alaska. However, ocean productivity impacted the Aleutians model more than the SE Alaska model. It is also clear that Pacific herring recruitment success was due to a combination of factors and was not the sole result of the PDO. This is to be expected in an environment where glaciers, bays, streams, and fjords have an influence. The models suggest that fishing played a structuring role in the dynamics of both ecosystems mainly through removing Atka mackerel in the Aleutians and herring in SE Alaska. Given the initial settings, sea lion mortality caused by killer whale predation in 1963 was equivalent in both models, but followed different trajectories. The impact of killer whale predation had the greatest impact when sea lion abundances were low (i.e., in the 1990s in the Aleutians and in the 1960s in SE Alaska).

The competition with large flatfish was one of the more interesting predictions of the simulations. Pacific halibut in the Aleutians and arrowtooth flounder in SE Alaska have increased dramatically in the last 40 years. The impact of these large flatfish is relatively small compared with the other factors, but their predatory effect on the most important prey species of their respective ecosystems makes them important over time. Halibut does not seem to play this role in SE Alaska probably because it did not increase as dramatically and it is only a minor competitor for Pacific herring. The competition with flatfish has also been pointed out in simulations with the Eastern Bering Sea models in two different contexts. Simulations from the 1980s Bering Sea model highlighted considerable overlap in diet of Steller sea lions and large flatfish and showed that their removal could increase the sea lion populations (Trites et al. 1999). Using a slightly different model for the Bering Sea, Aydin (2002) showed that increasing the fishery for flatfish and, depending on the initial assumptions, a decrease in the walleye pollock and Pacific cod fisheries could also result in an increase in sea lions.

The biomass of killer whales and their prey preferences are highly uncertain in both ecosystem models. In such models, the proportion of the diet made up by any one species depends on the initial diet used in the model and the changes in biomass that occur in the ecosystem. In the Aleutians, results showed that killer whale biomass and the proportion of Steller sea lions in their diet needed to be high in order for the observed 1990s decline in sea lions to have occurred. The model also assumed a strong predator–prey relationship existed between both species. However, other plausible scenarios of predation and behaviour cannot be discounted. For example, the same end results could have been obtained if several pods of killer whales had started to specialize in hunting sea lions in the 1980s (e.g., Matkin et al. 2002). For instance, the “Kodiak killers”, a group of six killer whales that frequents the waters around Kodiak Islands (GOA), are believed to have specialized hunting on sea lions (NPUMMRC 2006). There are other indications that some killer whales may develop specialized hunting behaviour, such as attacking sea otters (Estes et al. 1998), gray whale calves (*Eschrichtius robustus*) (Matkin et al. 2006), or beluga whales (*Delphinapterus leucas*) (Shelden et al. 2003) in difficult to access areas in spite of dangers of getting stranded (Frost et al. 1992). The structure of our model does not account for pod-based changes in behaviour. However, there seems to have been little incentive for killer whales to switch prey types given the high initial abundance of sea lions and the small number of killer whales in the Aleutians. The SE Alaska model also assumed a strong predator relationship between killer whales and sea lions, but the low numbers of sea lions could only have constituted a small proportion of the killer whales’ diet in the 1960s. Furthermore, there was no incentive for killer whales to switch to sea lions at any given time in the simulations, since there were always enough small mammals in the ecosystem model for them to consume.

Models that considered only the predator–prey relationships between transient killer whales and Steller sea lions yielded different conclusions about the potential impact of killer whales. Considering the central and eastern Aleutians, Springer et al. (2003) used a ratio of transient killer whales to sea lions of about 0.0025, which is similar to that of our SE Alaska model and 10 times larger than that calculated for our Aleutians model. Although Springer et al. (2003) were not explicit on the proportion of sea lions in killer whale diets, they suggested that it would take only a small change in diet to cause the sea lion decline. In contrast, our model results suggest that it would take a large change in diet to have provoked the decline. Other attempts to test the sequential megafaunal collapse theory have also failed to find support for the assumptions and conclusions drawn by Springer et al. (2003) (see DeMaster et al. 2006; Trites et al. 2006a; Wade et al. 2006).

Barrett-Lennard et al. (1995) modelled the effect of killer whales on Steller sea lions using a low proportion of sea lions in the killer whales’ diet (10%–15%), an estimate of 258 killer whales, and a maximum of 200 000 sea lions in the entire Northeast Pacific (Aleutian Islands to northern Washington coast), for an abundance ratio of 0.001. They found that depending on the functional predator–prey relationship (type II or III), the number of killer whales that

would maintain the sea lion population constant would vary from 200 to 275 killer whales given an initial population of 200 000 sea lions. Our model results showed that when sea lion numbers declined in the Aleutians, predation mortality increased, although the importance of each species prey in the killer whales diet shifted slightly. In addition, our model results suggested that a low proportion of sea lions in the killer whale diet would not have been sufficient to cause a decline in killer whales in the 1990s. Barrett-Lennard et al. (1995) favoured the type III functional response based on observations that killer whales can specialize to hunt other species, and sea lions can use rookeries as refuge. Our model produces a type III functional response because sea lions alter their behaviour and remain in refuges for larger periods as their abundance decreases. However, our model did not explicitly consider a change in killer whale predatorial behaviour (though this would be straightforward to include).

Using the 1950 Bering Sea ecosystem model (Trites et al. 1999) and Ecosim predictions, a National Research Council committee was unable to fit the observed abundance trajectories for fish and Steller sea lions (National Research Council 2003). The National Research Council committee did not use any of the Pacific production indices (e.g., PDO) to force primary production anomalies (although they did use a forcing function estimated by Ecosim) and were unable to test the hypothesis of increased killer whale predation because they did not consider transient killer whales separately. Nevertheless, their modelling exercise showed that fishing and sea lion killings alone were insufficient to explain the decline.

The two ecosystems we considered did not allow us to examine the relationship between the increase in Pacific herring and walleye pollock because walleye pollock fishing was not important in these two areas. Further work should concentrate on the Bering Sea and the central GOA to examine these questions. The ecosystem modelling was successful at integrating climate, competition, fisheries, and predation as potential causes of change in each ecosystem. It appears that climate impacted several species in both ecosystems, including species such as Atka mackerel and Pacific herring that form an important part of the Steller sea lion diet. Thus, change in ocean productivity appears to have had a major, indirect effect on sea lions. Fishing was important on target species and dominated the definition of biomass trends for several of them (e.g., sablefish and Pacific ocean perch) but did not seem to change the structure of the ecosystems. The direct effects of fishing appeared as a secondary factor in determining sea lion abundance in both ecosystems, although simulation results suggest that killer whale predation increased as feeding time increased in SE Alaska. Given the very large initial numbers of sea lions in the Aleutians, killer whale predation seems to not have played a role in the sea lion decline until the mid-1980s when sea lion numbers were substantially lower.

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