

## KILLER APPETITES: ASSESSING THE ROLE OF PREDATORS IN ECOLOGICAL COMMUNITIES

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**Abstract.** Large body size, carnivory, and endothermic costs lead to exceptionally high caloric demands in many mammalian predators. The potential impact on prey resources may be marked but is difficult to demonstrate because of the mobility, sparseness, and cryptic nature of these animals. In this study, we developed a method based on comparative bioenergetics and demographic modeling to evaluate predator effects and then used this approach to assess the potential impact of killer whales on sea otter and Steller sea lion populations in the Aleutian Islands. Daily caloric requirements of killer whales determined from allometric regressions for field metabolic rate show that an adult killer whale requires 51–59 kcal·kg<sup>-1</sup>·d<sup>-1</sup> (2.5–2.9 W/kg). Caloric values of prey items determined by bomb calorimetry ranged from 41 630 kcal for an adult female sea otter to sequentially higher values for male otters, sea lion pups, and adult Steller sea lions. Integrating these results with demographic changes in marine mammal populations show that fewer than 40 killer whales could have caused the recent Steller sea lion decline in the Aleutian archipelago; a pod of five individuals could account for the decline in sea otters and the continued suppression of sea lions. The collapse of the historical prey base of killer whales due to human whaling may have contributed to a sequential dietary switch from high to low caloric value prey, thereby initiating these declines. This study demonstrates that a combined physiological–demographic approach increases our ability to critically evaluate the potential impact of a predator on community structure and enables us to define underlying mechanisms that drive or constrain top-down forcing in dynamic ecosystems.

**Key words:** Aleutian Islands; caloric intake; community structure; energy consumption; *Enhydra lutris*; *Eumetopias jubatus*; killer whale; metabolism; *Orcinus orca*; predators; sea otter; Steller sea lion.

### INTRODUCTION

Large endothermic predators, by virtue of their size, mobility, and nutritional requirements, have the potential to place extraordinary pressures on their prey populations (Terborgh 1990, Seidensticker and McDougal 1993), which in turn may lead to marked effects on the structure and function of ecosystems (Berger et al. 2001, Soulé et al. 2003). Despite a small number of reasonably compelling case studies (see Estes et al. 2001), few researchers have defined and quantified the ecological roles of large carnivorous predators. This lack of information is not surprising, as direct experimental analyses are extremely difficult due to the sparseness, rapid movements, large ranges, and cryptic nature of these animals. Marine mammals, in particular, often hunt at depth, making the direct assessment of foraging behavior and predator-prey interactions impossible for most species (Davis et al. 1999). Given

these difficulties, theories concerning the role of large carnivores in shaping ecological communities abound, while critical evaluation of these theories is exceptionally rare.

The strength of top-down effects by any predator will be determined by abundance, diet, and per capita consumption rate with the latter dictated by the predator's metabolic rate and the quality of its prey. Many species of eutherian mammals that specialize in vertebrate prey maintain basal metabolic rates that are 1.4–2.0 times higher than predicted by the standard “mouse-to-elephant” curve describing metabolism in relation to body mass (Kleiber 1975, McNab 1986, 1988, Williams et al. 2001). These include carnivorous predators from both terrestrial and aquatic environments such as cheetahs (Taylor and Rowntree 1973) and other felids (McNab 2000), Cape hunting dogs (Taylor et al. 1971), river otters (Iversen 1972), killer whales (Kreite 1995), and bottlenose dolphins (Williams et al. 2001). Although incompletely understood, the comparatively high metabolic demands have been

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attributed to the energetic cost of a carnivorous diet (McNab 1986), mobility, and endothermy.

High caloric demands require a large intake of prey. The resulting effect on an ecosystem will depend in part on predator abundance, the abundance and demography of preferred prey items, and the hunting range of the predators. When hunting is focused in a relatively small area or on specific prey, the predator can have a significant impact. For example, in the case of the sea otter, high caloric demands (Costa and Kooyman 1984), great abundance (Estes 1990), and specialization on sea urchin prey result in strong effects on the nearshore kelp forest community (Estes and Palmisano 1974). Similarly, predation by large mammals may regulate various terrestrial ecosystems through top-down control and trophic cascades (McLaren and Peterson 1994, Crooks and Soulé 1999, Terborgh et al. 1999, 2001, Ripple and Larson 2000, Berger et al. 2001). Admittedly, the effects of such predator-prey interactions can be mediated by prey behavior (e.g., the mere presence of wolves causes elk to avoid high-risk areas; Ripple and Beschta 2003). Demography and physiology, however, set limits for the long-term consequences of such predator-prey interactions.

Here we used bioenergetic analyses in combination with demographic models to evaluate the needs of large predatory mammals and their consequent potential effects on prey populations. Such an integrated analysis, widely employed by fish ecologists (Kitchell et al. 1977, Kitchell 1998, Essington et al. 2002), can be used to refine and test theories of community importance for a wide variety of ecosystems. To illustrate this interdisciplinary approach, we compared the relationship between caloric demand and prey intake of killer whales (*Orcinus orca*) to the demography and nutritional composition of their prey populations. This case study was selected for several reasons. First, the system is empirically intractable due to the remote location and feeding behavior of killer whales. As such, it provides a "worst-case" example for our approach. Second, predation by killer whales has been implicated in the recent declines in pinniped and sea otter populations in the Aleutian Islands (Estes et al. 1998, National Research Council 2003, Springer et al. 2003), but the role of top-down forcing in these declines remains controversial.

## METHODS

### General approach

Four types of energetic information are measured or estimated to calculate the impacts of individual predators on different prey: (1) the caloric needs of individual predators, taking into account differences in body mass and reproductive status; (2) the caloric value of individual prey; (3) the digestive efficiency of the predator, which determines the ability to use caloric energy in prey tissue; and (4) the likely or possible

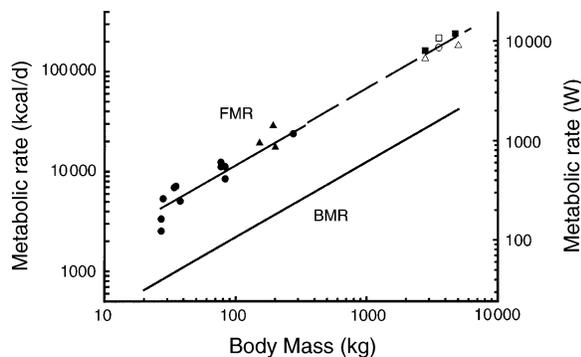


FIG. 1. Field Metabolic Rate (FMR) in relation to body mass for marine mammals. The solid line through the data points is the least-squares linear regression for measured field metabolic rates of pinnipeds (circles) and dolphins (triangles). Calculated FMR values for male and female killer whales in this study are shown by the solid squares; the dashed line indicates the extrapolation from the regression. These values are compared to FMR estimates from pinniped ingestion rates of wild killer whales (open circle; Baird 1994), activity budgets of free-ranging killer whales (open triangles; Kriete 1995), and captive whale food consumption rates (open square; Barrett-Lennard et al. 1995). Pinniped values include Northern fur seals, California sea lions, Antarctic fur seals, and Galápagos fur seals (Costa and Williams 1999); and Steller sea lions (R. Davis, unpublished data). Values for dolphins are from Costa and Williams (1999). The lower solid line is the predicted basal metabolic rate (BMR) of mammals from Kleiber (1975).

prey preferences of individual predators. This information on individual bioenergetics is then compared to population-level estimates of the number of predators, the dynamics of prey numbers, and the demographic rates governing the prey population in the absence of predation. For these analyses, we estimated the population-wide losses to predation needed to generate the observed changes in the prey population if all losses arise from predation (Estes et al. 1998). Using individual energetic analysis, we then determined whether the caloric intake of the predator population would be sufficient to account for these losses.

### Energetic requirements of killer whales

An allometric regression determined from the measured field metabolic rates (FMR) of smaller marine mammals was used to predict the caloric requirements of free-ranging, adult killer whales. Field metabolic rates assessed by the doubly labeled water method have been reported for one species of small odontocete (bottlenose dolphins) and a wide variety of pinniped species (Fig. 1), with remarkably consistent results. Regardless of swimming style, foraging patterns, geographic location, or species, average FMR is nearly six times the Kleiber (1975) calculated basal metabolic rate (BMR; Costa and Williams 1999), or approximately three times measured BMR for marine mammals (Williams et al. 2001). Because the resting metabolic rate measured for killer whales (Kriete 1995) follows trends for

smaller marine mammals, we assumed a similar pattern for field metabolic rate. The following allometric regression developed from the FMR of active pinnipeds and cetaceans was used to predict the FMR of adult female (2800 kg) and male (4733 kg) killer whales:

$$\text{FMR} = 19.65M_b^{0.756} \quad (1)$$

where FMR is in watts and  $M_b$  is body mass in kilograms (Fig. 1). These masses were chosen to represent the average size of mature killer whales of each gender (Dahlheim and Heyning 1999) for whom metabolic measurements were available (Kriete 1995). Note that the calculations are for adults only and assume no growth or reproductive costs. For killer whales, food consumption rates increase with age at least through age 20 years and may be altered by seasonal changes in water temperature and reproductive status (Kastelein et al. 2003). In view of this, the metabolic rates and caloric intake rates presented here are considered conservative estimates of average energetic demands for adult, non-lactating whales.

#### *Energy content of prey items*

Caloric value and water content were determined for tissues from sea otters (*Enhydra lutris*) and Steller sea lions (*Eumetopias jubatus*). Because killer whales typically ingest whole sea otters (see Plate 1) and sea lion pups (Estes et al. 1998; T. M. Williams, *personal observation*), entire carcasses were analyzed. Fresh adult sea otter carcasses were obtained from the Aleutian Islands ( $n = 1$ ) and California ( $n = 2$ ) following accidental death. Similarly, the carcass of a healthy Steller sea lion pup was obtained following accidental injury on a rookery in the Aleutian Islands. Each carcass was frozen ( $-30^\circ\text{C}$ ) within 2 to 24 hours of death until analysis. Frozen carcasses were ground whole and three aliquots taken from the homogenate for calorimetry measurements.

In contrast to smaller prey items, only portions of adult Steller sea lions are consumed by killer whales (Matkin 1994). Skeletal muscle, skin, and fat comprise >60% of the mass of adult Steller sea lions (R. W. Davis, *unpublished data*) and are the primary edible tissues for killer whales. Therefore, only skeletal muscle (*m. pectoralis*) and blubber from fresh carcasses of healthy, adult females ( $n = 2$ ) were analyzed, representing the edible portions of the animal. All tissues were frozen at  $-30^\circ\text{C}$  until homogenized and divided into three aliquots for analysis.

Tissue aliquots from all carcasses were dried to constant mass in a  $100^\circ\text{C}$  oven or freeze dryer over 48 hours. Water content for each sample was determined from the difference between initial and final sample mass. Dried subsamples were pulverized, compressed into pellets, and immediately analyzed. Caloric content for three subsamples ( $\sim 1.0$  g) of each tissue were determined using adiabatic bomb calorimetry (Parr Instrument Company, 1341 Plain Oxygen Bomb Calo-



PLATE 1. Predator versus predator: killer whale (*Orcinus orca*) skull in relation to the sea otter (*Enhydra lutris*) skull. Recent studies indicate that the whales have become the top carnivorous predator in areas of the Aleutian Islands where the Alaskan sea otter was once the major predator. Photo credit: T. M. Williams..

rimeter, Moline, Illinois, USA) at  $22.5^\circ\text{C}$ . The calorimeter was calibrated between samples using benzoic acid standards and was accurate to within 0.1%. The resulting caloric value for each dry tissue sample was converted to wet mass energy values using water contents determined for the original tissues and a conversion factor of 4.1868 joules per calorie.

#### *Demographic analysis*

The Aleutian archipelago defined the geographical range of our demographic analyses because the abundance trends for sea otters are best known for this area (Doroff et al. 2003), and because a substantial proportion of the overall decline in Steller sea lion and sea otter populations has occurred in this region (Estes et al. 1998, Springer et al. 2003). The limited movements of individual sea otters (Garshelis and Garshelis 1984) and sea lions (Calkins and Pitcher 1997) indicate that populations are reasonably closed within these boundaries. Potential influences of killer whale predation on sea lion and sea otter populations were evaluated from pre-decline abundance estimates and Leslie transition matrices that were parameterized with the best available data on age-specific fertility and mortality rates for a stable population. Changes in mortality rates needed to generate the observed patterns of population decline were then determined. Because sea otter and Steller sea lion populations underwent rapid, catastrophic declines (Springer et al. 2003) that exceeded

the rate of reproductive replacement, density-dependent responses were not considered in this analysis.

For sea otters, we used empirically derived estimates from Amchitka Island (Monson et al. 2000), adjusting the mortality rate of the zero age class (birth to one year; absent in Monson et al. 2000) to make the annual population growth rate,  $\lambda$ , equal to one. Our field studies suggested that mortality from killer whale predation was nonselective by sex and age class; thus, in the model we spread the additional mortality evenly across all age classes (Estes et al. 1998). The simulation began with 77 435 sea otters, the estimated pre-decline population size (Doroff et al. 2003). With minimal data on the pattern of decline through time, we fit a model with a constant number of otters lost to predation per year, setting this rate to that needed to generate the observed 78% decline in numbers between 1990 and 1997 on Adak Island and similar declines throughout the Aleutians (Estes et al. 1998, Doroff et al. 2003).

We used a similar but more detailed approach for Steller sea lions. A life table for female Steller sea lions reported by York (1994) was used to parameterize a Leslie matrix of baseline (pre-decline) vital rates. To simulate total population numbers, we assumed that female and male survival rates were the same. The simulation began with a stable age distribution for 70 412 sea lions, the estimated pre-decline population size in the Aleutian Islands (National Marine Fisheries Service [NMFS], November 2000 Biological Opinion, *available online*).<sup>6</sup> Because the size and relative vulnerability of sea lions differ with age (York 1994), multiple simulations were run assuming either elevated mortality spread evenly across all age classes or a two-fold increased risk for pups and juveniles (age 1–3 years). In contrast to the sea otter model, we were able to use census data collected between 1975 and 2000 to more finely estimate the pattern of sea lion declines. With these data, we fit the additional mortality rates needed to best match changes in the actual population with those predicted by the models. Added mortality was modeled as a time-dependent logit function for survival from added predation. For the model in which all animals suffered from the same, time-dependent predation risk, overall survival of age  $i$  animals,  $S_i$ , was modeled as

$$S_i = S_{i,\text{baseline}} \left[ \frac{\exp(a + b\Delta t)}{1 + \exp(a + b\Delta t)} \right]$$

where  $S_{i,\text{baseline}}$  is the survival estimate from York (1994),  $\Delta t$  is the year expressed as the amount of time elapsed since 1979, and  $a$  and  $b$  govern the magnitude of time-constant and time-varying survival from predation, respectively. The model with higher risk for pups and juveniles was identical, except that in any year the additional predation mortality for these ages was twice as large as that for adults. To estimate the

maximum likelihood values for  $a$ ,  $b$ , and observation error (a nuisance parameter that must still be included in this model-fitting exercise), we fit of the model's predicted population numbers through time to those observed, assuming normally distributed observation errors (Hilborn and Mangel 1997). As for the sea otters, we used the best-fit model to estimate the number of additional sea lion deaths required in each year of the decline to account for the observed population changes. We estimated the two-dimensional maximum-likelihood profile and 95% confidence limit for combined values of  $a$  and  $b$  for each model by a direct search of parameter space, while fitting observation variance as a free parameter (Hilborn and Mangel 1997).

## RESULTS

### *Energetic requirements of killer whales*

The estimated FMR for free-ranging killer whales using Eq. 1 was 163 738 kcal/d (7934 W) for a 2800-kg adult female and 243 501 kcal/d (11 800 W) for a 4733-kg adult male (Fig. 1). In comparison, caloric intakes based on daily fish ingestion for smaller, relatively sedentary whales in captivity was ~145 000 kcal/d (7026 W) for a 2692-kg adult female and 180 000 kcal/d (8722 W) for a 3750-kg adult male (Kreite 1995). Barrett-Lennard et al. (1995) added a 25% factor to these values to account for the activity level of whales in the wild with a resulting estimate of 220 000 kcal/d (10 661 W) for a 3550-kg, free-ranging killer whale.

The ingestion rates predicted for killer whales in the present study result in an average mass specific energy intake of 51–59 kcal·kg<sup>-1</sup>·d<sup>-1</sup> (2.5–2.9 W/kg) with male and female whales delineating the lower and upper range limits, respectively. This range is slightly lower than the 62 kcal·kg<sup>-1</sup>·d<sup>-1</sup> (3.0 W/kg) assessed from the rate of prey intake of transient killer whales feeding on harbor seals (Baird 1994) and may be explained by the digestive efficiencies associated with eating whole prey rather than just edible tissues. In general, carnivores digest and absorb about 90% of ingested food (Jorgensen 1977). In marine mammals, metabolizable energy ranges from 80.3% to 91.6% for a variety of pinnipeds placed on fish diets (Costa and Williams 1999). Likewise, captive killer whales show assimilation efficiencies of 82% on a fish diet (Kreite 1995). If we assume an average assimilation efficiency of 84.7% to account for the effect of ingesting whole prey items as well as edible tissues, then the actual caloric intake of killer whales is higher than our original estimates (i.e., the above ingestion rates only account for 85% of what the whale must consume). Based on this assimilation efficiency, a typical adult female killer whale would need to ingest 193 211 kcal/d in prey items; male killer whales would need 287 331 kcal/d to meet basic energetic demands.

<sup>6</sup> <http://www.nwr.noaa.gov/1publcat/allbiops.htm>

TABLE 1. Comparative energy values and water contents for common marine mammal prey items of killer whales.

Species	Energy values			Percentage water	n
	kcal/g wet mass	kJ/g wet mass	n		
Sea otter ( <i>Enhydra lutris</i> )					
Whole adult	1.81 ± 0.02	7.58 ± 0.08	4	66.6 ± 0.60	6
Steller sea lion ( <i>Eumetopias jubatus</i> )					
Whole pup	2.61 ± 0.08	10.97 ± 0.33	3	64.7	1
Adult					
muscle	1.45–1.47	6.07–6.15	2	72.2–72.7	2
blubber	6.78 ± 0.04	28.36 ± 0.19	4	24.4–24.9	2
Northern fur seal (whole) ( <i>Callorhinus ursinus</i> )	2.50	10.47	...	64.0	...
Ringed seal (whole) ( <i>Phoca hispida</i> )	3.55	14.86	...	...	...
Whale muscle (unspecified)	2.21	9.25	...	...	...

Notes: Values for the sea otter and Steller sea lions were determined in the present study by bomb calorimetry. Depending on the sample size, the values represent the range or mean ± 1 SE ( $n \geq 3$ ). Mean values for other species are from Stansby (1976) and Perez (1990) are provided for comparison.

#### Energetic content of prey items

The energy and water contents of a variety of common prey items for killer whales are listed in Table 1. In comparison to other marine mammals, sea otters provide the lowest energy content per kilogram of body mass ( $1.81 \pm 0.02$  kcal/g wet mass or  $7.58 \pm 0.08$  kJ/g wet mass); this may be attributed to their relatively low body fat content (Kenyon 1969, Riedman and Estes 1990). Accounting for their size, a typical adult male sea otter weighing 34 kg provides 61 540 kcal ( $34 \text{ kg} \times 1.81 \text{ kcal/g wet mass}$ ) or 257 656 kJ; a 23-kg adult female otter provides 41 630 kcal ( $174 296 \text{ kJ}$ ). Steller sea lion pups, which maintain blubber layers of 3–8 mm across the body (T. M. Williams, unpublished data), provide over 40% more calories per kilogram than sea otters. In this analysis, the average mass for the Steller sea lion pups was 40 kg (T. M. Williams, personal observation).

The caloric content of lean skeletal muscle from an adult Steller sea lion averaged 1.46 kcal/g wet mass ( $6.11 \text{ kJ/g wet mass}$ ), while blubber from the same animal had an energy content that was nearly five times higher. Likewise, the blubber layer of other pinnipeds and cetaceans contribute to relatively high caloric contents if whole prey items are ingested.

#### Demographic analysis

For sea otters, we estimate that 9982 additional deaths annually would generate the population declines observed from 1990 to 1997 across the Aleutian ar-

chipelago (Doroff et al. 2003), assuming the probability of increased mortality is the same for all individuals and no density-dependent increase in survival in the remainder of the population. Increasing prey densities during the otter decline (Estes et al. 1998) and documentation of elevated juvenile mortality at very high densities in this and other sea otter populations (Kenyon 1969, Estes 1990, Riedman and Estes 1990) suggests that density dependence does occur. However, given the rapidity of the decline, and the lack of a reproductive response to density in sea otters (Monson et al. 2000), our estimate is reasonable for the time scales relevant to the current synthesis.

The observed rates of decline for Steller sea lions were high from 1979 to 1988, and lower thereafter (Fig. 2a). Models with either uniform risk of predation or higher risk to young animals predict that the observed population decline would have required either 10 885 or 11 575 additional deaths annually between 1979 and 1988, respectively, with a rapid fall-off to only several hundred additional deaths per year in the 1990s (Fig. 2b). Under the best-fit model with uniform predation risk 14% of all added deaths were pups, with the remaining deaths occurring in the adult segment of the population. This compares to 24% of added deaths attributed to pups for the added-risk model (Fig. 2c).

The best-fit values for the predation survival parameters  $\{a, b\}$  for the uniform and added-risk models are  $\{1.385, 0.099\}$  and  $\{0.742, 0.110\}$ , respectively. Parameter values falling within the 95% maximum like-

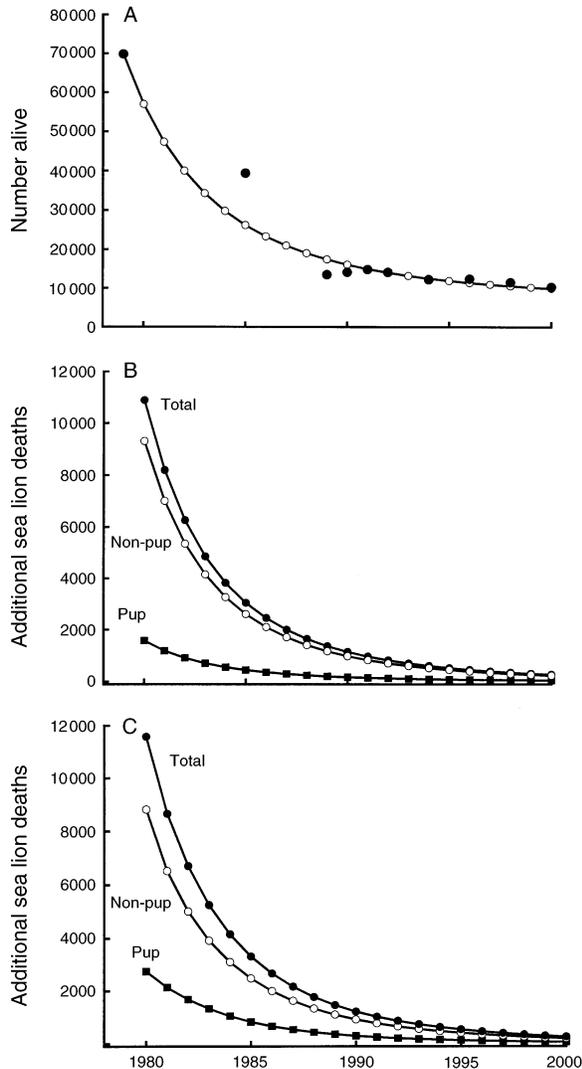


FIG. 2. Model predictions for (A) population number and (B, C) added mortality due to predation for Steller sea lions in the Aleutian Islands. In panel (A), the observed (solid circles) and modeled (open circles) total population numbers are compared for each year from 1978 to 2000. The curves in panels (B) and (C) show the predicted numbers of additional deaths needed to generate the observed population declines during this time period. Results are shown for total deaths attributed to predation (solid circles), adults and juveniles combined (open circles), and for first year pups (solid squares). The simulation in panel (B) assumed that predation was indiscriminate among age classes. This compares with the simulation in panel (C) that assumed that the risk of predation to juveniles and pups was double that of adults.

likelihood confidence limits for the uniform model ranged between 0.75 and 1.85 for  $a$  and 0.0362 and 0.2113 for  $b$ , and were strongly negatively correlated (Pearson  $r = -0.98$ ). Results were similar for the added-risk model ( $a$  from 0.056 to 1.229;  $b$  from 0.041 to 0.229; Pearson  $r = -0.98$ ). For parameter sets within the 95% confidence limits, the uniform model predicted between

19 340 and 9206 additional deaths between 1979 and 1980, with similar results for the added-risk model (19 356 to 9883). As with the sea otters, there is some evidence of negative density dependence in Steller sea lion populations (Calkins et al. 1998, Pitcher et al. 2000), again suggesting that our estimates of predation-caused deaths are likely to be conservative.

#### SYNTHESIS AND DISCUSSION

##### *Assessing the plausibility of top-down control of sea otter and sea lion populations*

With reasonable values for population abundance and field metabolic rates of killer whales (Fig. 1), the caloric value of individual prey items (Table 1), and demographic changes in prey populations (Fig. 2), it is a relatively simple bookkeeping exercise to determine the effect of the killer whales' energetic demands on their prey community. Putting these demands in terms of numbers of prey taken and accounting for digestive efficiency, we find that a large number of sea otters would be needed to meet the daily energy requirements of an adult killer whale. An adult male killer whale with a daily digestible caloric demand of 287 331 kcal/d (13 924 W) must ingest five male or seven female sea otters per day. An adult female killer whale will need three male or five female sea otters per day. It follows that an individual killer whale specializing in sea otters as prey would consume 1095–2555 otters per year, depending on the size of predator and prey. Because these calculations assume no growth or reproductive costs, they are conservative estimates for reproductively active, free-ranging killer whales.

Fewer Steller sea lions would be needed to meet the energy requirements of a killer whale due to the larger size and higher caloric content of both pups and edible portions of adults (Table 1). Calculations similar to those conducted for sea otters demonstrate that an average killer whale would require 2–3 Steller sea lion pups per day or about 840 pups per year when feeding exclusively on young Steller sea lions. In comparison, only one-third to one-half of an adult female sea lion per day (~160 per year) would be needed to satisfy the killer whale's appetite.

Scaled up to a population of killer whales, we can now assess the potential impact of such a large, mobile predator on prey resources. Killer whale abundance can be estimated from data obtained during surveys conducted in 1994 of the area from the Alaska Peninsula and Aleutian archipelago south 200 nautical miles (370 km), between 154° to 180° W. Applying standard line-transect methods to these data provides a density estimate of 3.6 individuals/1000 km<sup>2</sup> (K. Forney, unpublished data). Killer whale abundance for waters surrounding the Aleutian archipelago (1 080 000 km<sup>2</sup> of ocean surface within 200 nm of land) is thus estimated at 3888 individuals (range based on 95% CI = 1707–8857 killer whales). Obviously, this estimate depends

on the areal boundaries. In view of the exceptional mobility of killer whales (Dahlheim and Heyning 1999), we expect that animals in this and even more distant regions have easy access to coastal-living sea lions and sea otters.

It is unlikely that all of these killer whales would specialize in eating marine mammal prey. Rather, behavior, pod size, social structure, geographical movements, morphological characteristics, genetics, and patterns of vocalizations of killer whales indicate two distinct ecotypes in the northeastern Pacific Ocean (Bigg et al. 1987, Dahlheim and Heyning 1999), one that specializes in eating fish and another that preys primarily on marine mammals (Matkin 1994, Baird and Dill 1996). A third ecotype of offshore killer whales was recently described (Saulitis et al. 2000), although the diet of these animals remains uncertain. In well-studied areas around Vancouver Island (British Columbia), Prince William Sound (Alaska), and southeastern Alaska, mammal-eating killer whales represent a comparatively small proportion of the total killer whale population. Depending on area and season, mammal-eaters represent 14–40% of local killer whale numbers in Alaska (Leatherwood et al. 1984). More recent surveys of killer whales in the western Gulf of Alaska and the Aleutian Islands indicate that ~10% of the animals (170–886 whales) specialize on mammalian prey (M. E. Dahlheim, unpublished data). To provide a conservative estimate of potential ecological impact, we used the lowest value, 170 mammal-eating killer whales for this region.

The potential impact of mammal-eating killer whales on sea otter and sea lion populations is marked (Fig. 3). Based on the calculated prey intake, a single pod of mammal-eaters (where a pod is composed of one male and four females; Bigg et al. 1987, Matkin 1994, Baird and Dill 1996) could ingest over 8500 sea otters per year; 170 whales could take 290 476 otters over the same time period, a loss rate that would have driven the Aleutian Islands population to extinction in only three to four months (Fig. 3a). The number of Steller sea lions taken will depend on whether predation is indiscriminate across all age classes or if younger animals are taken preferentially. Indiscriminate predation by age results in nearly 1200 Steller sea lions eaten per year to meet the caloric requirements of one killer whale pod (assuming 16% pups and 84% juvenile and adult sea lions taken based on the life table for Steller sea lions; York 1994). This is increased to 39 644 sea lions for a population of 170 whales, approximately three times the highest annual removal rate needed to drive the observed sea lion declines (Fig. 3b). Altering the risk of predation by age changes these calculations considerably, to the detriment of the sea lions. If pups are four times more vulnerable and juveniles three times more vulnerable to predators than adults, then 1907 Steller sea lions would be needed per year to satiate a pod of five killer whales; 170 whales would

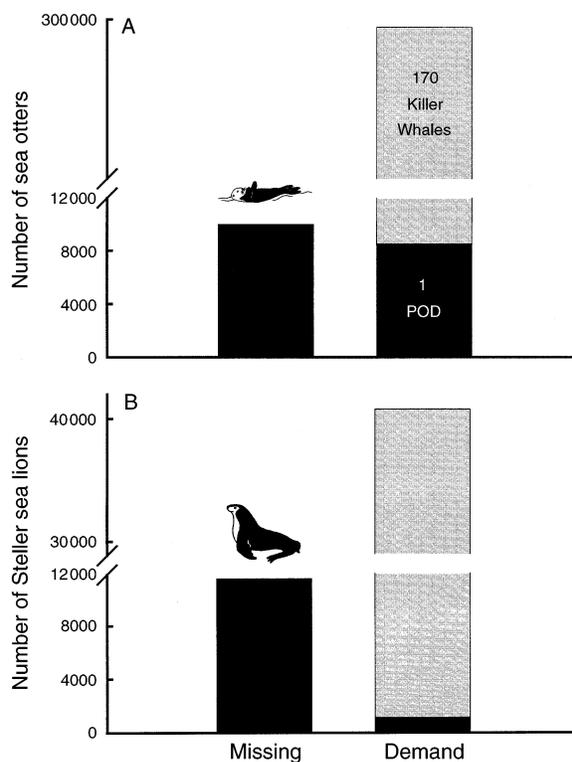


FIG. 3. Number of (A) sea otters and (B) Steller sea lions missing from the Aleutian archipelago populations compared to the energy demand of killer whales. Black bars on the left represent the calculated maximum number of animals lost to predation in a single year during the height of the declines. These are compared to the annual energy requirements for a single pod of killer whales composed of one adult male and four adult females (right black bar) and for 170 mammal-eating killer whales (gray bar). Analyses are based on the metabolic rate of free-ranging killer whales and the energy content of sea otters and Steller sea lions as described in the text.

consume 64 838 sea lions over the same time period. In sum, the minimal estimated population size of mammal-eating killer whales is considerably larger than necessary to drive the rapid declines of both Steller sea lions and sea otters in the Aleutian region.

In the absence of prey species' life histories, we can still estimate the effective pressure from predators on a particular prey resource by comparing the total energy available from a prey population (Energy Resource,  $E_R$ ) with the energy required to support the metabolic demands of a population of predators (Energy Demand,  $E_D$ ).  $E_R$  is calculated from the product of population size and the energy content of specific prey (Table 1), while  $E_D$  is the product of energy intake (Fig. 1) and the number of predators in a population. The ratio  $E_D/E_R$ , termed the Predation Pressure Index, is an estimate of the effective pressure by a predator population on each prey type. As a simplified version of catch estimates used in fisheries impact models (see, for example, Overholtz et al. 1986), the Predation Pressure

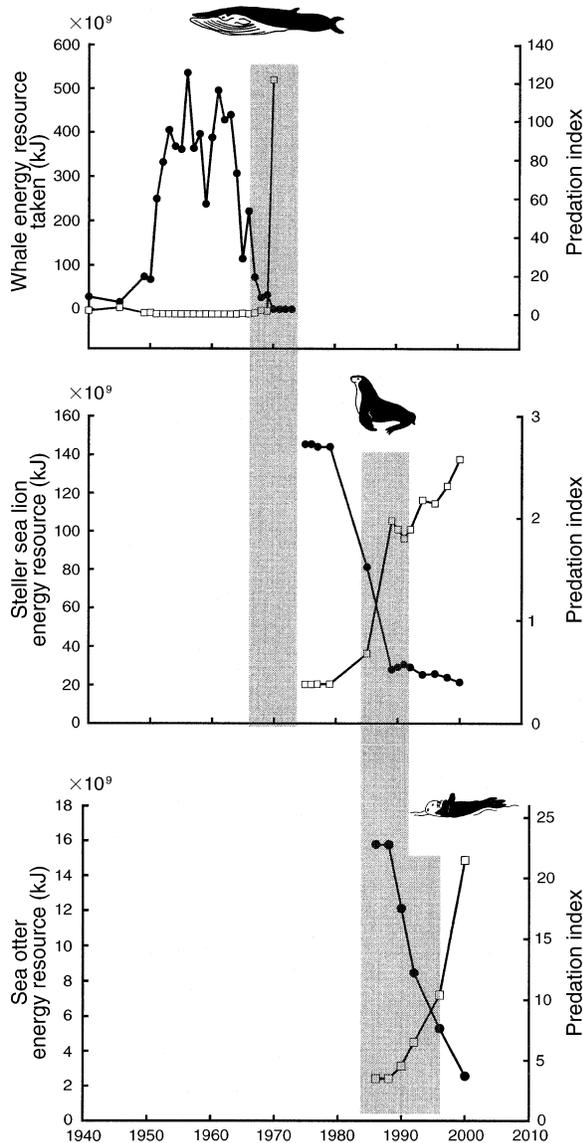


FIG. 4. Energy Resource (solid circles) and Predation Pressure Index (open squares) in relation to year. The energy available from (A) great whale, (B) Steller sea lion, and (C) sea otter populations in the Aleutian Islands are shown for each year. Because exact numbers for the population of great whales are unknown, we have substituted the number of whales removed from the population by human hunters as a minimum indication of available prey (Springer et al. 2003). Predation Pressure was calculated for 170 killer whales, the minimum number of mammal-eating whales in the study area. Gray bars indicate the point at which the energy demand of the predator population exceeds the energy available in the prey population as denoted by a Predation Pressure Index  $> 1$ . Note the sequential change to less profitable prey as the Energy Resource declines and Predation Pressure rises.

Index provides an assessment of instantaneous predation mortality on a prey resource.

Fig. 4 illustrates the interactive effect of Energy Resource and Predation Pressure for killer whales feeding on different marine mammal species. When  $E_R$  is high relative to other sources of mortality and to  $E_D$ , Predation Pressure is low and the prey population remains relatively stable or increases. This may occur when the prey species is exceptionally large, of high caloric value, or abundant. As Predation Pressure increases and eventually exceeds 1.0 (where the energy demand of the predators exceeds the total energy available) the prey population quickly declines.

Despite being conservative estimates, our calculations demonstrate that relatively minor changes in killer whale feeding habits could easily account for the recent changes in sea otter and Steller sea lion populations observed for the Aleutian Islands (Fig. 2). Energetics data indicate that only four male or six female killer whales could account for the estimated annual added mortality of 9982 sea otters needed to drive the observed population decline. The energy demands of as few as 27 male or 40 female killer whales (minimally 23% of the mammal-eaters or 2.3% of the total population) could account for the estimated 10 885–11 575 Steller sea lions lost per year at the height of the decline. Furthermore, predation losses to a single pod of five killer whales could prevent the present Steller sea lion population from recovering.

If elevated predation is indeed responsible for the observed population declines in sea otters and Steller sea lions, then a change in killer whale behavior or abundance during the past 30 years is needed to bring them about. There is little reason to believe that killer whale numbers have increased substantially. This species is especially numerous in productive, high-latitude seas (Corkeron and Connor 1999). The reported density of 3.6 individuals/1000 km<sup>2</sup> for our area of interest is comparable to the value of 2.5 individuals/1000 km<sup>2</sup> estimated for the eastern Bering Sea (Waite et al. 2001) and 2.3 to 7.6 individuals/1000 km<sup>2</sup> reported for the Southern Ocean (Branch and Butterworth 2001). Even if the killer whale population has grown, the low intrinsic rate of population increase for these marine mammals limits the potential magnitude of change. Using an  $r_{max}$  of 0.0402 for killer whales (assuming survival equal to 1 until senescence and observed fertility; Bigg et al. 1987) and hindcasting from a population size of 3888 individuals in 1994 produces a minimum population of 1517 killer whales in 1970. If only 10% of these whales were mammal-eaters, they could have removed the necessary numbers of sea otters and sea lions to drive the observed population declines. In view of this, a change in foraging behavior by killer whales is the more likely explanation for increased predation rates.

Changes in prey resources for killer whales occurring in the Aleutian Islands during this time period could

initiate such a dietary shift. One recent hypothesis concerning a change in the prey base of killer whales begins with the demise of the great whales through intensive post-World War II commercial whaling (Springer et al. 2003). Large mysticetes and odontocetes represent an important component of the killer whale's diet as evident from historical accounts (Scammon 1874), current behavioral observations (Goley and Straley 1994, George and Suydam 1998, Guinet et al. 2000, Pitman et al. 2001), and scarring patterns on great whales (Weller 2002). Certainly, skull and dental morphology (Slijper 1976, Dahlheim and Heyning 1999), speed and power capabilities, (Fish 1998), alimentary tract characteristics (Williams et al. 2001), and social structure of killer whales (Baird and Dill 1996, Dahlheim and Heyning 1999) also indicate a predator that can hunt, capture, and assimilate large prey.

In the absence of this once abundant prey resource, killer whales that fed on the great whales would have been forced to find other means of satisfying their high energy demands. We hypothesize that pinnipeds, including harbor seals, Steller sea lions, and possibly northern fur seals, and then sea otters were taken sequentially as the killer whales progressively fed on less profitable prey (Table 1, Fig. 4). Such a shift in energy value of the whales' diet has been revealed in the stomach contents of stranded killer whales; prey items identified in these stomachs show a general trend from high-energy content items (harbor seals, salmon) to progressively lower energy items (Steller sea lions, halibut) over the period of 1973 to 1994 (Barrett-Lennard et al. 1995). The timing of these dietary changes is consistent with population trends for marine mammals in the western Gulf of Alaska and the Aleutian Islands (Fig. 2; Springer et al. 2003), in which the final decline of great whales by the mid 1970s was followed by the rapid onset of harbor seal losses, concurrent population declines in Steller sea lions and northern fur seals, and then the rapid loss of sea otters in the Aleutian Islands from about 1990 to present (Fig. 4).

The proposed scenario requires prey switching, about which little is known for individual killer whales. However, in view of the remarkably broad range of vertebrate species reportedly eaten by killer whales (Jefferson et al. 1991, Matkin 1994), novel prey must be taken routinely by at least some individuals. This response by large obligate predators is not unprecedented, especially under the pressure of abrupt environmental change. Numerous species of consumers including Asian tigers (*Panthera tigris*) and leopards (*Panthera pardus*; Seidensticker and McDougal 1993), sea otters (*Enhydra lutris*; Watt et al. 2000, Estes et al. 2003), and others (Murdoch 1969, van Baalen et al. 2001) display dietary changes in response to changing prey availability.

Our results demonstrate that changes in the killer whale's historical diet of great whales by human hunters may have instigated the proposed dietary switch to

smaller marine mammals. The subsequent effect on pinniped and sea otter populations was marked due to the high caloric needs of the killer whale and the comparatively low caloric value of these small marine mammals. From this example, we find that a combined physiological–population analysis increases our ability to critically evaluate the impact of a predator on community structure where the purported keystone species is impossible to manipulate experimentally, extraordinarily difficult to observe, and for which few data exist to directly measure its community effects.

#### *Using bioenergetics to assess theories of community control*

In recent years, there has been a growing appreciation for the importance of large mammalian carnivores in food web dynamics (Terborgh et al. 1999, Estes et al. 2001), although nearly all of the evidence is based on comparisons of ecosystems in which these large carnivores are present or absent. Fish ecologists have frequently used bioenergetics models to estimate the impact of predation on prey populations (Kitchell et al. 1977, Schindler et al. 2002). We find that the integration of bioenergetics and demography, as employed in these various studies and used here, provides an approach for assessing the importance of top-down forcing by large, apex predators in a wide range of systems. In a similar analysis, Alroy (2001) used human population growth, hunting patterns, and the population dynamics of large mammalian herbivores to assess the potential role of human hunting on post-Pleistocene megafaunal extinctions in the New World, an idea that had been debated for 30 years. Admittedly, neither Alroy's analysis nor ours can demonstrate unequivocally that population declines or extinctions were driven by increased predation. However, such computations place the hypotheses within the biological limitations of the key players.

In addition to addressing the relative importance of top-down and bottom-up forcing, this approach may help to resolve a variety of widely debated questions in ecology. By comparing the potential impact of consumers in aquatic and terrestrial ecosystems, one might answer Strong's (1992) question "Are trophic cascades all wet?". Integrating energetics and demography may also be used to determine the physiological feasibility of wide-spread predation in studies such as Terborgh et al. (2001), where remarkable impacts of predators have been inferred, but where the act of predation is rarely seen. Similarly, this approach could provide a better understanding of systems where the natural compliment of large, predatory mammals are missing (Berger et al. 2001) or where predation has been shown to be a major source of mortality, but appears to have little effect on prey populations (e.g., lions and African buffalo; Sinclair 1977).

Lastly, this approach has value in both conservation and management schemes. In particular, the means by

which a predator meets its metabolic demands in the context of changing resources must be considered. In view of the reduced pinniped and sea otter populations in the Aleutian Island archipelago, the obvious question is how will mammal-eating killer whales satisfy their high energy demands? The answer to this is especially important due to currently reduced stocks and seasonal changes in many of the marine mammal populations in the Aleutian Islands. Using the same techniques as outlined here and current marine mammal population estimates from Pfister and DeMaster (*in press*), we can calculate the impact of 170 killer whales on their major prey species in this area. Of the available species, including sea otters, pinnipeds (Steller sea lions, harbor seals, fur seals) and cetaceans (great whales, Dall's porpoise, harbor porpoise), only the great whales represent a sustainable resource. For the remaining species, reproductive turnover rates would not occur quickly enough to counter the level of predation required to meet the energy demand of this number of mammal-eating killer whales. The problem is exacerbated by the seasonal movements of fur seals and great whales out of the Aleutian archipelago during the winter months (Pfister and DeMaster, *in press*). For nearly six months the primary coastal prey resources for killer whales are sea otters, Steller sea lions, and harbor seals, the same species that have declined precipitously (Fig. 4).

Recent reports of transient killer whales feeding on harbor seals in southeast Alaska and Puget Sound, Washington (D. Noren, *personal communication*), indicate that the predators may simply move into new areas. Photo-identification studies have demonstrated long-distance movements of mammal-eating killer whales exceeding 1500 km (Leatherwood et al. 1984, Goley and Straley 1994). In the latter account, at least three killer whales from Glacier Bay, Alaska, were sighted in central California attacking gray whales. If the same individuals had chosen to feed on sea otters, the entire threatened population of almost 2500 California sea otters could have been eliminated in less than four months. Without data from long-term studies and direct observation of hunting behavior, it is difficult to determine the factors that influence prey choice in killer whales. However, by defining physiological requirements (Fig. 1) and taking into account ecologically effective population sizes (Soulé et al. 2003), the integrated approach described here provides a means of assessing the basic requirements critical for the conservation of apex predators and the ecosystems in which they live.

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