The effect of predation (current and historical) by humpback whales (*Megaptera novaeangliae*) on fish abundance near Kodiak Island, Alaska

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Abstract—Humpback whales (*Megaptera novaeangliae*) are significant marine consumers. To examine the potential effect of predation by humpback whales, consumption (kg of prey daily) and prey removal (kg of prey annually) were modeled for a current and historic feeding aggregation of humpback whales off northeastern Kodiak Island, Alaska. A current prey biomass removal rate was modeled by using an estimate of the 2002 humpback whale abundance. A historic rate of removal was modeled from a prewhaling abundance estimate (population size prior to 1926). Two provisional humpback whale diets were simulated in order to model consumption rate. One diet was based on the stomach contents of whales that were commercially harvested from Port Hobron whaling station in Kodiak, Alaska, between 1926 and 1937, and the second diet, based on local prey availability as determined by fish surveys conducted within the study area, was used to model consumption rate by the historic population. The latter diet was also used to model consumption by the current population and to project a consumption rate if the current population were to grow to reach the historic population size. Models of these simulated diets showed that the current population likely removes nearly 8.83×10^6 kg of prey during a 5-month humpback whale feeding season, which could include around 3.26×10^6 kg of juvenile pollock (*Theragra chalcogramma*), 2.55×10^6 kg of capelin (*Mallotus villosus*), if these species are consumed in proportion to their availability. The historic humpback whale population may have removed over 1.76×10^7 kg of prey annually.

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Numerous studies have revealed that an increased awareness of trophic-level interactions is essential in assessing the status of complex marine ecosystems (Overholtz et al., 1991; Hairston and Hairston, 1993; Pascual et al., 1993; Estes, 1994; Kenney et al., 1997; Trites et al., 1997). Such studies have shown that predator-prey relationships in marine systems can have direct and indirect effects on all ecosystem members, but predictions of their effects cannot be made without multispecies models.

Cetaceans are top predators in marine ecosystems and consume significant amounts of prey. Knowledge of the distribution, abundance, and foraging habits of cetaceans is, therefore, an essential element of any pelagic ecosystem study (van Franeker, 1992). Many species preyed upon by cetacean populations are targeted by other marine predators and commercial fisheries or are linked to fisheries through complex food webs. Previous studies have reported that prey removal due to cetacean consumption approaches or exceeds removals due to commercial fishing (Laws, 1977; Laevastu and Larkins, 1981; Bax, 1991, Markussen et al., 1992; Nordøy et al., 1995; Kenney et al., 1997). Such high levels of consumption can have significant effects on the distribution and abundance of prey species and the structure of marine communities (Perez and McAlister, 1993; Kenney et al., 1997; Croll et al., 1998). Therefore, examining consumption by cetaceans contributes information about complex ecosystem relationships and the long-term sustainability of marine resources (Perez and McAlister, 1993; Kenney et al., 1997; Tamura and Ohsumi[1]).

Humpback whales (*Megaptera novaeangliae)* feed in the waters off Kodiak Island and, because they are considered apex predators, may influence the structure of the Kodiak Island marine ecosystem (Fig. 1) (Trites et. al., 1997; Croll et. al., 1998). Modeling the amount of prey consumed (kg of prey annually) by feeding humpback whales is, therefore, a useful tool for evaluating their role as marine predators.

Cetaceans, in general, are described as opportunistic in their food selection, although species tend to select broad categories of prey such as cephalopods, fish, or zooplankton (Tomilin, 1954; Nemoto, 1959; Klumov, 1966; Sigurjónsson and Víkingsson, 1998). Humpback whales are classified as generalists and target a wide variety of prey species (Nemoto, 1970; Perry et al., 1999). They have been shown to be seasonal feeders on euphausiids (*Thysanoessa* spp.*)* and schooling fish species up to 30 cm in length, including capelin (*Mallotus villosus*), Pacific herring (*Clupea pal-*

[1] Tamura, T., and S. Ohsumi. 2000. Regional assessments of prey consumption by marine cetaceans in the world. International Whaling Commission document SC/52/E6, 45 p. Website: www.icrwhale.org/eng/SC52E6.pdf [Accessed on 30 November 2002].

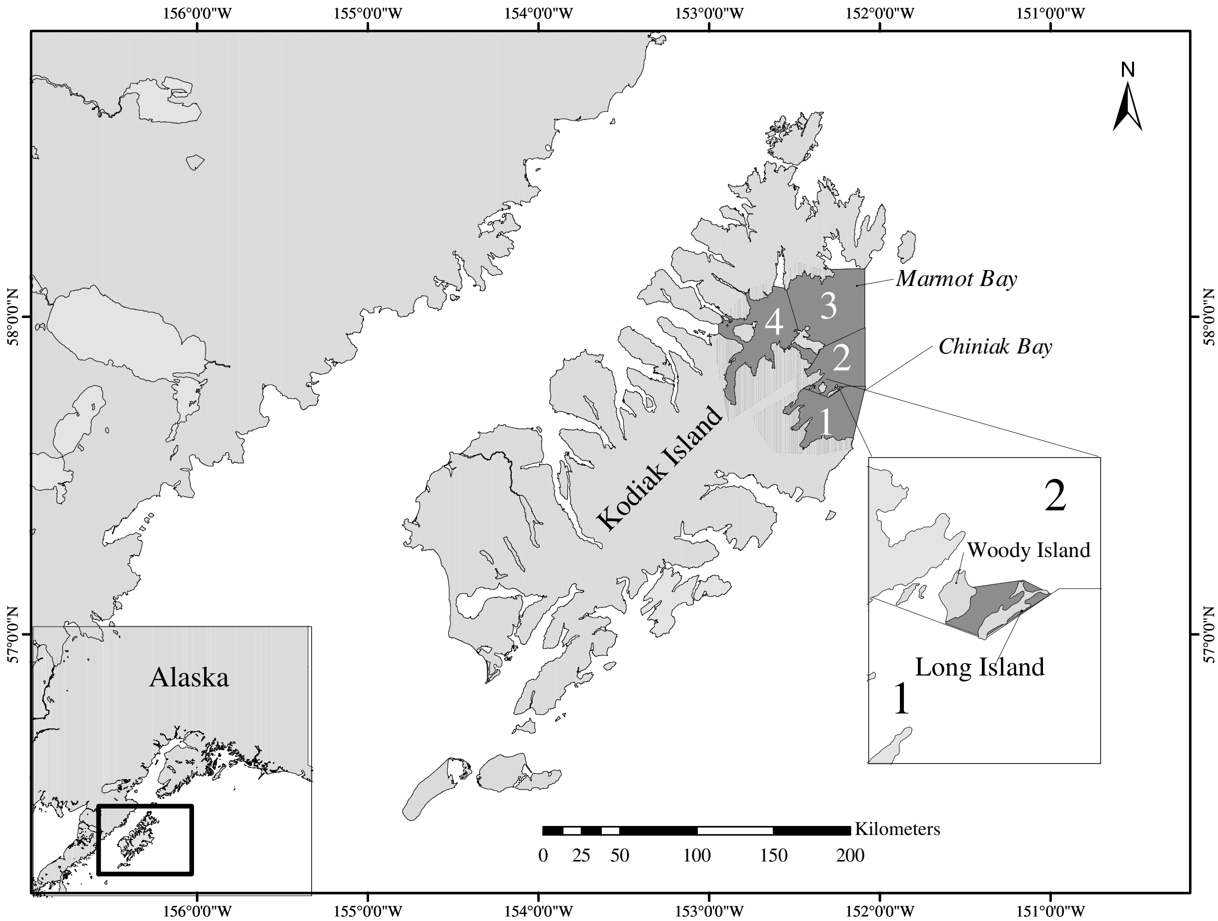

Figure 1

Map of Kodiak Island study area. Study area is shown as shaded area and subareas (1–4) are outlined and numbered. In detail is the nearshore subarea between Woody Island and Long Island.

lasi), walleye pollock (*Theragra chalcogramma*), Atka mackerel (*Pleurogrammus monopterygius),* cod (*Gadus* spp.), sardines (*Sardinops* spp.), and sandlance (*Ammodytes* spp.) (Nemoto, 1957, 1959; Mitchell, 1973; Payne et al., 1990). The variety, as well as the amount, of prey removed from Kodiak waters may therefore be significant. Resource removal from Kodiak waters is of particular importance when considering the high value of Kodiak Island commercial fisheries, which totaled 63.3 million dollars in exvessel (wholesale) value in 2002 (NMFS[2]).

Modeling consumption by humpback whales as they recover from severe population declines could shed light on patterns of change seen in prey and sympatric consumer populations, such as marine birds and pinnipeds (Merrick, 1997; Anderson and Piatt, 1999). Commercial whaling in the 1900s significantly reduced the number of humpback whales, both within coastal Kodiak waters and throughout the North Pacific (Rice, 1978). Following the protection of humpback whales in 1965, however, their numbers in the central North Pacific increased, possibly by as much as 10%, between the early 1980s and early 1990s for some North Pacific stocks (Baker and Herman, 1987; Calambokidis et al.[3]). Removal and subsequent recovery of a marine predator of this magnitude may cause large variations in the biomass removal of prey in the ecosystem, as has been hypothesized in other studies (Laws, 1985; Springer et al., 2003). However, no empirical evidence exists to demonstrate such trophic interactions in the Gulf of Alaska. In this article,

[2] NMFS (National Marine Fisheries Service). 2002. Unpubl. data. Website: http://www.st.nmfs.gov/pls/webpls/MF_LPORT_YEARD.RESULTS [Accessed on 31 May 2003.]

[3] Calambokidis, J., G. H. Steiger, J. M. Straley, T. Quinn, L. M. Herman, S. Cerchio, D. R. Salden, M. Yamaguchi, F. Sato, J. R. Urbán, J. Jacobson, O. von Ziegesar, K. C. Balcomb, C. M. Gabriele, M. E. Dalheim, N. Higashi, S. Uchida, J. K. B. Ford, Y. Miyamura, P. Ladron de Guevara, S. A. Mizroch, L. Schlender, and K. Rasmussen. 1997. Abundance and population structure of humpback whales in the North Pacific basin. Cascadia Research Cooperative Final Contract Report 50ABNF500113 to Southwest Fisheries Science Center, La Jolla, CA 92038, 72 p. Website: http://www.cascadiaresearch.org/reports/rep-NPAC.pdf. [Accessed on 19 April 1999.]

we model the historic and current consumption rate by humpback whales within waters of northeastern Kodiak Island in order to assess the impact these whales have as predators on local prey populations.

Materials and methods

Study area

The study area encompassed waters of northeastern Kodiak Island, including Chiniak and Marmot Bays (Fig. 1). The study area was divided into four subareas of approximately equal size in order to equalize sampling effort and maximize coverage of the study area. Subareas were also used to separate sightings of humpback whales for the purpose of weighting diet composition in relation to prey availability. An additional subarea, including the waters near Woody and Long Islands, was not considered a survey subarea but was designated in the poststudy period for calculating diet composition ("nearshore," Fig. 1).

Sightings and abundance of humpback whales

Data on humpback whale sightings were collected during vessel surveys conducted between June and September in 2001 and 2002. Individual whales were identified from photographs of the black and white pigment patterns (and other natural markings) on the ventral surface of their tail flukes (Katona et al., 1979). A humpback whale sighting was defined as a sighting of an individual whale on a single day. Therefore, no whale was counted twice on one day, but may have been counted multiple times during the study period. Humpback whale sightings were summed by month and then by subarea for calculation of whale diet (see "Materials and methods" section: "Composition of simulated diets").

These sightings and fluke photographs were used in an associated study to estimate current humpback whale abundance within the study area (Witteveen, 2003). The estimate determined from this associated study was used in conjunction with historic catch data from the Port Hobron whaling station to estimate historic humpback whale abundance. The whaling grounds of Port Hobron encompassed most of eastern Kodiak waters—an area approximately four times that of the study area. To account for the size difference between whaling grounds and the study area, catch values were divided by four under the assumption of a random harvest throughout the grounds. The prewhaling and current estimates of humpback whale population size in the study area are 343 individuals (95% CI: 331, 376) and 157 individuals (95% CI: 114, 241), respectively (Witteveen, 2003).

Composition of simulated diets

Two diets were simulated: one that reflected the historic diet and the other that reflected the current diet for humpback whales. The diets were simulated because direct observation of humpback whale feeding behavior is rare and, even when observed, cannot produce a precise account of the prey species being eaten.

Diet A simulated historic target species and was based on the stomach contents of 39 humpback whales harvested at the Port Hobron whaling station from southeast Kodiak waters between 30 May and 9 August 1937 as analyzed by Thompson (1940).

Diet B simulated current target species and assumed no prey selectivity. It was based on the assumption that humpback whales will eat prey of a suitable size (<30 cm) in proportion to the relative occurrence of the prey in areas used by humpback whales. Euphausiid proportions in the diet were based on historic stomach contents and assumed to be constant over time (no current euphausiid abundance estimate is available).

Information on seasonal prey availability was collected from mid-water trawl surveys that were conducted within eastern Kodiak waters in July 2001 and from June through September 2002. Multiple passes with a commercial mid-water trawl net with a 22-mm mesh codend liner were made through acoustic scattering layers, ensuring an accurate representation of mid-water fish composition and occurrence. Species composition, species counts, and fish size were determined for each tow and grouped within the study subareas. Only data from tows conducted during the study period in 2001 and 2002 in areas utilized by humpback whales were included in our analysis. Therefore, prey surveys overlapped humpback whale sightings both temporally and spatially. A separate series of acoustic and purse-seine (center panel with a 3.2-mm mesh net) surveys was used to determine prey availability within the nearshore subarea from June through September 2002 (Foy[4]). Prey composition determined by these surveys was assumed to be homogeneous throughout the nearshore habitat within the study area.

To calculate diet B, the occurrence of fish smaller than 30 cm was determined from the mid-water trawl surveys within each subarea and month for both 2001 and 2002. Tow data were first separated by subarea and month. Percent composition of prey species in each tow was calculated by dividing the total number of fish of each species caught by the total number of all fish caught in each tow, excluding species larger than 30 cm (Nemoto, 1959) and species that were not previously documented as prey, such as flatfish and other nonschooling fishes (Nemoto, 1957, 1959; Klumov, 1963; Krieger and Wing, 1984, 1986; Perry et al., 1999).

To calculate diet B for the entire study area, prey proportions were weighted by the number of whales in each subarea. The weighted proportions were then summed across all months and subareas and multiplied by one minus the percentage of assumed euphausiid

[4] Foy, R. 2002. Unpubl. data. Fishery Industrial Technology Center, University of Alaska Fairbanks, Kodiak, AK 99615.

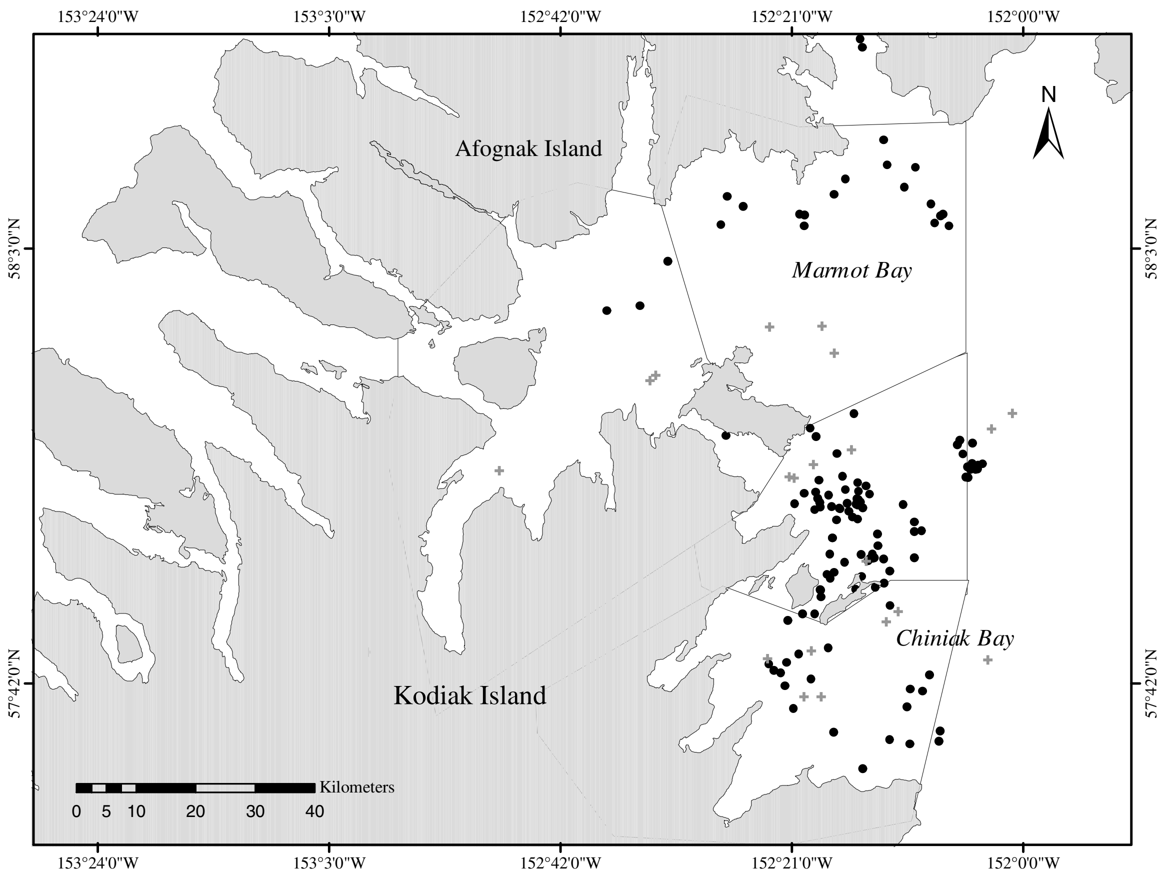

Figure 2

A close-up of the study area showing locations of humpback whale (*Megaptera novaeangliae*) sightings and prey tows (+) for 2001 and 2002. Only mid-water trawl locations are shown.

occurrence within the diet. Thus, diet B simulated a weighted availability of prey species based on temporal and spatial overlap between prey surveys and humpback whale sightings within the study period (Fig. 2).

Consumption rate

A seasonal consumption rate was estimated for both the current humpback whale population and the prewhaling humpback whale population. The prewhaling consumption rate was estimated by using diet A only. Diet B was used to estimate the consumption rate by the current humpback whale population and to project the consumption rate by a humpback whale population at the prewhaling abundance level.

The active metabolic rate (kcal/day) of feeding humpback whales was estimated in this study as $E=192M^{0.75}$, where Kleiber's (1961) model for basal metabolic rate (BMR; $E=70M^{0.75}$) was modified by using average oxygen consumption estimates for feeding baleen whales, where M is average body weight (kg) (Wahrenbrock et al., 1974: Sumich, 1983; Perez and McAlister, 1993).

Daily prey consumption was then estimated as

$$I = \frac{E}{K}\frac{1}{1{,}000},$$

where I = total prey consumption (kg/day);
E = estimated daily energy requirements (kcal/day); and
K = the estimated energy density (kcal/gram wet weight) of presumed prey.

The average body mass for humpback whales (M) was set equal to 30,408 kg (Trites and Pauly, 1998). The total energy density (K) of each diet was calculated by multiplying the average seasonal energy density of each prey species sampled in the study area by the percentage of that species within each diet and summing across all species. Values of K for individual prey species came from proximate compositions that were determined from prey collected during 2002 trawl surveys for all months within the study period (Foy[4]). For each month, energy density was calculated by multiplying percent lipid by 9.4 kcal/g and percent protein by 4.3 kcal/g, which are conversion factors based on heat produced during metabolism of food (Schmidt-Nielson, 1997). Carbohydrates were considered to be bound and not available for nutrition (Gaskin, 1982). The average seasonal energy density of each prey species was calculated by summing all values of energy density and dividing by the number of months in the study period. Previously published proximate composition values for surf smelt (*Hypomesus pretious)* and energy density data for euphausiids (*Thysanoessa* spp.*)* were used (Davis et al., 1997; Payne et al., 1999).

Seasonal prey consumption for the population was estimated by multiplying I by estimates of abundance (N) and the total number of days in the humpback whale feeding season. Consumption estimates were calculated for both the upper and lower 95% confidence limits on the abundance estimates to show a possible range of consumption. The length of the feeding season was presumed to be 152 days (Perez and McAllister, 1993).

Table 1

Number of sightings of humpback whales (*Megaptera novaeangliae*) for 2001 and 2002 by subarea and month in the Kodiak Island study area.

	2001 and 2002				
Area	June	July	August	September	Total
1	10	7	10	3	30
2	29	89	22	3	143
3	20	8	0	12	40
4	0	3	0	7	10
Nearshore	5	14	0	0	19
Total	64	121	32	25	242

Results

Analysis of sightings showed that humpback whales were not uniformly distributed within the study area (Table 1). Occurrence of humpback whales within subareas was variable, indicating within-season shifts of habitat use. Peak humpback whale sightings occurred in subarea 2 in July of both years. No humpback whales were sighted in the nearshore area after the month of July in either year.

Only two prey items were identified in the 27 stomachs that contained appreciable quantities of prey of 39 stomachs analyzed by Thompson (1940). Surf smelt were found in 21 of 27 (78%) stomachs and euphausiids were found in 6 of 27 (22%) stomachs (Table 2). These percentages represent diet A. Energy densities of these two species combined to give a total energy density of 1.31 kcal/gram (Table 3).

The fish species in areas used by humpback whales in 2001 and 2002, as shown by mid-water trawl surveys, were pollock (36.96%), capelin (28.89%), eulachon (7.60%), Pacific sandlance (4.44%), Pacific sandfish (0.08%), and Pacific herring (0.03%) (Table 2). These percentages represent diet B. Calculated energy densities of prey species ranged from a high (eulachon) of 2.52 kcal/gram to a low of 1.12 kcal/gram (juvenile pollock). The total energy density for diet B was 1.19 kcal/gram (Table 3).

Based on energetic content of the above diets, the model indicated that each humpback whale in the study area would consume 338 kg/day on diet A and 370 kg/day on diet B. Using a prewhaling estimate of 343 (95% CI=331–376) animals in the study area, we determined that humpback whales feeding on diet A prior to 1927 would have removed an estimated 1.76×10^7 kg of prey annually (95% CI= 1.70×10^7 to 1.93×10^7), including nearly 3.87×10^6 (3.74×10^6 to 4.24×10^6) kg of euphausiids and approximately 1.37×10^7 (1.32×10^7 to 1.50×10^7) kg of surf smelt (Table 4). If diet B accurately reflects prey selection by the estimated 157 (95% CI=114–241)

Table 2

Composition and relative occurrence of prey species represented in simulated humpback whale (*Megaptera novaeangliae*) diet A (historic) and diet B (current).

Diet	Prey species	Common name	Percent of total diet
A	*Hypomesus pretious*	surf smelt	78.00%
	Thysanoessa spp.	euphausiid spp.	22.00%
			Total 100%
B	*Theragra chalcogramma*	walleye pollock	36.96%
	Mallotus villosus	capelin	28.88%
	Thysanoessa spp.	euphausiid spp.	22.00%
	Thaleichthys pacificus	eulachon	7.60%
	Ammodytes hexapterus	Pacific sandlance	4.44%
	Trichodon trichodon	Pacific sandfish	0.08%
	Clupea harengus pallasi	Pacific herring	0.03%
			Total 100%

Table 3

Monthly and average energy densities (kcal/gram) of prey species represented in simulated humpback whale (*Megaptera novaeangliae*) diets A and B based on lipid and protein composition. Energy densities were used to estimate consumption by humpback whales. Average values in parentheses have been adjusted to reflect standard deviations of lipid and protein composition. N/A = not available.

	Energy densities (kcal/gram)				
Species	June	July	August	September	Average
Capelin	1.1285	1.2632	1.1956	1.4298	1.2542 (1.1665, 1.3755)
Pacific sandlance	1.4179	1.4179	1.4179	1.4179	1.4179 (1.3211, 1.5590)
Pacific sandfish	0.8661	1.2126	1.1165	1.1165	1.0779 (1.0449, 1.1300)
Eulachon	2.1582	2.5218	2.6758	2.7424	2.5245 (2.3761, 2.6860)
Herring	2.0999	2.0999	1.9454	2.1205	2.0664 (1.9432, 2.2942)
Juvenile pollock	1.0144	1.0657	1.1380	1.2461	1.1160 (0.9730, 1.2994)
Euphausiids	N/A	N/A	N/A	N/A	0.7430
Surf smelt	N/A	N/A	N/A	N/A	1.4698

Table 4

Daily and annual (over a 152-day feeding season) consumption of prey from two different diets off northeastern Kodiak Island by humpback whales (*Megaptera novaeangliae*) at two levels of population abundance: the current population of 157 and the historic population of 343 (also presumed to be the carrying capacity to which the current population will recover). Diet A is the simulated diet of the historic population through analysis of stomach contents of 39 whales in 1937; Diet B is the simulated diet of the historic and current population based on currently available prey of suitable size for consumption.

		Annual prey removal (kg)		
Prey species	Daily prey removal (kg)	Mean	Lower limit	Upper limit
Historic population				
Diet A				
Surf smelt	90,301	13,725,715	13,245,515	15,046,264
Euphausiids	25,469	3,871,355	3,735,914	4,243,818
Total	115,770	17,597,070	16,981,429	19,290,083
Diet B				
Euphausiids	27,934	4,246,006	4,097,458	4,654,514
Walleye pollock	46,924	7,132,406	6,882,876	7,818,614
Capelin	36,671	5,573,943	5,378,936	6,110,211
Eulachon	9,652	1,467,057	1,415,731	1,608,202
Pacific sandlance	5,635	856,475	826,511	938,876
Pacific sandfish	98	14,907	14,386	16,342
Pacific herring	33	5,038	4,862	5,523
Total	126,974	19,300,028	18,624,808	21,156,882
Current population				
Diet B				
Euphausiids	12,786	1,943,507	1,411,209	2,983,345
Walleye pollock	21,478	3,264,687	2,370,537	5,011,399
Capelin	16,785	2,551,338	1,852,564	3,916,385
Eulachon	4,418	671,510	487,593	1,030,789
Pacific sandlance	2,579	392,031	284,659	601,780
Pacific sandfish	45	6,824	4,955	10,474
Pacific herring	15	2,306	1,675	3,540
Total	58,119	8,834,124	6,414,587	13,560,661

humpback whales currently feeding in the study area, these whales would be removing nearly 8.83×10^6 (6.41×10^6 to 1.36×10^7) kg annually, including 3.26×10^6 (2.37×10^6 to 5.01×10^6) kg of pollock, nearly 2.55×10^6 (1.85×10^6 to 3.92×10^6) kg of capelin, and 6.71×10^5 (4.88×10^5 to 1.03×10^6) kg of eulachon. If the same diet were consumed by a population of humpback whales allowed to return to prewhaling abundance, the projected population would remove 1.9×10^7 (1.86×10^7 to 2.12×10^7) kg of prey annually, including approximately 7.13×10^6 (6.88×10^6 to 7.82×10^6) kg of pollock, 5.57×10^6 (5.38×10^6 to 6.11×10^6) kg of capelin, and 4.25×10^6 (4.10×10^6 to 4.65×10^6) kg of euphausiids (Table 4).

Discussion

Consumption rate

Estimating the energy requirements of large cetaceans is inherently difficult and values presented in the present study may be subject to substantial uncertainty. Previous studies in which consumption rates for cetaceans were estimated have used a range of values to adjust BMR (E=70$M^{0.75}$) for active metabolism. These values generally range from approximately 1.5 to 3 times BMR (Hinga, 1979; Lockyer, 1981; Sigurjónsson and Víkingsson, 1998). Our value of 192 is 2.7 times larger than 70 and is, therefore, a reasonable estimate because it fits within this range and is based on the observed oxygen consumption rates of baleen whales. However, the consumption estimates are highly sensitive to perturbations of model input; a 5% error in this value would cause deviation of the same percentage (5%) in final consumption values. Further, all values in our consumption model are assumed to be constant when body mass, physiological status, and assimilation efficiency are likely subject to large seasonal fluctuations (Innes et al., 1987; Perez and McAlister, 1993, Kenney et al., 1997; Trites et al., 1997; Sigurjónsson and Víkingsson, 1998). Our model, however, did account for seasonal changes in the energy density of local prey sources; previous models, on the other hand, did not account for these changes (Perez and McAlister, 1993). Further research is necessary to obtain reliable field estimates of metabolic rates if model uncertainty is to be reduced.

The historic prevalence of surf smelt in diet A could imply a dramatic change in surf smelt availability, misidentification, or an overestimation of smelt found in stomachs. Thompson's (1940) analysis resulted from "samples of stomach contents" obtained from catcher vessels; therefore, these samples may have completely missed less prevalent species. Further, stomach samples may have only reflected the most recent meal of the whale and therefore be biased toward a single species. This potential bias, however, could have been minimized by sampling stomachs throughout the season (May 30–August 09) (Thompson, 1940). Diet B was dominated by walleye pollock, a species not present in historic diet A. The increased importance of juvenile pollock in contemporary humpback whale diet B could reflect changes in prey species availability and use, foraging selectivity, or reflect our diet reconstruction method.

Diet B is considered provisional for two reasons. First, it is assumed that humpback whales eat prey species in proportion to their availability within foraging areas. Humpback whales select preferred prey species and consumption, therefore, may be disproportional to availability. That is, they may be selectively foraging from all available prey sources. Previous foraging studies have described humpback whale distribution as being correlated with areas of capelin (Whitehead and Carscadden 1985; Piatt et al. 1989) and sandlance abundance (Payne et al. 1986; Kenney et al. 1996) and this correlation may indicate a possible preference for small forage fish species. Given that in the decades since whaling, the Gulf of Alaska has shifted from a system dominated by forage fish to one dominated by pollock and other groundfish (Merrick 1997; Anderson and Piatt 1999; Benson and Trites 2002), a shift in prevalence from surf smelt in the historic diet to pollock in the current diet is not unexpected. Pollock have been shown to be a dominant prey source of humpback whales harvested in Russia (Klumov, 1963). Additionally, humpback whales in southeastern Alaska have been observed near schools of juvenile pollock and are believed to eat pollock to an unknown, but potentially large, extent in some years (Gabriele[5]).

The second source of uncertainty in diet B stems from the assumption that our mid-water trawl surveys provide unbiased samples of all available prey. Because these surveys were not designed to sample zooplankton, they may have produced a biased estimate of euphausiid availability. This bias may not be significant, however, because the 22% value we used in diet B was based on historic usage and falls within the range of euphausiid consumption (5–30% of the total diet) estimated in other humpback whale studies (Perez and McAlister, 1993; Kenney et al., 1997).

Further, diet B was constructed from the results of mid-water trawl surveys that may underestimate the availability of some forage fishes, particularly Pacific sandlance. Pacific sandlance are often small enough to swim through the meshes in the net or are found in benthic habitats and cannot be captured by mid-water trawl methods. To minimize this potential sampling bias, we supplemented our trawl surveys with purse seine sampling in the nearshore subarea. Despite this effort we may have underestimated the prevalence of Pacific sandlance in the area because it was found to dominate the diets of other coastal piscivores; stomach contents of 34 coho salmon (*Oncorhynchus kisutch*) and Pacific halibut (*Hippoglossus stenolepis*) in 2002 (Witteveen[6]) and regurgitants from blacklegged kittiwakes

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[5] Gabriele, C. 2001–2002. Personal commun. Glacier Bay National Park, P.O. Box 140. Gustavus, AK 99826-0140.

[6] Witteveen, B. H. 2002. Unpubl. data. Fishery Industrial Technology Center, University of Alaska Fairbanks, Kodiak, AK 99615.

in 2001 (n=96) and 2002 (n=147) were dominated by Pacific sandlance (Murra et al., 2003).

Ecological effects from humpback whale prey consumption

Although estimates of consumption are highly dependent on estimates of population abundance and metabolic rates, these values indicate that humpback whales were, and still are, significant predators within the Kodiak Island ecosystem.

Historic commercial whaling reduced the population in our study area to an estimated low of 27 animals by 1938 (Witteveen, 2003). The removal of so many large consumers likely had significant impacts on the surrounding ecosystem. As modeled, reducing historic consumption to that of current levels would release nearly 10,000 tons of prey within the study area in a single feeding season. Such a release could have caused a trophic cascade effect.

Cetacean removals in the Southern Ocean have demonstrated how trophic cascades can affect marine ecosystems through removal of large marine predators, including whales (Laws, 1985). It has been hypothesized that a similar reorganization of the marine community may have occurred in the Bering Sea and Gulf of Alaska, although the mechanisms of such a cascade are not well understood (Merrick, 1997; Trites, 1997; Springer et al. 2003). Removal of whales during commercial harvest reduced predation on certain fish, cephalopod, and zooplankton species, which were then available to other consumers. This large number of unconsumed prey, when combined with environmental factors such as the 1977 regime shift, may have contributed to the growth of sympatric marine predator populations from the late 1940s to late 1970s. It is hypothesized that whale stock resurgence, coupled with the 1977 regime shift that favored the proliferation of groundfish species, may have reduced prey availability to other piscivores in the system and may have led to declines seen in harbor seal (*Phoca vitulina)*, Steller sea lion, northern fur seal (*Callorhinus ursinus),* common murre (*Uria aalge*), thick-billed murre (*U. lomvia*), and red-legged kittiwake (*Rissa brevirostris*) populations (Merrick, 1995, 1997; NRC, 1996; Trites, 1997). The Gulf of Alaska and Bering Sea ecosystems may still be affected by changes caused by baleen whale removals and their recovery (NRC, 1996).

Assuming that the Kodiak Island study area was similarly affected by this trophic reorganization, an estimate of the current consumption by humpback whales would help elucidate the role that a humpback whale recovery is playing in ecosystem dynamics. If our diet composition and subsequent consumption estimates are accurate, our results indicate that the diet of humpback whales in Kodiak waters directly overlaps those of sympatric piscivores and the biomass that is removed may be substantial. The top species modeled in the humpback whale diet represent important sources of energy for multiple higher-trophic-level species and are known to be significant dietary species for Steller sea lions (Wynne[7]), harbor seals (Jemison[8]), tufted puffins (*Fratercula cirrhata)* (Piatt et al., 1997), blacklegged kittiwakes (Murra et al., 2003), adult pollock, Pacific halibut, and arrowtooth flounder (Livingston, 1993; Yang, 1995; Merrick, 1997; Best and St. Pierre[9]).

Our model indicates that humpback whales within the study area may currently be consuming a significant amount of fish, including over 3.26×10^6 kg of juvenile pollock and nearly 3.62×10^6 kg of small forage fish, such as capelin, eulachon and Pacific sandlance, during a 152-day feeding season. In comparison, tufted puffins consume less juvenile pollock (6.40×10^4 kg) between mid-July and mid-September, but this amount still accounts for one-tenth of the age-0 pollock stock in the Gulf of Alaska during early July (Hatch and Sanger, 1992). In addition, gadid removal by Steller sea lions in 1998 was estimated to be 1.79×10^8 kg, or 12% of the total gadid biomass that is removed by commercial fisheries for that year (Winship and Trites, 2003). This amount, although nearly 55 times the amount of pollock removal due to consumption by humpback whales, includes all gadid (not only pollock) species removals in all Alaskan waters. More importantly, these fish are likely larger (≥60 cm vs. ≤30 cm) than fish targeted by humpback whales.

Although humpback whales generally feed on smaller age classes than are targeted by commercial fisheries or Steller sea lions (Perez and McAlister[1]; Kenney et al., 1997), consumption of younger age classes may affect future recruitment into the fishery. Barrett et al. (1990) stated that consumption of young cod (*Gadus morhua)* and saithe (*Pollachius virens)* by shags (*Phalacrocorax aristotelis)* and cormorants *(P. carbo)* in the Northeast Atlantic could be a limiting factor in recruitment in years of low stock size, even if consumption of these species was overestimated by an order of magnitude. Thus, it is noteworthy that the removal by humpback whales of an estimated 3.26×10^6 kg of pollock (age 0–2) equals 30% of the 2002 commercial pollock harvest of 1.09×10^7 kg (ages 3 to 8) for the entire Kodiak Island management area and 2.1% of the 2002 spawning biomass of pollock for the entire Gulf of Alaska, which was estimated at 1.58×10^8 kg (NMFS[10]; NPFMC[11,12]).

These comparisons are based on mean estimates of prey removal and do not take into account model uncer-

[7] Wynne, K. M. 2002. Unpubl. data. Fishery Industrial Technology Center, Univ. Alaska Fairbanks, Kodiak, AK 99615.

[8] Jemison, L. A. 2001. Summary of harbor seal diet data collected in Alaska from 1990–1999. *In* Harbor seal investigations in Alaska (R. J. Small, ed.), p. 314–22. Ann. Rep. NOAA Grant NA 87Fx0300. Alaska Departmart of Fish and Game, P.O. Box 240020, Douglas, AK 99824.

[9] Best, E. A., and G. St. Pierre. 1986. Pacific halibut as predator and prey. International Pacific Halibut Commission Technical Report 21, 27 p. Website: http://www.iphc.washington.edu/halcom/pubs/techrep/tech0021.pdf. [Accessed on 31 May 2003.]

[10, 11, 12] *See next page for footnote text.*

tainty. When uncertainty is considered, comparison to even the lower end of estimates of prey removal are still of note. For example, assuming that removal of juvenile pollock is equal to the lower estimate, or 2.37×10^6 kg, the removal of pollock by humpback whales could still equal 21.7% of the 2002 commercial pollock catch and 1.5% of 2002 spawning biomass. Thus, it follows that if true consumption is actually closer to the upper estimates, the impact of prey removal by humpback whales would likely increase.

The humpback whale represents only one of a myriad of marine consumers within the Kodiak Island ecosystem whose ecological role cannot be determined without sophisticated multispecies models and an analysis of ecosystem interactions. This study was designed to provide essential baseline data and a model for estimating prey removal by foraging humpback whales. Our results show that the potential for biomass removal due to consumption by humpback whales is significant and that the foraging strategies of these whales warrant further investigation. Continued research efforts can improve estimates of biomass removal by identifying target prey, determining the degree of prey selectivity, and assessing variable foraging efficiency.

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[12] NPFMC. 2002. SAFE report for the groundfish resources of the Gulf of Alaska, Assessment of Walleye Pollock Stock in the Gulf of Alaska, 90 p. Website: http://www.afsc.noaa.gov/refm/stocks/Historic_Assess.htm [Accessed on 24 February 2004.]

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