Ecosystem Models of the Aleutian Islands and Southeast Alaska Show that Steller Sea Lions are Impacted by Killer Whale Predation when Sea Lion Numbers are Low

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Abstract. We constructed ecosystem models using the Ecopath with Ecosim software to evaluate whether predation by killer whales might explain the decline of Steller sea lions since the late 1970s in the central and western Aleutian Islands. We also sought to understand why sea lions increased in the presence of killer whales in Southeast Alaska. Modelling results reproduced the time series of abundances for exploited species and sea lions in both ecosystems. Simulation results suggest that killer whale predation contributed to the decline of sea lions in the central and western Aleutians, but that predation was not the primary cause of the population decline. However, predation could have become a significant source of mortality during the 1990s when sea lion numbers were much lower. In Southeast Alaska, predation was also determined to be a significant source of mortality in the 1960s when sea lions were low, but ceased to control population growth through the 1980s and 1990s. Overall, the ecosystem models suggest that large populations of Steller sea lions can withstand predation, but that small populations are vulnerable to killer whales.

Introduction

Steller sea lions declined in the Aleutian Islands and Gulf of Alaska from the late 1970s to the late 1990s, while the population in Southeast Alaska and British Columbia increased (Trites and Larkin, 1996; Calkins and others, 1999). Various hypotheses have been formulated to explain the declines, including an increase in predation by transient (marine-mammal eating) killer whales in the west compared to the eastern portion of the sea lion range (National Research Council, 2003; Springer and others, 2003). A second hypothesis is that the carrying capacity for sea lions is lower due to bottom-processes that affected the relative abundances of prey available to sea lions in the Gulf of Alaska and Aleutian Islands (Trites and others, 2006b). A third hypothesis is that the large-scale fisheries modified the ecosystem structure and function to the detriment of the western population of sea lions (Alverson, 1992; Dillingham and others, 2006).

Our objective was to reproduce the observed times series of species abundance in southeast Alaska and the central and western Aleutians and to examine the possibility that marine mammal eating killer whales (transient) were responsible for the decline of Steller sea lions in the central and western Aleutians.

Methods

The Model

Ecosystem models account for the biomass of each functional group of species, their diet composition, consumption per unit of biomass, mortality from predators and fishing, accumulation of biomass and net migration. The principle behind this ecosystem modelling approach is that, on a yearly basis, biomass and energy in an ecosystem are conserved. We built models for southeast Alaska and of the central and western Aleutians for 1963 using the Ecopath with Ecosim software (EwE) (Christensen and Walters, 2004). The Aleutians Islands are contained within 170°E and 170°W around the islands, to the 500 m depth contour, for a total area of 56,936 km^2. The eastern cut off point was Carlisle Island and did not include Unimak Pass, a known aggregation area for marine mammals. The Southeast Alaska study area consisted of the continental shelf east of 140°W to 1,000 m depth and included the eastern part of the Yakutat region (140–137°W) and the coastal region east of 137°W. The southern limit was the border between British Columbia and Alaska (Dixon Entrance).

The models each comprised 39 functional groups, and were built with the Steller sea lion and their principal prey species in mind (see Guénette and Christensen, 2005). Commercially important species were considered separately to ensure that we adequately accounted for the most important fisheries. Catch, biomass, and fishing mortality for 1963–2000 were assembled from stock assessment reports and related publications. Starting from 1963 we fitted our models to biomass and catch data using time series of fishing mortality. The criterion was a weighted sum of squares of deviations (SS) between logarithms of observed and predicted biomasses and catches, for all species for which time series were available. The Pacific Decadal Oscillation (PDO) was used to modify primary productivity and account for changes in oceanic productivity in the Pacific Ocean (Hare and Mantua, 2000; Benson and Trites, 2002). Monthly values of PDO (http://jisao.washington.edu/pdo/PDO.latest) were transformed to obtain a range of one and were used directly in Southeast Alaska, to improve the fit to the time series. In the Aleutians, it was necessary to use the inverse PDO (Heymans, 2005). This

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is consistent with the fact that the PDO is inversely related to sea surface temperature in the Aleutians and positively correlated in Southeast Alaska (Mantua and others, 1997). During the simulations, the proportion of a prey in the diets of their predators was allowed to change in response to changes in biomass.

The Data

As all of the data used in our model cannot be listed here, we only summarise the abundance data for sea lions and killer whales, which directly pertains to the objectives of our paper. Of the 219 transient whales catalogued so far in the Pacific Northwest, 6 percent have only been seen in SEAK, 50 percent have been seen in SEAK and BC, and 44 percent in British Columbia and Washington (Ford and Ellis, 1999). Transients are believed to be constantly on the move and may cover large distances within a month (Ford and Ellis, 1999). Thus, we assumed that 123 transients were present in Southeast Alaska during the 1990s and that they stayed in SEAK for 2–3 months and travelled as far as Washington State in other months. This amounted to 24 whales year round in Southeast Alaska.

Attacks and killings by killer whales in British Columbia and Southeast Alaska have been observed on harbour seals (53 percent), Steller sea lions, Dall's porpoises, and harbour porpoisse (Ford and others, 1998). Minke and gray whales remains have been found in stomachs of stranded whales (Ford and others, 1998; Ford and Ellis, 1999; Ford and others, 2005; Mizroch and Rice, 2006). Harassment and killing of birds were rarely followed by consumption and are thought to be hunting skill practice (Matkin and Dalheim, 1995; Ford and others, 1998), and given their body weight, their contribution was set at 1 percent. We assumed that a large proportion of the sea lions attacked were pups and juveniles (<3 yrs old) as killer whales spend more time around haul-outs and near-shore areas during the pupping season (Heise and others, 2003). Mentions of deer and river otters (Matkin and Dalheim, 1995) were classified as imports and were given a weight of 2 percent in the SEAK model. Sea otters were never seen attacked in SEAK, presumably because of their odour, low fat, and dense fur (Matkin and Dalheim, 1995). In addition there is sufficient numbers of the preferred prey of killer whale, namely harbour seals and seal lions in the system.

For the Aleutians, the diet was adapted to include 78 percent small mammals (seals and porpoises), 1 percent birds, 4 percent sea otters, 16 percent Steller sea lions and 1 percent baleen whales. The baleen whales were reduced from 3 percent to 1 percent. The percentage of sea otters in the diet was set at 4 percent. The 16 percent of sea lions in the diet was broken down into 1 percent pups, 9 percent juveniles and 6 percent adults.

Springer and others (2003) estimated that 3,888 killer whales occurred in the 1,080,000 km^2 of water surrounding the Aleutian Islands. We assumed that 7 percent of killer whales were the transient ecotype and that 14 of them were in the area of the models (for a biomass of 0.0006 $t{\cdot}km^{-2}$). An alternative estimate of 63 killer whales was counted by Fiscus and others (1981) in the central Aleutian Islands (from the Rat Islands to the Fox Islands). Assuming that 10 percent (6) of these 63 whales were transients (Waite and others, 2002), the total biomass would be 0.0003 $t{\cdot}km^{-2}$.

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). The number of sea lions increased from 4,960 in 1963 to 21,186 animals in 1999 in Southeast Alaska. In the central and western Aleutians, the population numbered 50,834 animals in 1963, increased to 72,274 in 1979 and declined to 32,296 in 1991.

Results

Ecosim predicted a small drop in sea lion abundance in Southeast Alaska between 1963 and 1973, followed by exponential growth (1973–90) and stabilisation (1990–2002) (fig. 1). The model generally captured the dynamics of all species except for salmon because most aspects of the life history of salmon occur outside of the study areas. This poorer fit of predicted to observed Steller sea lion numbers in the 1990s may be due to the model not adequately describing the dynamics of salmon, as salmon is an important prey. The Southeast Alaska model matched the increase in biomass of arrowtooth flounder, Pacific herring, Pacific cod and Pacific Ocean perch (fig. 1).

For the central and western Aleutians, the Ecosim predictions of sea lion numbers corresponded well with the reference time series—showing an initial increase in the sea lion population followed by a steep decline after 1975 (fig. 2). The model predictions also provided good fits for species such as the Pacific Ocean perch that were mainly influenced by the overexploitation that occurred during the 1960s throughout the Gulf of Alaska (although the model predicted a bigger recovery in the 1980s than what was observed). The predictions for species such as Pacific cod and arrowtooth flounder resembled the time series data while Ecosim predictions for Atka mackerel matched the stock assessment trends except for the 1970s and late 1990s. The model also predicted that the biomass of Atka mackerel in 1963 was similar to that of 1992. Note however the lack of data for the 1960s.

Given the uncertainty about killer whale parameters, we used the model to evaluate the impact of various assumptions about diet and abundance in the central and western Aleutian Islands (fig. 3a). The first scenario assumed a low abundance of killer whales (0.003 $t{\cdot}km^{-2}$) and a low proportion of sea lions in the killer whale diet in 1963 (16 percent); the second scenario assumed a low abundance of killer whales that ate predominantly sea lions (80 percent); and the third scenario assumed high killer whale abundance (0.006 $t{\cdot}km^{-2}$) with a preference for sea lions and high predation levels (80 percent). All scenarios showed the same pattern of decrease in sea lion abundance in the 1980s (fig. 3A). The difference between

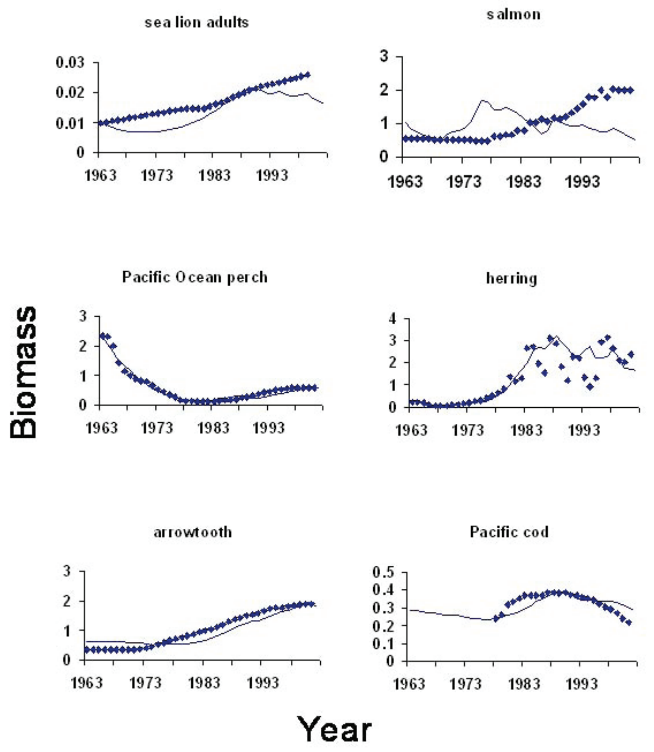

Figure 1. Comparison of observed biomass (t·km^{-2}) (dots) and simulation results (continuous line) for 6 of the principal functional groups of the Southeast Alaska model between 1963 and 2002. The functional groups include Steller sea lion pups (SSL pup) and adults (SSL ad), Pacific herring, Pacific Ocean Perch (POP), Pacific cod, and arrowtooth flounder.

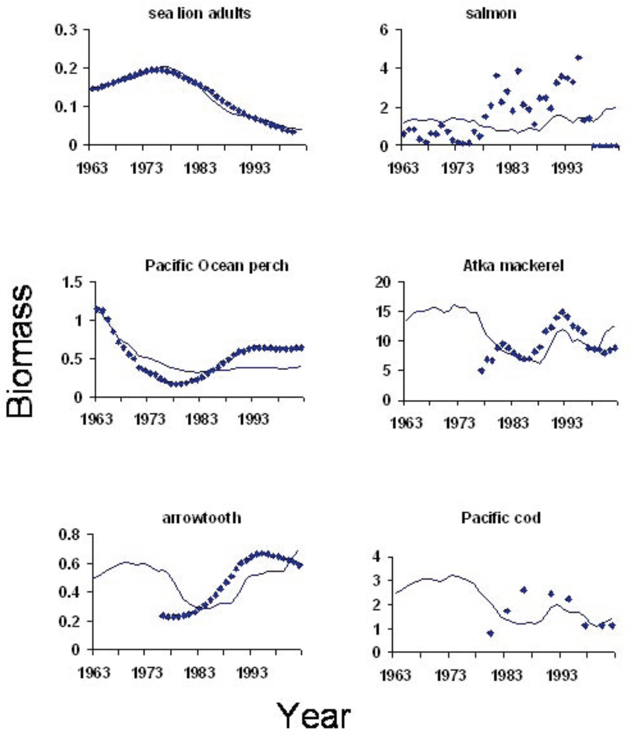

Figure 2. Comparison of observed biomass (dots) and simulations results (continuous line) for the 6 of the principal functional groups of the central and western Aleutian Islands model between 1963 and 2002. The functional groups include Steller sea lion pups (SSL pup) and adults (Steller adult), and Atka mackerel (Atka).

scenarios was the steepness of the decline of sea lions in the 1990s which correspond to increases in predation mortality in the 1990s (fig. 3A). Sea lion abundance predicted using Scenario 3 were the closest to the observed time series data while light levels of predation result in a smaller decline in sea lion abundance. In contrast, in Southeast Alaska, predation mortality induced by killer whales in the model at its highest in the late 1960s when the abundance of sea lions was low (fig. 3B).

Discussion

For Southeast Alaska, our simulations showed that the model captured the trends of several exploited species but failed to adequately replicate the trends of salmon and Steller sea lions. Further work will be necessary to explain the discrepancy between predictions and observed abundances for sea lions. The simulation results for the Aleutians were problematic because of the lack of data in the 1960s for Atka mackerel, Pacific cod and arrowtooth flounder. The model was not entirely successful at reproducing the trends of several of the exploited species except for Pacific Ocean perch. Further work will be necessary to explore the implications of this lack of data by using various scenarios about initial abundance and diets.

Simulations with various level of killer whale predation on sea lions in the central and western Aleutians suggest that killer whales had the highest impact in the 1990s when sea lion numbers were low. However, the initial abundance of killer whales and the proportion of sea lions in their diet modified the trajectory of sea lion abundance in the 1990s. This emphasises the importance of initial assumptions about the diet preference of killer whales. However, similar results could be obtained if several pods of killer whales increased their dietary preference for sea lions by hunting them more frequently.

The decline in sea lion abundance in the central and western Aleutians can only be explained by killer whale predation if numbers of whales were much higher than current estimates suggest were present, or if Steller sea lions constituted a much bigger (i.e., 80 percent) portion of the killer whale diet than has ever been reported. However, recent information about killer whales in the Aleutians and reviews of existing dietary data for killer whales do not support the higher assumed estimates of diet and numbers (DeMaster and others, 2006; Matkin and others, 2006; Mizroch and Rice, 2006; Trites and others, 2006a). The three simulations shown

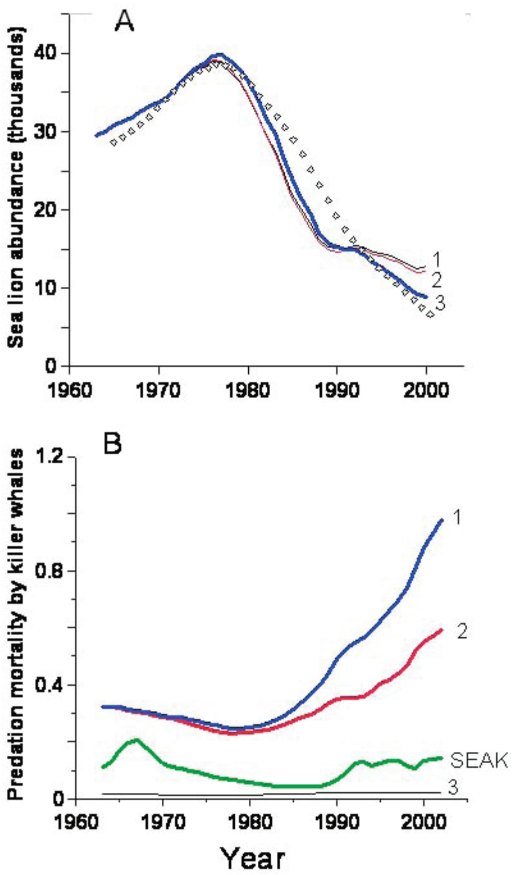

Figure 3. (A) Comparisons of observed sea lion numbers in the central and western Aleutians (dots) with simulation results (lines) corresponding to three scenarios that considered different combinations of whale numbers and dietary makeup: Scenario 1: low killer whale abundance and low (16 percent) predation on sea lions; Scenario 2. high killer whale abundance and low (28 percent) predation; Scenario 3. high killer whale and high predation (80 percent). and (B) Trajectory of adult sea lion mortality in Southeast Alaska and the central and western Aleutians.

in figure 3a imply that Steller sea lions would have declined during the 1980s in the absence of killer whales (given the small difference between scenarios), and that the most pronounced effect of killer whales would only have occurred when sea lion numbers were low (i.e., during the 1990s).

This modelling exercise is a first step in trying to examine the effect of killer whale predation on sea lions within the framework of an ecosystem model that includes fishing. Further work is needed to delineate the relative impact of fishing, predation, and ocean productivity on the sea lion abundance trends in both ecosystems.

Implications

The ecosystem model built for Southeast Alaska could be modified to address concerns of Glacier Bay National Park. It could be used to compare and rank the various hypotheses about the trends in harbour seals in Glacier Bay. This would require careful compilation of the catch and abundance of harbour seals throughout its geographical range to give a basis for comparison and to provide some insight into the regional declines of harbour seals.

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