# ABUNDANCE AND FEEDING ECOLOGY OF HUMPBACK WHALES (*Megaptera novaeangliae)* IN KODIAK, ALASKA

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A

THESIS

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# ABSTRACT

A feeding aggregation of humpback whales (*Megaptera novaeangliae)* in the Kodiak Island region has received little previous study. A mark-recapture experiment was conducted in 2001 and 2002 to estimate its abundance. Historical abundance was back-calculated from this estimate, whaling records, and suspected survival and productivity values within a population model. The current population was estimated at 157 whales and the pre-whaling population at 343 whales. Prey consumption by humpback whales was modeled using three methods for two hypothetical diets based on prey availability surveys conducted within the study area and stomach contents of commercially caught whales. By assuming current consumption is proportional to prey availability, the current population removes an estimated 9,600 tons of prey annually. Historical populations may have removed over 19,000 tons of prey annually.

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# CHAPTER 1: INTRODUCTION

## *Thesis objectives and organization*

There are two main objectives of this study: (1) to estimate abundance of current, pre-whaling (pristine), and immediate post-whaling eastern Kodiak Island humpback whale (*Megaptera novaeangliae)* populations, and (2) to use consumption rates to estimate the prey biomass removed seasonally by the pre-whaling and current populations.

In chapter two, I report results of the photo-identification study conducted during the summers of 2001 and 2002. Models presented in this chapter estimate current, pre-whaling, and immediate post-whaling abundances. In chapter three, humpback whale consumption and prey biomass removal is modeled based on hypothetical diets of pre-whaling and current humpback whale populations. Chapter four discusses how this study leads to an increased understanding of the foraging behavior and population dynamics of the eastern Kodiak humpback feeding aggregation and how these whales may relate to the Kodiak marine ecosystem as a whole.

## *Humpback whale biology and life history*

Humpback whales are baleen, or mysticete, whales belonging to the Balaenopteridae family. Weighing two tons and measuring four to five meters at birth, the humpback whale will grow to nearly 30 tons and 13 to 15 meters in length. Sexual maturity is reached at roughly five years, followed by physical maturity at 10 years of age (Chittleborough 1965). The oldest documented humpback whale was 48 years old when it was harvested by commercial whalers, but humpback whales are thought to have life spans similar to those of humans (Chittleborough 1965). Female humpback whales give birth to a single calf every two years following a 12-month gestation period (Chittleborough 1958).

The humpback whale is found worldwide in all major ocean basins. They are migratory animals that, in general, spend the summer months feeding in higher latitude waters and the winter months in low-latitude tropical or subtropical waters where they mate and give birth (Perry et al. 1999). In the summer months, the North Pacific humpback whales inhabit coastal waters from Point Conception, California, north to the lower Chukchi Sea in Alaska, along the Aleutian Islands, and into northern Japan (Rice 1978). Barlow (1994) lists four separate stocks within the North Pacific based on resightings, genetics, and historical whaling records, while Angliss et al. (2001) report only three stocks for management purposes. The three management stocks are the Eastern North Pacific (known as the California/Oregon/Washington stock), the Central North Pacific stock, and the Western North Pacific stock (Angliss et al. 2001).

The exact migration routes of the North Pacific humpback stocks are not well known (Perry et al.1990; Waite et al. 1999). It is generally believed that whales belonging to the western stock migrate to winter grounds in Japan from the Bering and Chukchi Seas and Aleutian Islands, while those in the central stock migrate to Hawaii from the waters of northern British Columbia to Kodiak Island, and those in the eastern stock migrate to Mexico from Washington, Oregon, and California. Recent studies indicate an additional breeding area may exist off the coast of Central America (Rasmussen et al. 1999). Geographically separate feeding aggregations are found within each stock are. A small degree of interchange (2 to 3%) may occur between stocks and aggregations, but, for the most part, they are isolated from one another (Baker et al. 1986; Calambokidis et al. 1996; Waite et al. 1999; Urbán et al. 2000).

*Mark recapture and photo-identification*

To achieve a better understanding of the population sizes and migration patterns of the humpback whale stocks, photo-identification of humpback whale flukes has been widely used throughout the world and has resulted in reasonable distribution information along the coast of the Pacific Ocean (Darling and McSweeny 1985; Mizroch et al. 1990; Perry et al. 1990; Baker et al. 1986, 1992; von Ziegesar 1992; Calambokidis et al. 1993). Long-term research in feeding areas has provided estimates of local abundance and an understanding of the humpback whale's role as an apex predator. Despite the longevity and success of this research, humpback whales in some waters of Alaska, including Kodiak Island (Figure 1.1) and the western Gulf of Alaska, have remained largely unstudied.

The small amount of research that has taken place in the Gulf of Alaska has provided evidence of a geographically segregated feeding aggregation in the waters of Kodiak Island, Alaska. Waite et al. (1999) published results from an opportunistic photo-identification study that took place during killer whale (*Orcinus orca)* surveys between 1991 and 1994. The study suggested that there may be a separate group of humpback whales that spends the summer months feeding around Kodiak Island and that there is little interchange between this group and other feeding groups found in Prince William Sound and southeastern Alaska (Waite et al. 1999). However, since humpback whale

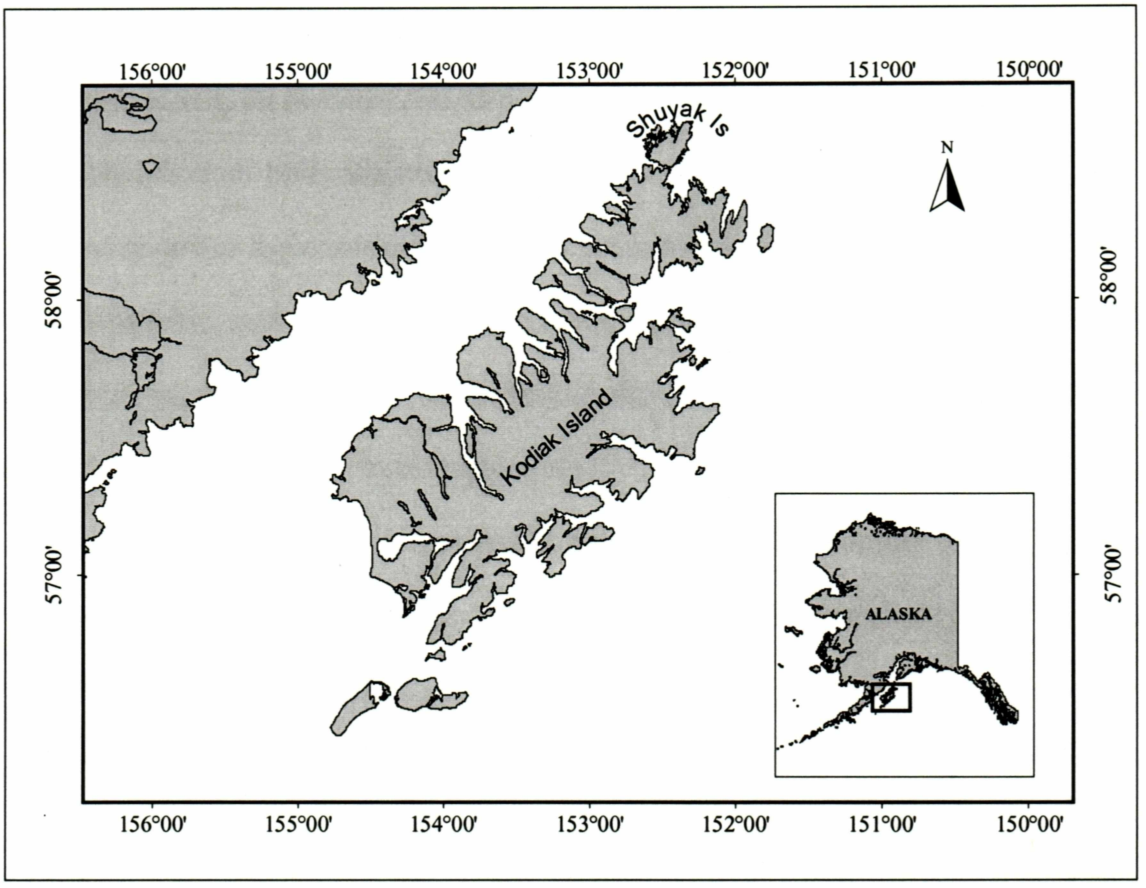

**Figure 1.1. Location of Kodiak Island.**

photos were only collected opportunistically further research was needed.

### *Ecosystem dynamics*

Cetaceans play important roles within marine ecosystems, though their role in these systems is often difficult to define (Katona and Whitehead 1988). Studies conducted in some oceans of the world, including the Southern Ocean and the Northeast Atlantic continental shelf, have shown how whales are significant predators and impact the environments in which they live (Laws 1985; Katona and Whitehead 1988; Kenney et al. 1997; Trites et al. 1997).

The depletions of blue (*Balaenoptera musculus)*, fin (*B. physalus)*, sei (*B. borealis)*, right (*Eubalaena glacialis)*, and humpback whales in the North Pacific by commercial whalers in the first half of the 20th century, may affect the degree to which a whale population influences ecosystem dynamics and cause reorganization of marine communities. The effects of removing cetacean biomass are not entirely understood. The reduction in cetacean biomass caused by commercial whaling could have significantly increased the amount of prey biomass available to other predators, essentially reorganizing trophic relationships (Katona and Whitehead 1988). It is generally believed that removing top predators, such as whales, will lead to an increase in the amount of available prey (NRC 1996; Trites 1997). This is known as trophic cascading and, though not widely studied in marine ecosystems, is seen frequently in freshwater systems. The trophic cascade hypothesis provides a conceptual framework for examining community processes and is based on the premise that ecosystems are driven by top-down, chainlike interactions between trophic levels (Stein et al. 1995). Trophic cascading results when changes in the density of predators results in a change in the density and species composition of prey and other predators (Carpenter et al. 1985).

Studies in the Southern Ocean have shown how trophic cascades can apply to cetacean removal. The exploitation of whales (including humpback whales) in the Southern Ocean heavily influenced the structure of the marine ecosystem by leaving large amounts of prey unconsumed (Laws 1985). The large reduction of whales in the Southern Ocean released an estimated 150 million tons of krill to other predators. Subsequent increases seals, birds, and unexploited whale species has been attributed to the increase prey biomass (Laws 1985). The species that experienced direct benefit from whale removal may now actually be hindering the recovery of whale stocks (Knox 1994).

Commercial whaling significantly reduced the number of humpback whales in the North Pacific, including the Gulf of Alaska. The North Pacific population of humpback whales is estimated to have been between 15,000 and 20,000 individuals before the commercial exploitation of this species began in the early 1900's (Rice 1978). Prior to international protection from harvest in 1967, humpback whales in the North Pacific may have been reduced to as few as 1,000 animals (Perry et al. 1990). Current population estimates list 6,010 animals in the central North Pacific and their numbers have not recovered to pre-exploitation levels (Calambokidis et al. 1997). Therefore, a situation similar to that in the Southern Ocean may have occurred in the North Pacific.

Presently, there is an increase in humpback whale abundance that may be influencing ecosystem dynamics. Humpback whales in the North Pacific may have increased by as much as 10% per year from the 1980s to early 1990s (Baker and Herman

1987; Calambokidis et al. 1997). This recent increase in the number of humpback whales feeding in Pacific waters may be affecting other apex predators, such as Steller sea lions (*Eumetopias jubatus),* through consumption of shared prey species.

Humpback whales in the North Pacific eat a highly varied diet of fish species, including herring (*Clupea harengus pallasi*), walleye pollock (*Theragra chalcogramma)*, capelin (*Mallotus villosus)*, and zooplankton (Nemoto 1957; Klumov 1963; Krieger and Wing 1984). Commercial fisheries and other apex predators target many of these same species. Therefore, humpback whales may exhibit a degree of prey overlap with other apex predators, including other marine mammals, bird species, and humans. This overlap could lead to competition for prey resources if prey is limited. Significantly limited prey resources or dietary overlap with other apex predators may affect the full recovery of the humpback whale to pre-whaling abundances (NRC 1996).

### *Kodiak Island ecosystem*

Humpback whales are established as apex predators within the Gulf of Alaska. The presence of a feeding aggregation of humpback whales around Kodiak could significantly affect ecosystem dynamics. Estimating abundance and examining foraging ecology of these whales would provide information essential to evaluating species interactions and the environmental impacts of feeding humpback whales. Estimation of consumption by humpback whales is of particular importance within the Kodiak region, as wide-sweeping biological changes have been seen throughout the Gulf of Alaska and Bering Sea within the last 30 to 40 years. The Gulf of Alaska and Bering Sea ecosystems have undergone a shift in community structure (Anderson and Piatt 1999). Beginning in the late 1970s, several marine mammal and bird species, as well as a variety of forage fishes, severely declined, while some gadid and flatfish species, such as walleye pollock and arrowtooth flounder (*Atherestes stomias)*, increased. One prominent shift is the decline in the western stock of Steller sea lions, by as much as 80% in some areas of western Alaska (NRC 1996; Merrick 1997). The cause of these changes is unclear, though several hypotheses have been proposed. One hypothesis states that changes in abundance of forage fish species (capelin, herring), and subsequent decline in marine mammal species, may have been brought about through a reorganization of the ecosystem caused by historical patterns of exploitation and climate changes (Merrick 1995; NRC 1996; Trites et al. 1999).

A large scale whaling operation run out of Port Hobron, Alaska from 1926 to 1937 resulted in the taking of nearly 1,600 humpback whales from the waters of the southeastern shores of Kodiak Island (Williams S. Lagen Collection unpub. data, University of Washington). Historical whaling data show humpback whales were consistently present in the eastern waters of Kodiak Island from May through October and that the Port Hobron whaling station, which was located on the southeastern side of Kodiak, "clearly specialized in catching humpbacks" (Leatherwood et al.1985). This implies that a large number of humpback whales once inhabited eastern Kodiak on a seasonal basis. The reduction in humpback population size caused by whaling was likely to have had effects on the surrounding ecosystem.

The relationship between the humpback's decline due to commercial whaling and changes in prey composition may be essential in understanding current and historical trends and predator-prey interactions in the Gulf of Alaska. At present, there is no reliable information on abundance for the Kodiak Island humpback whale feeding aggregation. Without abundance estimates and boundaries for this feeding aggregation, it is impossible to determine the amount of prey being consumed by these large predators. Historical and current abundance and predation data for the eastern Kodiak Island feeding aggregation of humpback whales can be combined to obtain an understanding of their role as apex predators. Further, this knowledge will provide insight into the Kodiak marine ecosystem as a whole and help to determine which apex predators may have potential to compete with one another for prey resources. Understanding the potential for competitive relationships may provide insights into the cause of recent declines in such species as the Steller sea lion, the increase of various groundfish species, and trophic dynamics of the Kodiak Island ecosystem.

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# CHAPTER 2: AN APPARENT FEEDING AGGREGATION OF HUMPBACK WHALES (*Megaptera novaeangliae)* NEAR KODIAK ISLAND, ALASKA: HISTORICAL AND CURRENT ABUNDANCE ESTIMATION[1]

## ABSTRACT

A photo-identification, mark-recapture study was conducted on a previously unstudied feeding aggregation of humpback whales (*Megaptera novaeangliae)* in the waters of eastern Kodiak Island. The Schnabel maximum likelihood estimator for closed populations was used to estimate current abundance. An estimated 157 (95% confidence interval (CI): 114, 241) whales were in the study area based on sightings of individual whales from June through September 2002. This estimate was used to back-calculate historical abundance using a delay difference model with a density dependent recruitment function. Estimated abundance within the study area just prior to commercial whaling, which began in 1926, was 343 (331, 376). Estimated abundance immediately following the cessation of whaling in the Kodiak region in 1938 was 27 (14, 61).

## INTRODUCTION

A group of feeding humpback whales (*Megaptera novaeangliae)* can be found year-round, with a peak in sightings occurring between June and October, in the Kodiak Archipelago in the western Gulf of Alaska (Waite et al. 1999; Zwiefelhofer unpub. data). These whales are currently assigned to the Central North Pacific (CNP) stock of humpback whales by the National Marine Fisheries Service (NMFS), though no directed

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[1] Prepared for submission to *Marine Mammal Science* as "An apparent feeding aggregation of humpback whales (*Megaptera novaeangliae) near Kodiak Island, Alaska: Historical and current abundance estimation."* By Briana H. Witteveen.

research has been conducted on this population (Angliss et al. 2001). These whales are not associated with any known feeding aggregation in Alaskan waters and their abundance has never been estimated. Understanding of the structure of North Pacific humpback whales, therefore, remains incomplete, making need for research efforts in this region critical to management.

Necessity for humpback whale research in the Kodiak Island area also stems from the need to monitor recovery rates of the population. Large-scale commercial whaling occurred on Kodiak Island between 1926 and 1937, significantly reducing the number of humpback whales in the area (Williams S. Lagen Collection unpub. data, University of Washington). All stocks of humpback whales diminished by commercial whaling are believed to be increasing, but data are inadequate to assess the rate of increase (Angliss et al. 2001).

In answer to the need for humpback whale research near Kodiak Island, a study to assess humpback whale numbers in this region began in 2001. This study estimated abundance for a portion of eastern Kodiak Island humpback whales based on photo-identification studies conducted in 2001 and 2002. Estimates of pre-whaling and immediate post-whaling populations are also constructed using a delay-difference population model (Quinn and Deriso 1999).

Photo-identification has been used for many years as a mark-recapture tool for estimating humpback whale populations and tracking their movements (Baker et al. 1986, 1992; Perry et al. 1990; von Ziegesar 1992; Calambokidis et al. 1993). Photo-identification studies have resulted in moderate understanding of humpback whale stocks in the North Pacific and have proven that, though they may converge on winter breeding grounds, humpback whales are isolated into regional aggregations during feeding seasons with very little exchange between them. Known feeding aggregations in the North Pacific are found along the California/Oregon/Washington coast and southeastern Alaska (Calambokidis et al. 1993; Straley 1994).

## METHODS

### *Study area*

The study area was limited to the waters of eastern Kodiak Island, including Chiniak and Marmot Bays. Kodiak Island is part of the Kodiak Archipelago and is located approximately 30 miles from the Alaskan mainland in the Gulf of Alaska. In 2002, the study area was divided into four subareas of approximately equal size (Figure 2.1). The subareas were established in order to equalize sampling effort and ensure thorough coverage within the study area. Due to low sample sizes, subarea data could not be used for abundance estimation.

### *Vessel surveys and field data*

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 (Figure 2.2) (Katona et al. 1979). Photographs were taken during vessel surveys with a 35 mm camera with 300 mm lens and black and white 3200 ASA speed film exposed at 800 ASA. Fluking behavior was not always observed and, in such cases, a photograph of the animal's dorsal fin was taken from the right side.

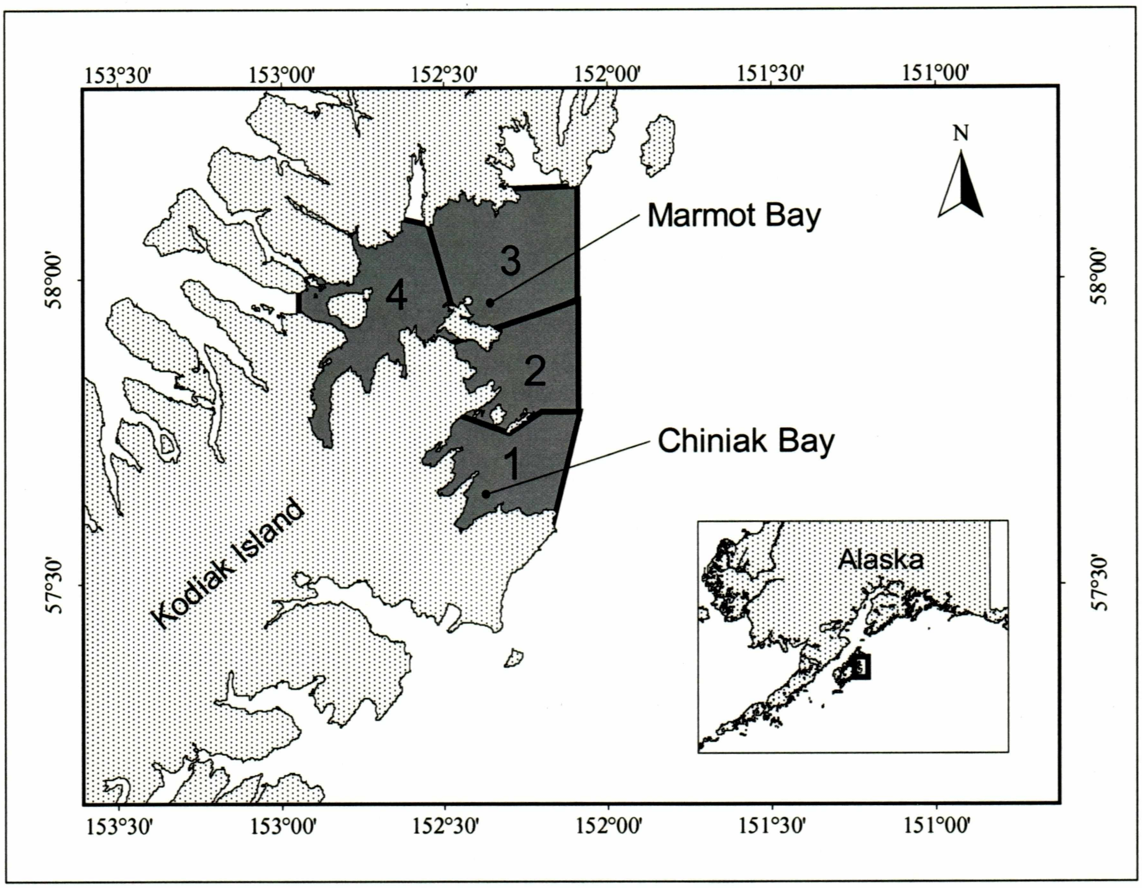

**Figure 2.1. Map of Kodiak Island study area. Study area is shown in shade with subareas outlined and numbered.**

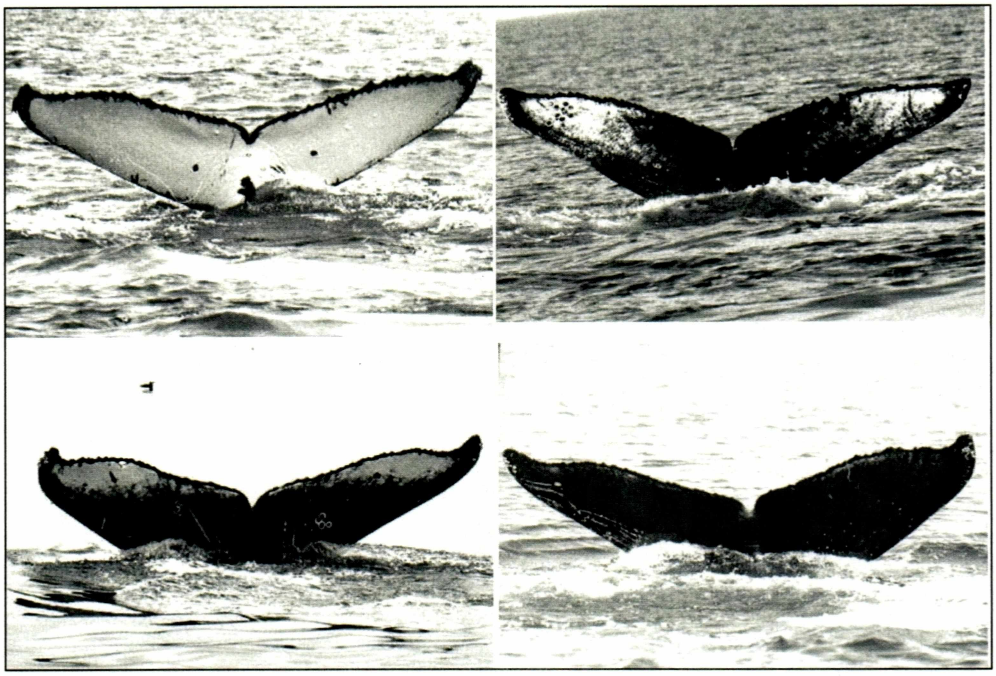

**Figure 2.2. Examples of black and white photographs of humpback whales flukes. Variation in pigmentation and distinctive marks were used to identify individuals.**

In addition to photographs, data collected included the date, time, latitude and longitude, nearest headland, and general behavior of the whale. Information about the number of whales in the group and the role (mother, calf, adult) of each whale was documented for each encounter.

Photographs of calves were not used in the analysis, due to the tendency of the fluke pattern of some calves to change prior to maturity. Dorsal fin photographs of whales were only used in sighting histories if the dorsal fin could be matched to a later dorsal fin with a fluke photograph. Cases in which only the dorsal fin photograph was collected were not used in abundance estimation.

### *Study and sample periods*

Vessel surveys were conducted during study periods in June through September of 2001 and 2002 from the R/V Soundwave, an 8.2-meter (27 foot) bowpicker. The study periods for each year were divided into sample periods. Sample periods were seven days in length with the exception of the final sample periods in both years (Table 2.1). In 2002, a survey of each subarea was attempted at least once during the sample period. Adverse weather conditions prevented surveys of each area during every sample period. Vessel surveys were often initiated in areas where whales were previously sighted.

The 2001 study period consisted of 10 total sample periods beginning June 13th and ending September 14th (Table 2.1). Surveys took place for 18 days and a total of about 74 hours. Effort in 2002 consisted of 15 sample periods beginning June 4th and ending September 17th. Surveys took place on 38 days for a total of about 224 hours.

**Table 2.1. 2001 and 2002 effort for humpback whale photo-identification vessel surveys.**

| | Year | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 2001 | | | | 2002 | | | |
| Sample Period | Period Start Date | Period End Date | Number of days sampled | Number of hours sampled | Period Start Date | Period End Date | Number of days sampled | Number of hours sampled |
| 1 | 11-Jun | 17-Jun | 2 | 4.9 | 3-Jun | 9-Jun | 4 | 27.9 |
| 2 | 18-Jun | 24-Jun | 3 | 14.4 | 10-Jun | 16-Jun | 4 | 29.1 |
| 3 | 25-Jun | 1-Jul | 2 | 8.6 | 17-Jun | 23-Jun | 3 | 17.9 |
| 4 | 2-Jul | 8-Jul | 1 | 8.3 | 1-Jul | 7-Jul | 5 | 28.8 |
| 5 | 9-Jul | 15-Jul | 3 | 14.6 | 8-Jul | 14-Jul | 3 | 17.8 |
| 6 | 16-Jul | 22-Jul | 1 | 4.6 | 15-Jul | 21-Jul | 2 | 10.7 |
| 7 | 23-Jul | 29-Jul | 1 | 2.1 | 22-Jul | 28-Jul | 2 | 10.5 |
| 8 | 30-Jul | 5-Aug | 3 | 9.1 | 29-Jul | 4-Aug | 4 | 23.7 |
| 9 | 3-Sep | 9-Sep | 1 | 3.0 | 5-Aug | 11-Aug | 2 | 10.3 |
| 10 | 10-Sep | 14-Sep | 1 | 4.0 | 12-Aug | 18-Aug | 1 | 5.3 |
| 11 | | | | | 19-Aug | 25-Aug | 3 | 13.9 |
| 12 | | | | | 26-Aug | 1-Sep | 1 | 4.9 |
| 13 | | | | | 2-Sep | 8-Sep | 1 | 7.0 |
| 14 | | | | | 9-Sep | 15-Sep | 1 | 8.8 |
| 15 | | | | | 16-Sep | 17-Sep | 2 | 7.7 |
| Total | | | 18 | 73.6 | | | 38 | 224.1 |

Survey effort was increased in 2002 primarily due to vessel availability. Survey effort by subarea in 2002 was fairly uniform (Table 2.2).

*Current abundance estimation*

An estimate of current humpback whale abundance within the study area was made using the Schnabel maximum likelihood estimator (MLE) (Seber 1982). The Schnabel MLE of $\hat{N}$ is the solution of the equation

$$1-\frac{r}{N}=\prod_{i=1}^{s}(1-\frac{n_i}{N}). \qquad (2.1)$$

Details of the Schnabel MLE are described in appendix A.1. A closed population is the primary assumption of the Schnabel MLE. Additional assumptions are outlined in detail in appendix A.2.

The Schnabel MLE was only applied to 14 sample periods in 2002 because no whales were seen in the shortened 15th sample period. Model input is summarized in appendix A.3. Small sample sizes in 2001 prevented estimation of abundance, due to four of the nine periods having a zero for the *m* parameter. The 2002 data were also pooled to three and five sample periods. Pooling was performed by separating the study period into three or five sample periods, as opposed to the original 15, and analyzing sighting histories within those periods. The pooled sample periods were created so that an equal number of seven-day sample periods were represented in each of the pooled periods.

A parametric bootstrap was performed to obtain 95% confidence intervals for $\hat{N}$ (Appendix A.4). Upper and lower 95% confidence intervals were calculated using the

**Table 2.2. Effort by subarea in 2002 for humpback whale photo-identification surveys.**

| Subarea | Number of Days | Number of Hours |
|---|---|---|
| 1 | 13 | 53.5 |
| 2 | 18 | 70.6 |
| 3 | 9 | 56.0 |
| 4 | 7 | 44.0 |
| Total | 47[*] | 224.1 |

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[*] Number of days totals 47 and not 38 due to survey of more than one area in a single day. 2001 effort was not tracked by subareas.

percentile method in which $\alpha$ equals 0.05 and the $\alpha/2$ and $1-\alpha/2$ percentiles of the bootstrap replicates represent the lower and upper confidence intervals. The bootstrap was performed with 1,000 replicates.

Alternatives to the closed population Schnabel MLE were also explored. A Jolly-Seber estimate was calculated for the 2002 data. This method of estimation assumes an open population and allows for recruitment and mortality to occur within the study period. In addition, robust estimators from program MARK, including the Pollock robust model that combined results from 2001 and 2002, were also explored (White and Burnham 1999).

*Historical abundance estimation*

Estimates of eastern Kodiak Island humpback whales within the study area were calculated for pre-whaling (pristine) and immediate post-whaling populations following an Allen-Clark delay-difference model (Quinn and Deriso 1999). The following equation, adapted from Breiwick et al. (1981), was used to calculate historical abundances, which were dependent upon the current abundance estimate and historical catch:

$$N_{t+1} = (N_t - C_t)(1 - M) + R_t \tag{2.2}$$

where $N_t$ = population size at the beginning of year $t$

$C_t$ = catch in year $t$

$M$ = natural mortality rate

$R_t = r_t N_{t-\tau}$ is the gross recruitment between the beginning of year $t$ and $t+1$

$\tau$ = lag time assumed for population response.

The recruitment rate was assumed to be a density-dependent function, according to the equation:

$$r_t = M + (1 - \frac{N_{t-\tau}}{N_o})(r - M) \tag{2.3}$$

where $r_t$ = recruitment rate in year *t*

$N_0$ = initial population size (pristine population size prior to commercial exploitation)

*(r-M)* = net recruitment rate.

An equilibrium solution for equation 2.2 when $C_t = 0$ is

$$\left(1 - \frac{N}{N_0}\right)(r - M) = 0. \tag{2.4}$$

Therefore, at equilibrium either $N = N_0$ or $r - M = 0$. The value of $N_0$ is defined as the carrying capacity for the population.

Net recruitment rates for humpback whales, and cetaceans in general, are difficult to estimate. Most estimates of net recruitment result from long-term population studies of female calving intervals and are often found to be around 0.06 (Clapham and Mayo 1987; Steiger and Calamobkidis 2000). Net recruitment values for humpback whales are low due to the fact that they are long lived whales that produce a single offspring every one to five years (Straley 1994). Currently, there are no estimates of net recruitment for humpback whale populations in the North Pacific. Therefore, the value of net recruitment was set equal to 0.04, which is equal to the general cetacean maximum productivity rate defined by Wade and Angliss (1997). The value of $M$ was taken as one minus survival rate. A survival rate of 0.96 came from the estimated survival rate for humpback whales in the North Pacific (Mizroch et al. in review). The values of $r$ followed from the fact that the net recruitment rate is equal to $r$ minus $M$. The value of $r$ was thus set equal to 0.08 in order to achieve a net recruitment rate of 0.04 given an $M$ of 0.04. The value of $\tau$ was set equal to five years, as per the age of average sexual maturity in humpback whales (Chittleborough 1958, 1959; Clapham and Mayo 1990).

The values for $C_t$ were taken from the William S. Lagen collection at the University of Washington. The collection contains catch history, including date, year, and number of kills for humpback whales harvested out of the Port Hobron whaling station in Kodiak, Alaska (Figure 2.3). Locations of most kills are given in the collection, but are very general and typically only account for approximate bearing and distance offshore in which the whale was harvested. The whaling grounds encompassed most of eastern Kodiak Island; an area approximately four times that of the study area (Figure 2.3). As a result, values of $C_t$ were divided by four to account for the size difference between whaling grounds and the study area.

Initial population size, $\hat{N}_0$, was estimated by first entering a trial value for $\hat{N}_0$ into equation 2.2 and projecting the population forward to 2002. The estimate for $\hat{N}_0$ was the value that resulted in $\hat{N}_{2002}$ corresponding to the MLE, given values of $C_t$, $R_t$, and $M$. The initial population size applies to the years 1920 through 1925 and is assumed to represent the carrying capacity prior to commercial exploitation. Once a value of $\hat{N}_0$

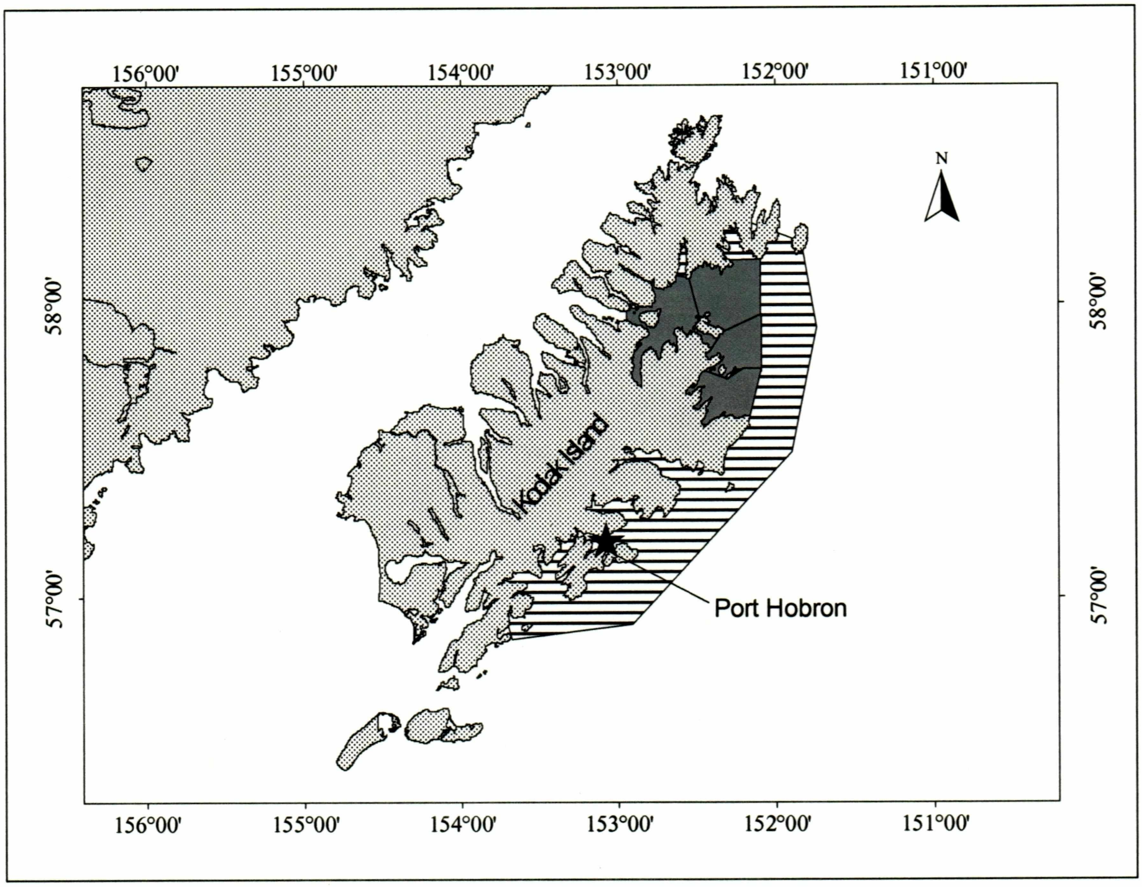

**Figure 2.3. Location of the Port Hobron whaling station. The approximate coverage area of commercial whaling operations is shown in stripes and the study area is shown in shade.**

was found, population size at any subsequent time period could be estimated. Thus, immediate post-exploitation abundance, $\hat{N}_{1938}$, was easily found by use of this method. The spreadsheet Excel was used to find the parameter estimate $\hat{N}_0$. Appendix A.5 shows model input. The values of $\hat{N}_0$ and $\hat{N}_{1938}$ were dependent on $\hat{N}_{2002}$, therefore confidence intervals for each followed from a parametric bootstrap in which $\hat{N}_0$ and $\hat{N}_{1938}$ were estimated based on the $\hat{N}_{2002}$ values from the previous 1,000 bootstrap replicates. Upper and lower 95% confidence intervals were calculated using the percentile method in which $\alpha$ equals 0.05 and the $\alpha/2$ and $1-\alpha/2$ percentiles of the bootstrap replicates represent the lower and upper confidence intervals.

*Sensitivity study of historical estimation to model parameters*

A sensitivity study of the $r$ and $M$ parameters in the delay-difference model was performed in order to determine which parameter was the most influential in the final estimation of historical population sizes. Changing the value of each of the parameters and re-running the model tested the sensitivity of the model to each parameter. New values of $M$ and $r$ were used to reflect both higher and lower values than the baseline model. The two parameters were tested independently from one another, meaning if the value of $M$ was changed, $r$ was not. Values of $M$ used came from the 95% confidence intervals of survival from Mizroch et al. (in review), which equaled 0.94 and 0.98. Therefore values of $M$ were 0.02 and 0.06. No confidence intervals were available for $r$, so values were set at 0.06 and 0.10 to reflect both lower and higher rates of recruitment. An additional scenario was examined in which $r$ and $M$ were both set equal to 0.04 to represent a situation in which net recruitment was zero. A final scenario set net recruitment equal to 0.10 between 1980 and 1990 inclusively to reflect a period of increased productivity (Baker and Herman 1987; Calambokidis et al. 1997).

### *Sensitivity study of historical estimation to catch numbers*

A sensitivity study of the historical catch ($C_t$) in the delay-difference model was performed in order to determine how influential catch was in the final estimation of historical abundance. To test the sensitivity of the model to catch, catch numbers were left as given values as well as divided by two to represent scenarios in which catch within the study area comprised either all or one half of the total number of humpback whale kills. Results were compared to the base model in which catch numbers were divided by four.

## RESULTS

### *Vessel surveys*

Vessel surveys in 2001 resulted in 68 sightings of 50 individual whales (Table 2.3). Nineteen of the 50 individual whales sighted were calves or animals for which only a dorsal photograph was obtained. These animals were excluded from the analysis; therefore fluke photographs of 31 individuals were captured in 2001. Adult whales were sighted in all months surveyed. The peak number of sightings occurred in sample period eight, representing dates from late July through early August. A total of 12 sightings were documented during this period. The fewest number of sightings (0) occurred in the 10th sample period.

**Table 2.3. Number of sightings and the number of flukes photographed by period. Photographs were collected during humpback whale vessel surveys conducted in 2001 and 2002.**

| | Year | | | |
|---|---|---|---|---|
| | 2001 | | 2002 | |
| Sample Period | Number of sightings (adults only)[*] | Number of flukes photographed | Number of sightings (adults only) | Number of flukes photographed |
| 1 | 3 | 2 | 4 | 3 |
| 2 | 7 | 7 | 8 | 6 |
| 3 | 5 | 5 | 13 | 11 |
| 4 | 4 | 4 | 11 | 10 |
| 5 | 5 | 5 | 29 | 28 |
| 6 | 2 | 1 | 1 | 1 |
| 7 | 2 | 2 | 7 | 5 |
| 8 | 12 | 11 | 9 | 7 |
| 9 | 5 | 3 | 1 | 0 |
| 10 | 0 | 0 | 0 | 0 |
| 11 | | | 3 | 2 |
| 12 | | | 4 | 4 |
| 13 | | | 2 | 2 |
| 14 | | | 11 | 11 |
| 15 | | | 0 | 0 |
| Total | 45 | 40 | 103 | 90 |

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[*] Number of sightings columns includes adult whales with dorsal fin only photographs.

Vessel surveys in 2002 resulted in 148 sightings of 103 individual whales (Table 2.3). As in 2001, some sighted whales were calves or animals with no associated fluke photograph. Thus, 2002 vessel survey data resulted in fluke photographs of 71 individual whales that were used in analysis. Adult whales were sighted in all months surveyed. The fifth sample period, representing dates in mid-July, had the most sightings with 29. Sample periods 10 and 15 both had zero animals sighted.

*Current abundance estimation*

The Schnabel MLE of abundance in 2002 was 157 (CV 18%) animals with a 95% confidence interval of (114, 241). Pooled estimates of $\hat{N}$ resulted in higher CVs and are not reported here. Estimated parameters in the Jolly-Seber method, such as capture probability and survival, were not biologically realistic (i.e. survival over 100%). Thus estimates of abundance from the Jolly-Seber method are not reported. Robust models produced highly unreasonable results, including negative estimates of abundance and capture probability, due to low sample sizes. Therefore, estimates from robust models are also not reported.

*Historical abundance estimation*

The delay difference model estimated the pre-whaling humpback whale abundance at 343 (CV 3%) animals within the study area given a value of $\hat{N}_{2002}$ equal to 157 (Figure 2.4). The 95% confidence interval was (331, 376). The model estimated post-whaling abundance, $\hat{N}_{1938}$, as 27 (CV 42%) animals, with a confidence interval of (14, 61).

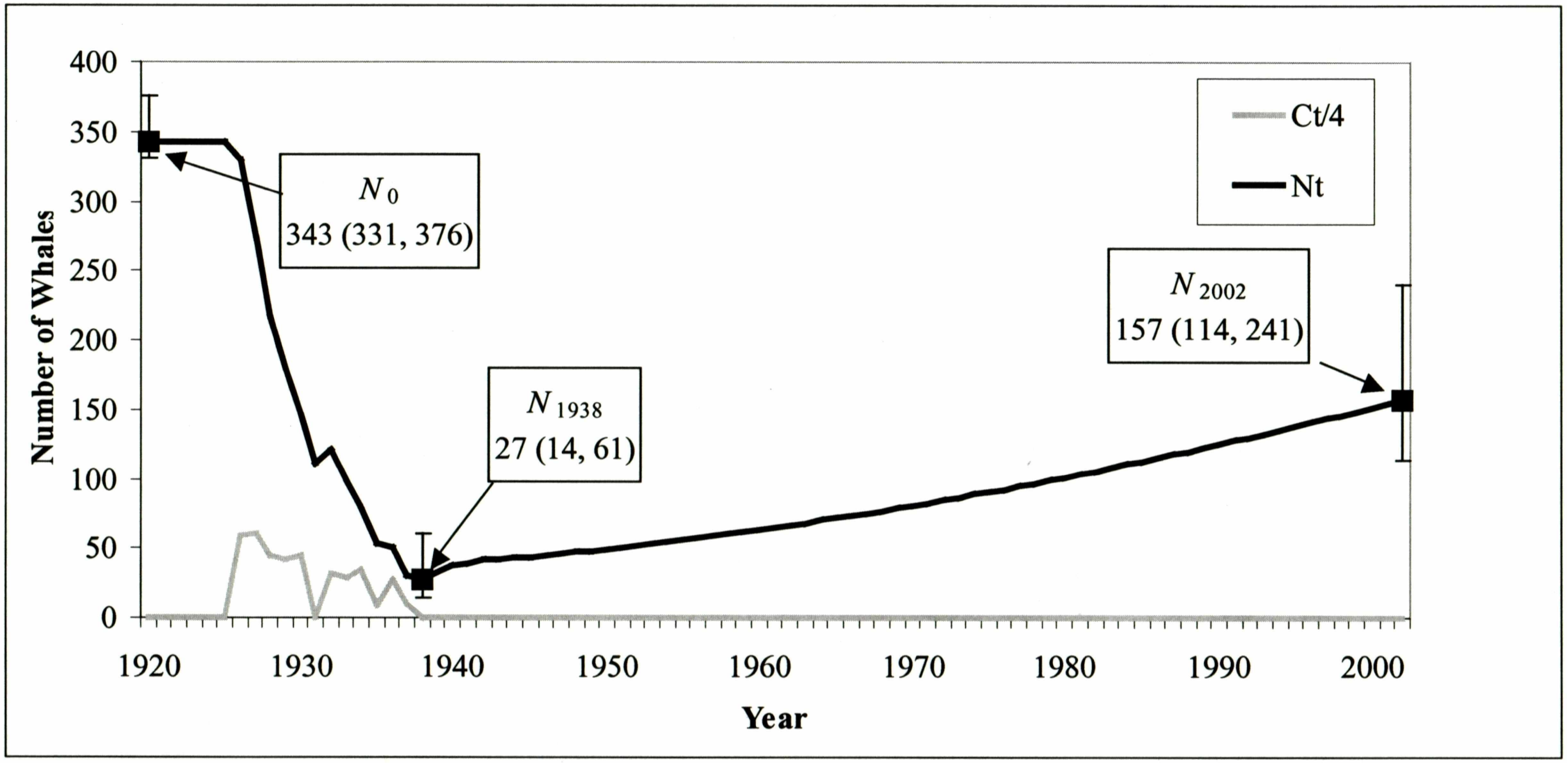

**Figure 2.4. Comparison of adjusted commercial catch ($C_t/4$) and estimated abundance ($N_t$). Abundance estimates (± 95% CI) from delay-difference model for $N_0$, $N_{1938}$, and $N_{2002}$ are shown.**

### *Sensitivity study of historical estimation to model parameters*

Pristine abundance was estimated at 341 and 373 when $M$ was equal to 0.02 and 0.06 respectively. $N_{1938}$ equaled 5 and 72 under the same parameterization (Figure 2.5). Pristine abundance was estimated at 392 and 371 when $r$ was set equal to 0.06 and 0.10, respectively. $N_{1938}$ was equal to 67 and 8 under the same parameterization. During the "1980" scenario pristine abundance was estimated at 332 and $N_{1938}$ was equal to 16 (Figure 2.6). Similar patterns of population growth and decay were seen for all values of both $M$ and $r$.

### *Sensitivity study of historical estimation to catch numbers*

When historical catch numbers were divided in half, representing a scenario in which one half of humpback whale kills occurred within the study area, pristine abundance was estimated at 645 and abundance in 1938 was estimated at 11. When catch numbers were not altered and 100% of the historical catch was assumed to occur within the study area, $N_0$ was estimated at 1258, while $N_{1938}$ was estimated at -11 (Figure 2.7).

## DISCUSSION

### *Vessel surveys and humpback whale sightings*

More humpback whales were sighted in the Kodiak Island study area in 2002 than in 2001. Supplemental information provides evidence that increased sightings in 2002 may have been due to both an increase in survey effort, both temporally and spatially, and an increase in the number of humpback whales occurring within the study area during that year. Results show that 2.5 whales were sighted per day in 2001, while 2.7 whales per day were sighted in 2002, yet, 0.61 whales were sighted per hour in 2001,

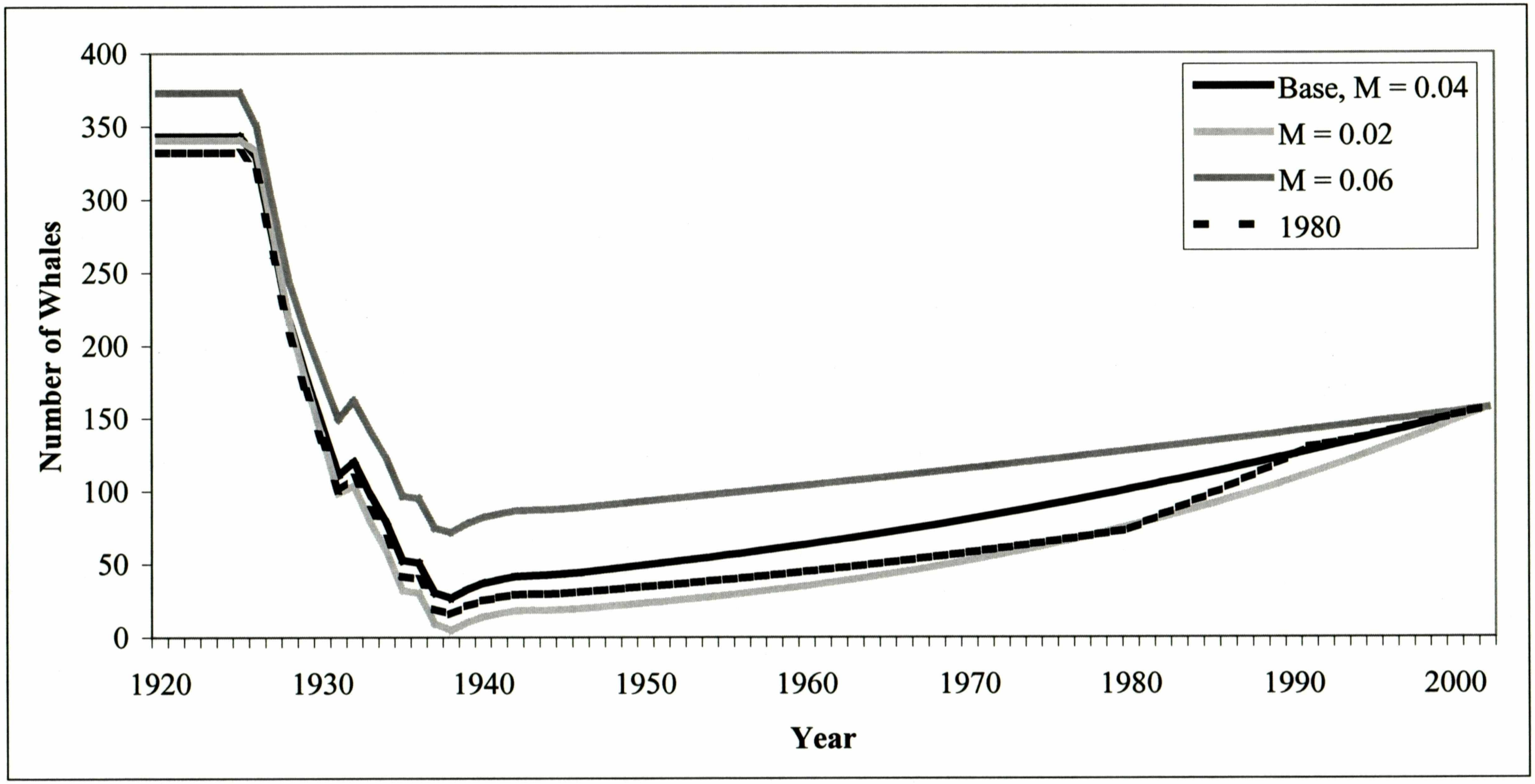

**Figure 2.5. Comparison of estimated abundance showing sensitivity of the delay-difference model to the mortality parameter *M*. Parameter *M* equals 0.02, 0.04 (base model), and 0.06 while parameter *r* remained fixed at 0.04. Also shown is the "1980" scenario in which (*r*-*M*) was fixed at 0.10 between 1980 and 1990.**

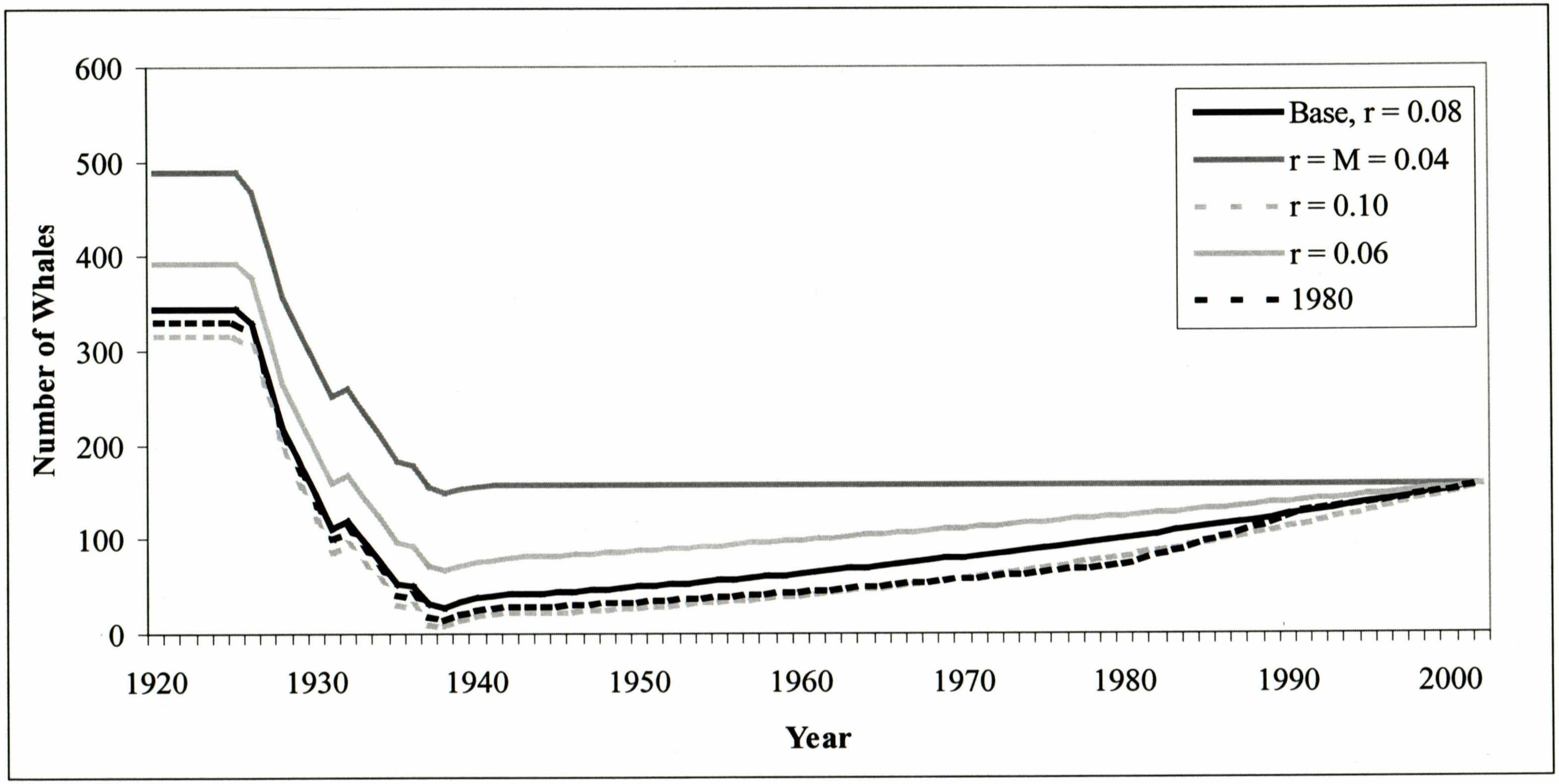

**Figure 2.6. Comparison of estimated abundance showing sensitivity of the delay-difference model to the recruitment parameter *r*. Parameter *r* equals 0.04 (*r=M*), 0.06, 0.08 (base model), and 0.10 while parameter *M* remained fixed at 0.04. Also shown is the "1980" scenario in which *(r-M)* was fixed at 0.10 between 1980 and 1990.**

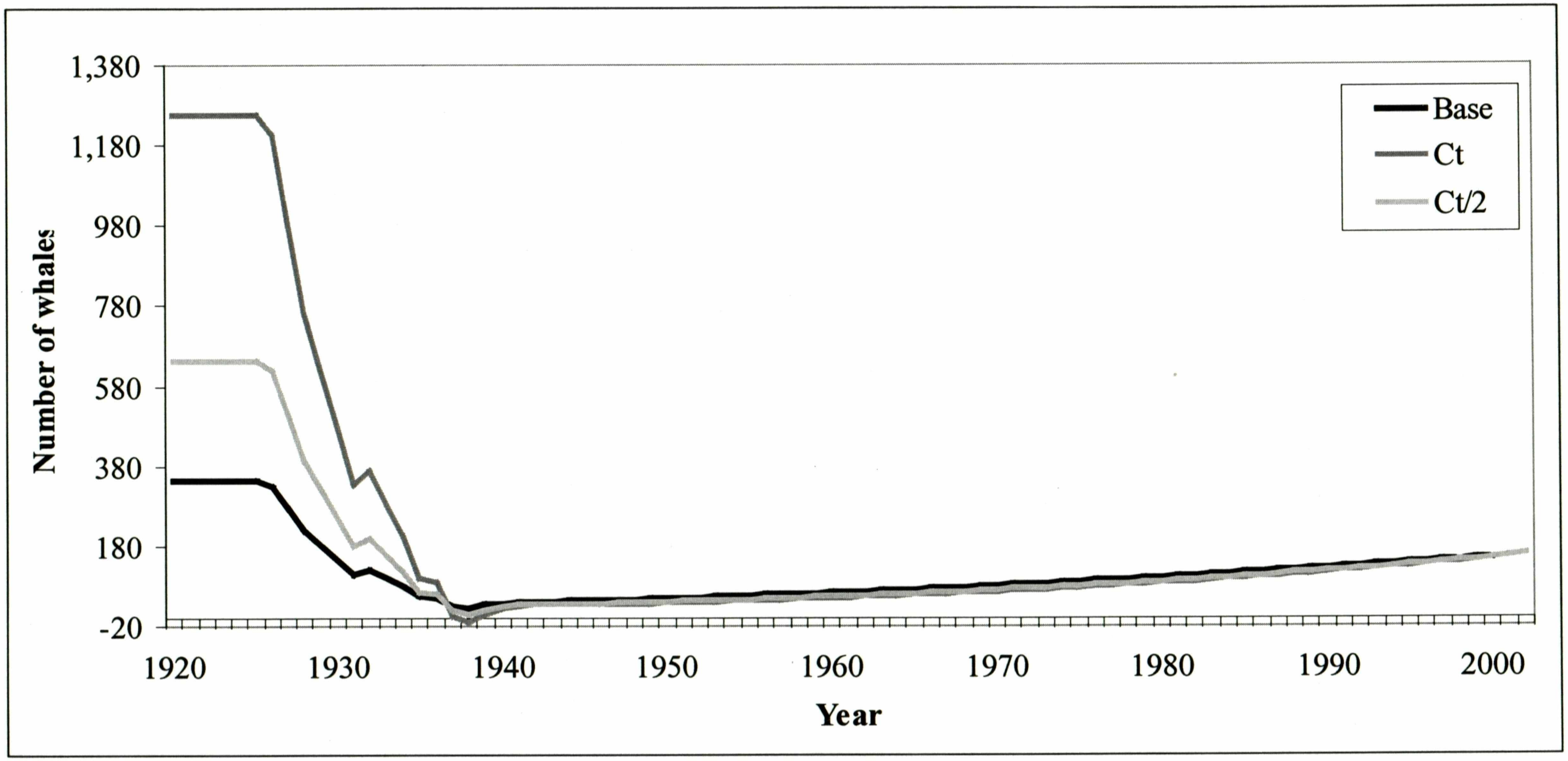

**Figure 2.7. Comparison of estimated abundance showing sensitivity of delay-difference model to catch ($C_t$). Shown are the scenarios in which $C_t$ equals total catch, one half of total catch, and one fourth of total catch (base model). All other parameters are fixed.**

while only 0.46 whales were sighted per hour in 2002. This would indicate that the increased number of sightings in 2002 may have been due, in part, to an increase in total hourly survey effort.

There is evidence to suggest that an increase in sightings in 2002 was also due to increased humpback whale occurrence within the study area in 2002. Monthly aerial surveys of Steller sea lion habitats conducted during the 2001 study period revealed no large concentrations of humpback whales anywhere around Kodiak Island. Similar aerial and vessel surveys in 2002, however, showed large aggregations of humpback whales both in the study area and in other areas along the east side of Kodiak Island, suggesting humpback whale abundance increased throughout the area (K.Wynne, unpubl. data).

The reasons for possible lower abundance in 2001 than in 2002 are unknown; food limitation did not seem to be a factor. Trawl surveys within the study area in 2001 showed episodes of forage fish moving into the area and a constant large biomass of juvenile pollock, a pattern similar to 2002 when more whales were sighted (R. Foy, pers.comm.). Piscivorous birds in the region experienced exceptional productivity in 2001 and were assumed to be feeding from the same prey base as the whales (C.L. Buck, pers. comm.).

Though prey was not limited within the study area in either 2001 or 2002, the availability of preferred prey or concentration of prey in other regions may have accounted for an absence of humpback whales in the study area during 2001. Humpback and other baleen whales are known to respond to concentrations of prey types (Piatt et al. 1989). Fluctuations in abundance of humpback whales have been seen to directly correlate to the concentration or availability of certain prey types, such as capelin or euphausiids (Krieger and Wing 1986). Such fluctuations can occur seasonally or annually. Thus, humpback whales that would normally feed in the waters near Kodiak may have abandoned the grounds in 2001 for a preferred or more abundant source of prey in another region of western Alaska, such as the Shumagin Islands, the Barren Islands, or Shuyak Island. Such a preferred or more abundant prey source may not have been available in 2002.

However, at present, too few data exist to make statements on patterns of use. Two years of data cannot be used to determine trends in humpback whale sightings. Continued research and uniform survey effort across years within the study area may lend insight into the inter-annual variability of humpback sightings within the Kodiak Island study area.

### *Current abundance estimation*

The Schnabel unconditional MLE estimated abundance for the Kodiak Island humpback whale population within the study area with a reasonable CV of just over 18%. However, the model may have not met at least two of its assumptions; closure and equal probability of capture.

A violation to the closure assumption stemmed from the limitation of the study area. The study area was defined based on historical accounts of humpback whale occurrence and vessel accessibility from the city of Kodiak and did not incorporate all areas around Kodiak Island in which humpback whales may feed. Thus, this study estimated only a proportion of the whales that may be part of a much larger feeding aggregation. The whales in the study area may belong to a feeding aggregation that utilizes waters not only around Kodiak Island, but waters throughout the western Gulf of Alaska as well. Whales may have migrated into and out of the study area throughout the study period, as humpback whales have been previously observed throughout the Kodiak archipelago. Areas of high concentration have been historically found along the east coast and in some northwest bays of Kodiak Island, as well as near Shuyak Island (Figure 1.1) (Reeves et al. 1985, Waite et al. 1999, K.Wynne, unpubl. data, Zwiefelhofer, unpubl. data). Within recent years, however, the study area has represented one of the areas of highest humpback whale concentration (K. Wynne, unpubl. data).

The amount of movement that may have occurred into and out of the study area cannot be estimated without photo-identification effort in other high use areas around the island. One survey of the entire east coast of Kodiak Island in September 2002 sighted 67 individual whales outside of the study area, of which only two whales had been previously sighted in the study area within the study period (B. Witteveen, unpubl. data). This would suggest some very limited movement between the whales within the study area and other feeding whales around Kodiak Island, but data were too few to draw conclusions about the degree of violation to the closure assumption within the study area.

Despite other areas of high use by humpback whales and slight evidence for movement out of the study area, the assumption of closure was probably justified due to the fact that only a single year of sighting histories was examined. However, if high enough degrees of mortality and recruitment, as well as immigration and emigration, were present during the study period, abundance would be overestimated (Seber 1982).

The assumption of equal probability of capture within each sampling period may not be satisfied. The Schnabel MLE allows for time-varying capture probabilities, meaning capture probability was equal for all animals at each time period, but not, necessarily, over all time periods. Equal capture probabilities for all whales at each sample period is highly unlikely.

Heterogeneity in capture probability affects abundance estimators at the most general level. Within the context of this photo-identification study, heterogeneity is defined by unequal probabilities of capturing fluke photographs of individual whales, primarily stemming from variations in fluking behavior. Nearly all estimators of animal populations are based on the fundamental equation

$$\hat{N} = \frac{n}{p},$$

where $n$ is the sample size and $p$ is the probability of capture (Seber 1982). When heterogeneity in $p$ is present within a population, the animals that are captured, photographed in this case, are those that are the most catchable and $p$ is overestimated. An overestimation in $p$ subsequently causes an underestimate of $\hat{N}$.

Program CAPTURE was used to evaluate the degree of heterogeneity in the 2002 sighting data (Rexstad and Burnham 1992). CAPTURE extends the Schnabel experimental design by applying sighting histories to increasingly complicated models in which the probability of capture varies with time, behavior, and heterogeneity. The program then recommends models that best represent the input data. Two of the top four models suggested by CAPTURE included heterogeneity as a factor in estimation, though the top recommended model did not. Thus, program output suggested that heterogeneity may be present to some extent.

Problems with model assumptions such as these may be rectified in the future as effort continues and sample size is increased. Additional research will further clarify habitat usage by humpback whales within the Kodiak Island study area and the degree of exchange between these whales and feeding humpback whales in other regions of western Alaska. This would allow for more advanced models that examine closure assumptions and heterogeneity in $p$ to be utilized (Pollock et al. 1990; White and Burnham 1999).

### *Historical abundance estimation*

The estimation of the historical populations of humpback whales was dependent on the estimate of current abundance. A negative bias associated with the current estimate would lead to underestimation of the historical estimates. However, the estimated carrying capacity was affected more by the whaling removals and choice of parameters $r$ and $M$.

Sensitivity study results show the delay-difference model was highly dependent on the values of $M$ and $r$. Changing each value by a few percent causes changes in estimates of abundance throughout the time scale by means of changes in net recruitment to the population. In cases when $r > M$, the population will continue to increase until carrying capacity is reached. When $r < M$, the population will decrease. The mortality parameter seems to exert more influence on the model, causing larger variations in estimates from the baseline (Figure 2.4).

In most scenarios examined here, parameters were kept constant throughout the time period. In reality, recruitment and mortality rates have significant annual variation and are not likely to remain constant throughout the time period. The delay-difference model is deterministic and does not allow for variations in these parameters over time when, in reality, variations over a long time period, such as the one represented here, are likely to occur.

The values for $M$ and net recruitment used in this model were taken from large-scale humpback whale research projects and are not specific to the Kodiak region. Using new values of $M$ and $r$ based on the Kodiak Island population would result in an improved assessment of historical population size and growth, but no data currently exist for such values to be estimated. Therefore the values of $M$, $r$, net recruitment, and subsequently estimates of the historical population, are provisional.

Examination of the scenario in which both $r$ and $M$ equal 0.04 not only demonstrates the influence of these parameters, but also allows for properties of the delay-difference model to be discussed. When the $r$ and $M$ parameters are set equal to one another, the population quickly reaches 157 animals and stabilizes at this value for a period of nearly 50 years (Figure 2.6). This is because the delay-difference equation is designed so that at equilibrium either abundance is equal to the carrying capacity, $N_0$, or $r = M$. The population may stabilize for a period of time when $r = M$ and $C_t = 0$, but does not imply the population has necessarily reached carrying capacity. Thus, in the model scenario in which $r$ was equal to $M$, equilibrium was quickly reached once commercial harvest stopped in 1937, though the population was well below the defined value for carrying capacity.

Historical abundance here was estimated only within the study area though humpback whale kills occurred throughout the east side of Kodiak. It is likely that historical abundance within the study area would be overestimated if catch had not altered to account for the size of the study area in relation to the whaling grounds because results show that the delay difference model is highly sensitive to changes in catch numbers. Applying all of the humpback whale kills to the study area results in a negative abundance in 1938 indicating a complete depletion of the population and showing the impracticality of not adjusting catch numbers. Specific information about kill location would allow for a more accurate proportion of catch to be applied and would result in a more realistic account of historical abundance within the study area. Reeves et al. (1985) gives a rough distribution of Port Hobron humpback whale kills based on the general locations given in the William S. Lagen collection. Examination of this distribution supports a one-quarter proportioned catch within the study area. Without more specific information, however, assuming that the study area comprises one quarter of the whaling grounds and applying that same proportion to the historical catch numbers results was the most conservative estimate of historical abundance within the study area. Thus, an estimate of 343 animals was the best estimate of historical abundance within the study area given the current level of data.

The total population utilizing the entire Kodiak area is clearly greater than that of the study area. Depending on the annual utilization of the study area, the population could be just slightly larger than that in the study area to several times the estimated population. The whales in the study area may belong to a feeding aggregation that utilizes waters not only around Kodiak Island, but waters throughout the western Gulf of Alaska as well. Further research is needed to accurately define the boundaries of feeding humpback whales in the Kodiak Island study area and in western Alaska in general.

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# CHAPTER 3: FORAGING ECOLOGY OF HUMPBACK WHALES (*Megaptera novaeangliae)* NEAR KODIAK, ALASKA[2]

## ABSTRACT

Feeding humpback whales (*Megaptera novaeangliae)* are significant marine predators. Their role as predators is highly dependent on the amount of prey they consume. Consumption and biomass of prey removed were modeled using three methods (I through III) for a feeding aggregation of humpback whales in eastern Kodiak Island, Alaska. Methods I and II estimated biomass removal based on a percentage of average humpback whale mass. Method III estimated removal using the energy requirements of humpback whales and the energy density of their prey. A current rate of biomass removal was modeled based on current estimates of humpback abundance. A historical rate of removal based on a pre-whaling population estimate within the study area was also modeled. Two hypothetical humpback whale diets were created. The first diet was based on the stomach contents of commercially caught whales. The remaining diet was created from prey availability surveys conducted within the study area. The first diet was used to model consumption for the historical population and the second diet for the current population. The second diet was also used to project consumption if the current population grew to reach the historical population size. Currently, feeding humpback whales may be removing nearly 9,600 tons of prey annually, including 3,500 tons of juvenile pollock (*Theragra chalcogramma*) and 2,800 tons of capelin (*Mallotus villosus*). Historical populations may have removed over 19,000 tons of prey annually.

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## INTRODUCTION

Determining the prey and amount of consumption due to humpback whale (*Megaptera novaeangliae)* feeding is a useful tool for evaluating their efficiency as a marine predator. This following paper reports on estimation of biomass removal due to humpback whale consumption within one area of eastern Kodiak Island. Removal was estimated by modeling consumption for both historical and current humpback whale populations estimated in chapter two. Hypothetical humpback diets used in the modeling exercise were created to reflect prey availability and probable target species of humpback whales.

Feeding humpback whales are found in the waters of eastern Kodiak Island (Figure 1.1). The degree to which these whales are consuming prey is likely significant and may influence the structure of the Kodiak Island marine ecosystem because humpback whales are considered a top-level predator in marine ecosystems (Trites et al.1997; Croll et al.1998).

Cetaceans, in general, are described as opportunistic in their food selection, though species have a tendency towards selection of 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 1973; Perry et al. 1999). They have been shown to be seasonal feeders on euphausiids and schooling fish species up to 30 cm in length, including capelin (*Mallotus villosus*), Pacific herring (*Clupea harengus pallasi),* walleye pollock (*Theragra chalcogramma*), Atka mackerel (*Pleurogrammus* *monopterygius),* and species of cod (*Gadus spp.*), sardines (*Sardinops spp.*), and sandlance (*Ammodytes spp.*) (Nemoto 1957, 1959; Mitchell 1973; Payne et al. 1990). Klumov (1963) states that humpback whales in the North Pacific are "ichthyophagus" and feed to a "slight extent on zooplankton." Soviet whaling records indicate walleye pollock as the dominant prey source of humpback whales in the Kuril Islands (Klumov 1963). Acoustic and trawl surveys have shown that humpback whales in southeastern Alaska feed primarily on euphausiids and fish species, such as herring, juvenile walleye pollock, and capelin (Krieger and Wing 1984, 1986). The variety, as well as the amount, of prey removed from Kodiak Island prey sources may therefore be significant.

Consumption by Kodiak Island humpback whales is of further importance due to the fact that the region has experienced a large fluctuation in cetacean populations due to commercial exploitation. Commercial whaling in the 1900's significantly reduced the number of humpback whales, not only within the Kodiak Island area, but also within the North Pacific as a whole (Rice 1978). Their numbers are currently believed to be increasing and the rate of increase may have been as high as 10% between 1980 and 1990 (Baker and Herman 1987; Calambokidis et al. 1997). Removal and subsequent growth of a marine predator of this magnitude is likely to cause large variations in the biomass removal of prey in the ecosystem.

## METHODS

### *Study area*

The study area was limited to the waters of eastern Kodiak Island, including Chiniak and Marmot Bays. Kodiak Island is part of the Kodiak Archipelago and is located approximately 30 miles from the Alaskan mainland in the Gulf of Alaska. In 2002, the study area was divided into four subareas of approximately equal size (Figure 2.1). The subareas were established in order to equalize sampling effort and ensure thorough coverage within the study area. Subarea three was not adequately covered in 2001. Subareas were also used to separate sightings of humpback whales for the purpose of weighting diet composition in relation to prey availability. An additional area called near-shore was defined as the waters near Woody and Long Islands (Figure 3.1). This area was not defined as a survey subarea and was designated in the post-study period for calculating diet composition only.

### *Data on prey availability*

Information on prey availability came from tows from mid-water trawl surveys that were conducted seasonally within eastern Kodiak Island waters in 2001 and 2002. Trawl surveys targeted acoustic scattering layers. Multiple passes with a commercial mid-water trawl net with a 22 mm cod end liner were made through acoustic scattering layers, ensuring an accurate representation of mid-water prey abundance (R. Foy, pers. comm.).

Prey data from surveys were available for July of 2001 and June through September of 2002. Data available from these surveys includes date and location (latitude and longitude), as well as species composition and species counts for each tow. Each tow was mapped and tows outside of the study area were not included in this analysis. In addition to mid-water trawls, seasonal acoustic surveys and a series of purse seine (center panel with a 3.2 mm net) surveys were used to determine prey availability

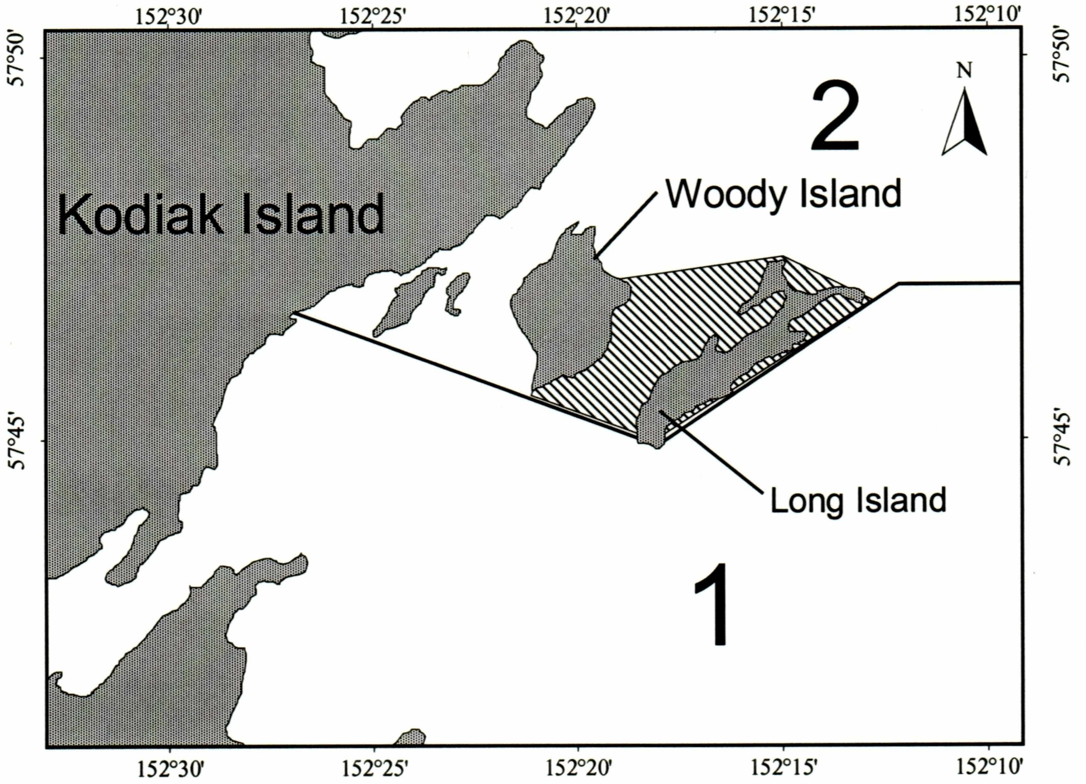

**Figure 3.1. Map of the near-shore subarea. The near-shore subarea is shown in stripes and a portion of subareas one and two of the Kodiak Island humpback whale study area.**

within the near-shore subarea. Purse seine hauls were performed at predetermined sites near south Chiniak Bay and near Long Island. Prey composition from these surveys was assumed to be homogeneous throughout near-shore habitat. Additional hauls targeting active surface schools of fish between Woody and Long Islands support this assumption (R. Foy, unpubl. data).

### *Diet composition*

Consumption was estimated based on two hypothetical diets. The diets were created to reflect both a historical and current account of possible humpback whale prey species. Diets were hypothesized because direct observation of humpback whale feeding behavior is rare and, even when observed, cannot produce a concrete determination of the prey species being eaten.

#### *Historical diet*

One diet (diet A) was created to reflect possible historical target species and was based on the stomach contents of humpback whales harvested at the Port Hobron whaling station on southeast Kodiak Island as analyzed by Thompson (1940).

#### *Current diet*

The second diet (diet B) was created to reflect possible current target species and was based on the assumption that relative occurrence of prey species less 30 cm within mid-water trawl surveys of fish was equal to the humpback whale diet. The diet was designed to be proportional to humpback whale sightings within subareas and reflect average prey availability within the study area for 2001 and 2002.

Mid-water trawl surveys did not contain information on euphausiid occurrence within the study area, but euphausiids are known to occur within a typical humpback whale diet (Nemoto 1957; Bryant et al. 1981; Dolphin and McSweeney 1983). In order to account for euphausiids within diet B without current information about their occurrence or speciation, it was assumed that the percentage of euphausiids within diet B remained constant from historical data.

Diet B was created through a multi-step process that began by separating humpback whale sightings by subarea and by month. The total number of sightings within a subarea by month was divided into the total number of sightings for both 2001 and 2002 to calculate monthly humpback whale sighting percentages by subarea.

Tow data from mid-water trawl surveys were then separated by subarea and month for both 2001 and 2002. Prey totals for walleye pollock, hereafter referred to as pollock, were adjusted to include only juvenile pollock under than 30 cm in length. Lengths of pollock were measured for fish collected during July mid-water trawl surveys only. The percent of juvenile pollock under 30 cm in the July tows was applied to pollock counts from the remaining months of trawl data.

Percent composition for prey species was then calculated by subarea and month for all species excluding non-traditional humpback whale prey. Non-traditional humpback prey were species larger than 30 cm (Nemoto 1959) and species that were not previously documented as prey, such as flatfish and other non-schooling fishes (Nemoto 1957, 1959; Klumov 1963; Kreiger and Wing 1984, 1986; Perry et al. 1999). Appendices B.1 though B.4 summarize monthly tow data and subsequent prey percentages.

The next step was to multiply the prey percentages by the average humpback whale sightings by month and by subarea. This properly weighted the compositions to reflect monthly area usage by humpback whales.

Finally, diet B was created by summing the percentages across all months and subareas and multiplying these by one minus the percentage of assumed euphausiid occurrence within the diet.

*Consumption and biomass removal*

Seasonal consumption was estimated for both the current humpback whale population and the pre-whaling humpback whale population. Pre-whaling consumption was estimated using diet A only. Diet B was used to estimate the consumption of the current humpback whale population. Finally, diet B was used to project consumption in the future if the current humpback whale population reached carrying capacity, which was equal to the pre-whaling population estimate.

Estimates of consumptions were calculated by three methods. Methods I and II estimated daily prey consumption from average humpback whale body weights only. Method I originated from Innes et al. (1986) with

$$I = 0.42M^{0.67} \tag{3.1}$$

where $I$ = daily prey consumption (kg/day)

$M$ = average body weight of a humpback whale (kg).

Constants used in method I were derived from general heart to body mass ratios of cetaceans originally presented by Sergeant (1969) (Innes et al. 1986).

Method II, taken from Klumov (1963), similarly estimated daily consumption by

$$I = 0.035M\ . \qquad (3.2)$$

The constant applied in method II was derived from stomach volumes of large cetacean species (Klumov 1963).

Method III accounts for humpback whale body weight, as well as the energy requirements (kcal/day) of whales and the energy density (kcal/g) of their prey. Energy requirements of humpback whales were based on the following equation from Perez and McAlister (1993).

$$E = aM^{0.75} \qquad (3.3)$$

where $a =$ an estimated coefficient for Mysticete whales and is equal to 192

$M =$ average body weight (kg).

Daily prey consumption was then estimated using the following equation:

$$I = \frac{E}{K}, \qquad (3.4)$$

where $I =$ total prey consumption (grams/day)

$E =$ estimated daily energy requirements (kcal/day)

$K =$ the estimated energy density (kcal/gram) of the diet.

*E* followed from equation 3.3. Values of *K* for local prey were calculated following estimates of proximate composition from Foy (unpubl.data). Details are discussed in the next section. The energy density of the diet was adjusted to account for each species in each diet. This was done by multiplying each species' *K* value by the percentage of the species within each diet. These values were then summed to obtain an overall value of *K*.

For all three methods, $M$ was set equal to 34,000 kg; the average weight of a mature humpback whale (Perry et al. 1999). Seasonal prey consumption for the population was obtained by multiplying each estimate of $I$ by estimates of abundance ($N$) and the total number of days for the season. The pre-whaling value for $N$ was equal to 343 and the current value of $N$ was equal to 157 (see chapter 2). The total number of days was set equal to 152 as per Perez and McAlister (1993). Estimate*s* of $I$ for all three methods were converted to tons for easy comparison between methods.

*Prey energy densities*

Proximate compositions of fat and protein were available for local prey species collected during 2002 trawl surveys for all months within the study period (R. Foy, unpubl. data). For each month, proximate values were converted into kilocalories per gram (kcal/gram) by multiplying percent fat by 9.4 and percent protein by 4.3, which are conversion factors based on heat produced during metabolism of foodstuffs (Schmidt-Nielson 1997). The converted values were then summed and weighted. The weighting was done for each species by summing the total number of fish of each species caught over the study period and dividing the number caught in a given month into the total. This gave an occurrence percentage for each month a species was present. This percentage was multiplied by the summed fat and protein conversions to obtained the weighted monthly energy density. Finally, the values were summed across months and the total was used as $K$ for each prey species represented in the diets. Pollock had the lowest energy density of the fish species caught in summer mid-water trawl surveys at 1.107 kcal/g. The species with the highest energy density was eulachon at 2.517 kcal/g

(Table 3.1). Appendices B. 5 through B.7 summarize prey totals and proximate compositions.

Proximate composition was not available for surf smelt (*Hypomesus pretious)* since none were caught in mid-water trawl surveys. However, Payne et al. (1999) published proximate composition of Gulf of Alaska surf smelt. These values were used to calculate an energy density of surf smelt. No data regarding proximate composition was available for local euphausiid species. Therefore, an energy density of 0.743 kcal/g for general euphausiids (*Thysanoeassa spp.)* from Davis et al. (1997) was used.

## RESULTS

### *Sightings of humpback whales*

Combined 2001 and 2002 humpback whales sightings show a peak in sightings occurred in July in subarea two (Table 3.2). The post-study defined near-shore area was utilized in June and July only. Subarea three showed the second highest number of sightings. This was based on 2002 sightings only, as subarea three was not adequately surveyed in 2001.

### *Diet composition*

#### *Historical diet*

Thompson (1940) analyzed the stomach contents of 39 commercially caught humpback whales. Of these, 27 contained appreciable quantities of prey. Surf smelt

**Table 3.1. Weighted monthly and total energy densities (kcal/gram) of prey species. Energy densities were used to estimate consumption by method III.**

| | Weighted Energy Densities (kcal/gram) | | | | |
|---|---|---|---|---|---|
| Species | June | July | August | September | Total |
| Capelin | 0.0029 | 0.9560 | 0.1451 | 0.1705 | 1.2745 |
| Pacific Sandlance | 0.2979 | 0.3753 | 0.3724 | 0.3724 | 1.4179 |
| Pacific Sandfish | 0.0495 | 0.4850 | 0.5423 | 0.0638 | 1.1406 |
| Eulachon | 0.0323 | 2.4763 | 0.0005 | 0.0080 | 2.5170 |
| Herring | 0.0000 | 0.0000 | 1.0475 | 0.9787 | 2.0262 |
| Juv. Pollock | 0.0988 | 0.6611 | 0.0492 | 0.2979 | 1.1069 |
| Euphausiids (general) | N/A | N/A | N/A | N/A | 0.7430 |
| Surf Smelt | N/A | N/A | N/A | N/A | 1.4698 |

**Table 3.2. Combined 2001 and 2002 sightings of humpback whale. Sightings are shown as percentages by subarea and month.**

| 2001 and 2002 | | | | | |
|---|---|---|---|---|---|
| Area | June | July | August | September | Total |
| 1 | 4.13 | 2.89 | 4.13 | 1.24 | 12.40 |
| 2 | 11.98 | 36.78 | 9.09 | 1.24 | 59.09 |
| 3 | 8.26 | 3.31 | 0.00 | 4.96 | 16.53 |
| 4 | 0.00 | 1.24 | 0.00 | 2.89 | 4.13 |
| Near Shore | 2.07 | 5.79 | 0.00 | 0.00 | 7.85 |
| Season | 26.45 | 50.00 | 13.22 | 10.33 | 100.00 |

occurred in 21 of 27 stomachs analyzed and euphausiids occurred in 6 of 27 stomachs analyzed (Figure 3.2).

#### *Current diet*

The additional diet that was created reflected available prey types in the study area and an assumed use of euphausiids. Pollock, capelin, and eulachon (*Thaleichthys pacificus*) were the three most prominent fish species (Figure 3.3). Both pollock and capelin represented a higher percentage of the diet than euphausiids. Other prey types in diet B included Pacific sandlance (*Ammodytes hexapterus*), Pacific sandfish (*Trichodon trichodon*), and Pacific herring.

### *Consumption and biomass removal*

#### *Daily rates of consumption*

Method I estimated the daily consumption rate of individual whales to be 0.46 tons. Method II calculated the highest rate of consumption at 1.19 tons per day per individual whale. Finally, method III estimates a daily removal of 0.37 tons per whale for diet A and 0.40 tons per whale for diet B.

#### *Methods I and II*

Neither methods I or II rely on the energetic content of the prey to estimate consumption. As a result, total seasonal biomass removal for both the pre-whaling and current humpback whale populations remained constant regardless of which diet was applied. Biomass removal due to the pre-whaling humpback population was equal to 23,795 tons using method I and 62,042 tons using method II (Table 3.3). Biomass

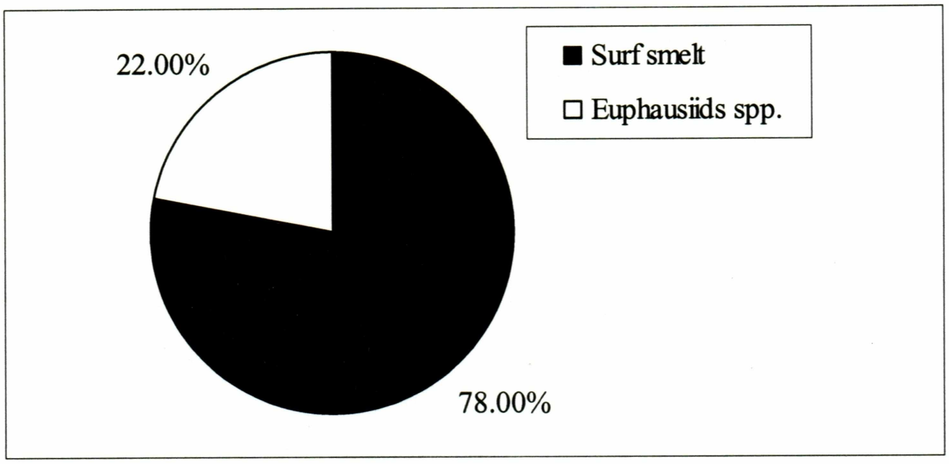

**Figure 3.2. Composition of diet A. Diet A was based on stomach contents (n=27) of commercially caught humpback whales from the Port Hobron whaling station in 1937.**

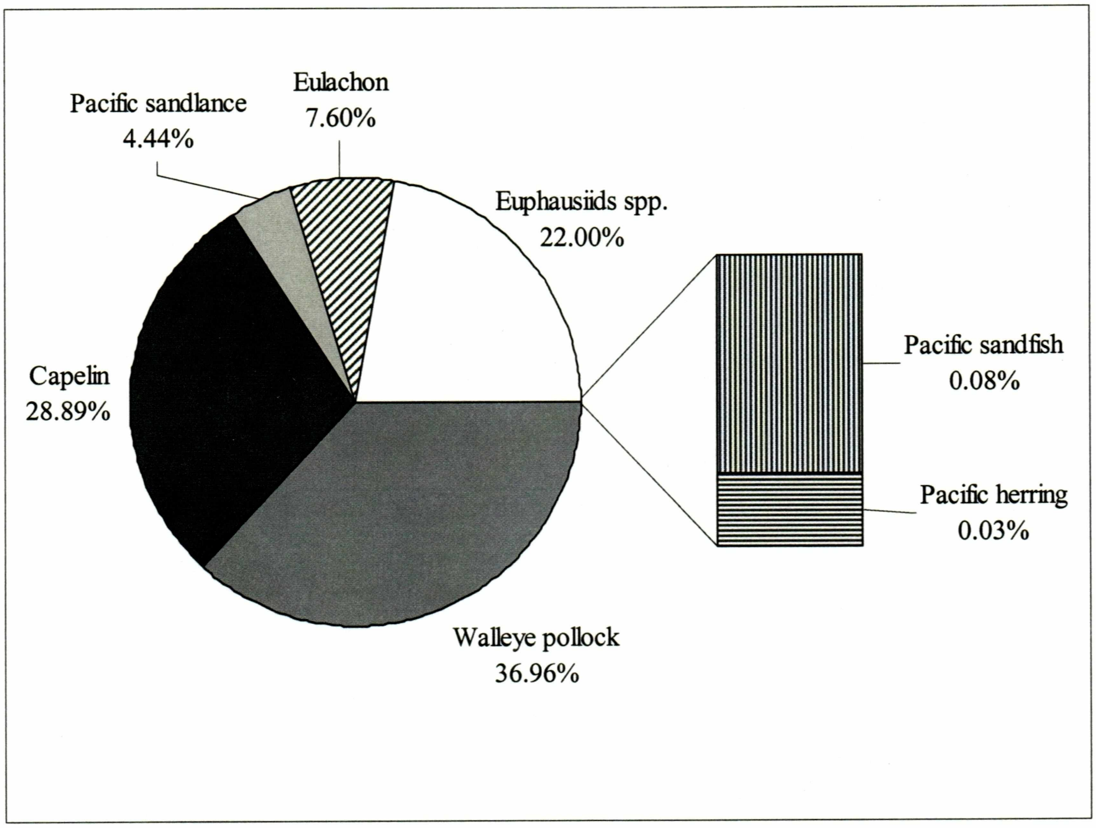

**Figure 3.3. Composition of diet B. Diet B was based on 2001 and 2002 Kodiak Island prey availability survey.**

**Table 3.3. Estimated seasonal biomass removal of prey by the humpback whale population at carrying capacity (*$N_0$*) and current abundance (*$N_{2002}$*). All three methods of consumption and both diets A and B are shown. All values are in tons.**

| | $N_0$ | | | $N_{2002}$ | | |
|---|---|---|---|---|---|---|
| | Method I | Method II | Method III | Method I | Method II | Method III |
| Diet A | 23,795 | 62,042 | 19,134 | 10,891 | 28,398 | 8,758 |
| Diet B | 23,795 | 62,042 | 20,951 | 10,891 | 28,398 | 9,590 |

removal due to the current population was equal to 10,891 tons using method I and 28,398 tons using method II. The biomass removal of individual prey species, however, did vary with methods I and II (Tables 3.4 to 3.6).

#### *Method III*

##### *Diet A*

Consumption and biomass removal for diet A was modeled for the pre-whaling population only. Method III estimated seasonal removal at 19,134 tons (Table 3.3). Consumption of individual prey species of diet A ranged from nearly 4,200 tons of euphausiids to approximately 15,000 tons of surf smelt annually (Table 3.4).

##### *Diet B*

Consumption and biomass removal for diet B was modeled for the current humpback whale populations and the projected population at carrying capacity. Biomass removal attributed to the current humpback whale population was estimated at nearly 9,600 tons (Table 3.5), including 3,500 tons of pollock. The projected population was estimated to remove 20,951 tons of prey, including approximately 7,800 tons of pollock (Tables 3.3 and 3.6).

## DISCUSSION

Feeding humpback whales in eastern Kodiak Island may currently be removing between 9,600 and 28,400 tons of prey annually. Pre-whaling population may have removed between 19,100 and 62,000 tons of prey annually. This indicates that humpback whales were, and likely still are, a significant predator within the Kodiak Island ecosystem.

**Table 3.4. Estimated consumption by the pre-whaling humpback whale population of species represented in diet A. Both seasonal and daily biomass removal are shown. All values are in tons.**

| | | Method I | | Method II | | Method III | |
|---|---|---|---|---|---|---|---|
| Prey Species | Percent of Diet | Daily removal | Seasonal removal | Daily removal | Seasonal removal | Daily removal | Seasonal removal |
| Surf smelt | 78.00 | 122.10 | 18,560 | 318.37 | 48,393 | 98.19 | 14,925 |
| Euphausiids spp. | 22.00 | 34.44 | 5,235 | 89.80 | 13,649 | 27.69 | 4,210 |
| | Total | 156.54 | 23,795 | 408.17 | 62,042 | 126.88 | 19,134 |

**Table 3.5. Estimated consumption by the current humpback whale population of species represented in diet B. Both seasonal and daily biomass removal are shown. All values are in tons.**

| | | Method I | | Method II | | Method III | |
|---|---|---|---|---|---|---|---|
| Prey Species | Percent of Diet | Daily removal | Seasonal removal | Daily removal | Seasonal removal | Daily removal | Seasonal removal |
| Euphausiids spp. | 22.00 | 15.76 | 2,396 | 41.10 | 6,248 | 13.88 | 2,110 |
| Walleye pollock | 36.96 | 26.48 | 4,025 | 69.04 | 10,495 | 23.32 | 3,544 |
| Capelin | 28.88 | 20.69 | 3,145 | 53.96 | 8,202 | 18.22 | 2,770 |
| Eulachon | 7.60 | 5.45 | 828 | 14.20 | 2,159 | 4.80 | 729 |
| Pacific sandlance | 4.44 | 3.18 | 483 | 8.29 | 1,260 | 2.80 | 426 |
| Pacific sandfish | 0.08 | 0.06 | 8 | 0.14 | 22 | 0.05 | 7 |
| Pacific herring | 0.03 | 0.02 | 3 | 0.05 | 7 | 0.02 | 2 |
| | Total | 71.65 | 10,891 | 186.83 | 28,398 | 63.09 | 9,590 |

**Table 3.6. Estimated consumption by the humpback whale population at carrying capacity of species represented in diet B. Both seasonal and daily biomass removal are shown. All values are in tons.**

| | | Method I | | Method II | | Method III | |
|---|---|---|---|---|---|---|---|
| Prey Species | Percent of Diet | Daily removal | Seasonal removal | Daily removal | Seasonal removal | Daily removal | Seasonal removal |
| Euphausiids spp. | 22.00 | 34.44 | 5,235 | 89.80 | 13,649 | 30.32 | 4,609 |
| Walleye pollock | 36.96 | 57.85 | 8,793 | 150.84 | 22,928 | 50.94 | 7,743 |
| Capelin | 28.88 | 45.21 | 6,872 | 117.88 | 17,918 | 39.81 | 6,051 |
| Eulachon | 7.60 | 11.90 | 1,809 | 31.03 | 4,716 | 10.48 | 1,593 |
| Pacific sandlance | 4.44 | 6.95 | 1,056 | 18.11 | 2,753 | 6.12 | 930 |
| Pacific sandfish | 0.08 | 0.12 | 18 | 0.32 | 48 | 0.11 | 16 |
| Pacific herring | 0.03 | 0.04 | 6 | 0.11 | 16 | 0.04 | 5 |
| | Total | 156.54 | 23,795 | 408.17 | 62,042 | 137.84 | 20,951 |

A large amount of variability was seen between the three methods of modeling consumption. Daily rate of consumption and total biomass removed estimated by method II were greater than two times those of methods I and III. Methods I and III were similar in rates of daily consumption and total consumption. Thus, method II was likely the least accurate of the three estimates.

Methods I and II both assume consumption based on a percentage of body mass only. Method II is based on the assumption that cetaceans are required to consume 3.5% of average body weight. The method stems from assumptions about stomach volumes and does not account for metabolic requirements while method I was based on heart mass to body mass ratios (Klumov 1963, Innes et al. 1986). It may be inappropriate to estimate food consumption of large whales by methods such as I and II because of failure to account for the energy content of the prey (Innes et al. 1987). Many recent studies modeling consumption use energy requirements and not only predator biomass assumptions (Perez and McAlister 1993; Kenney et al. 1997; Trites et al. 1997; Sigurjónsson and Víkingsson 1998). As a result, method III provides the best estimate of consumption of the three methods because it accounts for humpback whale mass and energy requirements and the energy density of the prey.

Method III is not without limitations. Data on energy and feeding of large cetaceans are limited. True accounts of consumption rely on reliable knowledge of body mass, physiological status, and environmental conditions (Innes et al. 1987), all of which are extremely difficult to obtain or even estimate for any species of marine mammal.

An assumption of method III is that the energy requirements of the whales are constant throughout the year and do not account for fasting species (Perez and McAlister 1993). Humpback whales are a fasting species since they do not feed while on the winter breeding grounds in low-latitude waters. Thus, the energy requirements of humpback whales may be significantly increased when they return to feeding grounds. The method also does not account for physiological demands on specific animals, such as lactation. Further, methods do not account for the fact that assimilation rates of prey may vary by species due to the differences in digestibility of protein and lipid.

Method III was adapted for seasonal changes in the energy density of prey sources. This was one limitation of the model presented in Perez and McAlister (1997), from which method III is based. Results presented here not only account for seasonal variability in the caloric content of prey, but do so for prey that is within the specified study area.

Of note is the difference in species composition between diets A, based on historical data, and diet B, based on current prey availability. One of the dominant prey species in diet B implies a relative importance of juvenile pollock in current humpback whale diets. Pollock was not present in diet A, suggesting either limited availability of this species during the whaling period or a tendency for historical humpback whale populations to selectively avoid pollock as a prey source, which would indicate an over representation of pollock in the current diet. The primary prey source in diet A was surf smelt, which was not represented even in small amounts in diet B. Surf smelt is a forage fish species that is currently rarely seen within the study area (R. Foy, pers. comm.). Surf smelt is not commonly listed as a major prey source for humpback whales. Thompson (1940) does not specify how stomach contents of humpback whales were identified to the species level. It may be that the surf smelt was misidentified and was actually another smelt species, such as eulachon, which are currently prevalent within the study area.

The differences between historical and present-day diets may be an artifact of a regime shift in the North Pacific and Bering Sea ecosystems. This shift is well documented and attributed to it are increases in groundfish biomass (including pollock) and decreases in forage fish biomass (Merrick 1997; Anderson and Piatt 1999; Benson and Trites 2002), which corroborates what is seen in the modeled humpback diets.

The current diet itself is based on limited sampling and may or may not reflect the true diet of the eastern Kodiak Island humpback whales. This diet reflects prey species that are available to humpback whales as determined by mid-water trawl surveys. Consumption analysis was predicated on an assumed high importance of pollock in the humpback diet, but their high occurrence in diet B may be skewed due to the tendency of mid-water trawl surveys to underestimate the availability of some of the smaller forage fishes, particularly Pacific sandlance. Prey surveys were able to assess the availability of Pacific sandlance in the near-shore area only, while these fishes may extend beyond that region. There was evidence that Pacific sandlance was more prevalent in the study area than what availability surveys indicated. Pacific sandlance was the primary prey species observed in the stomach contents of sport caught fish species, including coho salmon (*Oncorhynchus kisutch*) and Pacific halibut (*Hippoglossus stenolepis),* caught within the study area in 2002 (B. Witteveen, unpubl. data). Regurgitants collected from black-legged kittiwakes (*Rissa tridactyla)* foraging within Chiniak Bay in 2001 and 2002 were also dominated by Pacific sandlance (Murra et al. 2003). Thus, it may be that Pacific sandlance were underrepresented in the current diet.

Further, the humpback whales may have preferred prey species and consumption may be disproportional to availability. That is, they may be selectively foraging from all available prey sources. The high occurrence of surf smelt in the stomach of commercially caught whales may indicate a preference for smelt-like fishes by humpback whales. If this is true and the appearance of smelt was not simply an artifact of widespread availability, the current diet may place too high an importance on pollock and other non-smelt like species and a current diet closer to that of the historical diet may be more accurate. In such a case, eulachon, or other smelt species, would likely dominate the current diet and the consumption by humpback whales of some fishes presented here, pollock in particular, would be overestimated. In some regions of the North Pacific, however, pollock has been shown to be a dominant prey source of humpback whales; thus the high percentage of pollock in diet B may be realistic (Klumov 1963, C. Gabriele pers. comm.).

Unfortunately, without direct observation of foraging, selectivity cannot be described in this study and the assumption that humpback diet is equal to prey availability remains. Because the prey surveys overlapped humpback whale sightings both temporally and spatially, however, proposed diets may approximate true target prey availability.

Though zooplankton species are often listed as prey of humpback whales, data on their occurrence within the study area were not available. Diet B assumes a euphausiid consumption of 22% remained constant from whaling days. Other studies of humpback whale consumption estimate euphausiid species comprises anywhere from five to 30% of the total diet (Perez and McAlister 1993; Kenney et al. 1997). Consumption estimates would be different if true consumption of euphausiids was not near the assumed 22%. For method III, the difference would not only be in the overall tons of prey removed, but in the biomass removal of individual species as well. The most significant of these would be the degree of importance of pollock in the humpback diet. A greater than 22% euphausiid consumption would decrease the importance of pollock, while euphausiid consumption less than 22% would increase pollock in the humpback whale diet.

Total consumption, itself, was dependent on both the population size of the humpback whales and the length of the feeding season. The estimate of population abundance was assumed to be a minimum (see chapter 2). Consumption was based on a 152-day feeding season. If the feeding season began on the first day of the study period (June 4th) in 2002, the feeding would continue through November 2, 2002. Humpback whales were seen within the study area on November 12th, 2002 (K. Wynne, pers. comm.) and it is probable that humpback whales arrived in the study area prior to the start of the study period. Therefore, the feeding season may easily extend beyond 152 days. If the population size used in modeling was a minimum and the feeding season was actually longer than 152 days, then consumption estimates are conservative.

For these reasons, biomass removal estimated by method III for diet B represents the best minimum estimate of consumption by the 157 humpback whales within the study area: 9,590 tons of prey annually based on seasonal availability of prey as shown by mid-water trawl surveys. If the population continues to grow to carrying capacity, this figure grows to 21,000 tons. While there are obvious limitations in modeling consumption, the results presented here do provide essential baseline data and show a range of possible consumption scenarios. Estimates will improve as additional research is conducted and new techniques in determining feeding habits and prey species of humpback whales are applied. Further, this consumption exercise can provide information that may be used in cause-effect modeling of the Kodiak Island ecosystem in the future.

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# CHAPTER 4: CONCLUSION

The unknown cause of the recent decline of Steller sea lion (*Eumetopias jubatus)* abundance in the central and western Gulf of Alaska has brought attention to the necessity for understanding complex marine interactions, including those among apex predators (marine mammals, fish, birds, and humans). Despite limited knowledge of these interactions in the Gulf of Alaska and how they affect the Steller sea lion, severe restrictions on commercial fisheries throughout western Alaska have been put into effect. Numerous studies have revealed that an increased awareness of trophic level interactions and the roles played by marine species is essential in assessing the status of complex ecosystems (Overholtz 1991; Pascual et al. 1993; Hairston and Hairston 1993; Estes 1994; Trites et al. 1997; Kenney et al. 1997). Therefore, an increased understanding of potential and existing predator competition and other ecological interactions needs to be reached in order to make realistic judgments of current Gulf of Alaska trends, to produce educated fisheries management decisions, and to avoid negative socioeconomic consequences in the future.

One way to study ecosystem dynamics is to focus on the predators, such as marine mammals and birds, that comprise these ecosystems. Croll et al. (1998) suggests that there are six types of data that can be used in combination to increase understanding of foraging behavior and population dynamics of marine predators: (1) the distribution and abundance of the predators on large and small spatial scales; (2) the horizontal and vertical movements of individuals at large and small temporal scales; (3) the physical oceanography of the region from the literature, concurrent remote sampling, and/or onboard data collections; (4) measures of prey availability; (5) predator diet; and (6) fitness measures of foraging success such as growth, survival, and reproductive success.

Research on the humpback whales (*Megaptera novaeangliae)* presented in this thesis provides the first data that address the population size and consumption by this marine predator near Kodiak Island. Research of this nature is important in understanding the foraging ecology and population dynamics of marine predators (Croll et al. 1998).

A mark-recapture study estimated a minimum of 157 humpback whales feed in the eastern Kodiak Island study area. Though there are limitations associated with the method of estimation, results provide important baseline data that will aid in monitoring this population in the future. Further, the mark-recapture portion of the study is an essential first step to determining true boundaries of feeding aggregations within regions of western Alaska. Achieving a more accurate account of these boundaries is critical when evaluating the ecosystem impacts caused by humpback whale feeding. Already, comparison of fluke photographs between the Kodiak Island study area and the Shumagin Islands (Figure 4.1) revealed five whales sighted in both regions since 1999 (Witteveen and Straley 2002). Sightings such as these increase the likelihood that the whales feeding in Kodiak Island belong to the same feeding aggregation of whales in the Shumagin Islands. Further research in all regions of western Alaska will help to either solidify or disprove the initial findings. If continued effort showed additional matches between the two regions and provided ample evidence for a single feeding aggregation encompassing them, then the ecological impact of the feeding whales would need to be

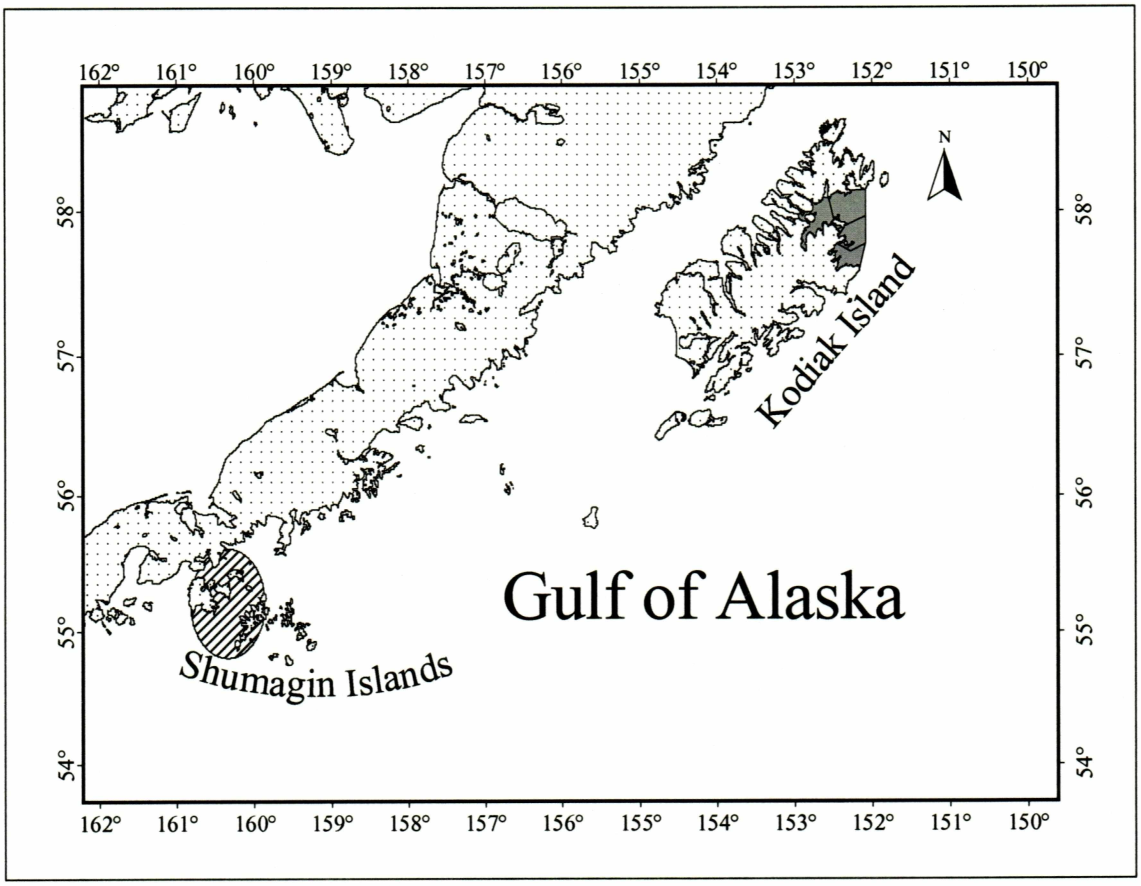

**Figure 4.1. Map of the Gulf of Alaska showing Kodiak Island and the Shumagin Islands. The Kodiak Island study area is shown in shade. The approximate area of photo-identification effort in the Shumagin Island is shown in stripes.**

reevaluated. The impacts of humpback whales would likely be far-reaching on a large spatial scale because of the wide reaching range of possible prey fields and potential interchange of humpback whales between feeding areas throughout western Alaska. Until information on a large scale becomes available, focus must be placed where effort has occurred, the Kodiak Island study area and the whales within it.

Humpback whales may be significant consumers of a variety of prey at their current level of abundance. Assuming humpback whale consumption of prey is proportional to its availability within the study area, these whales may be consuming over 3,500 tons of juvenile walleye pollock (*Theragra chalcogramma)* and nearly 4,000 tons of small forage fish, such as capelin (*Mallotus villosus)* and eulachon (*Thaleichthys pacificus)*, during a 152-day feeding season. Therefore biomass removal of these fish species may be substantial. The humpback whales' removal of an estimated 3,500 tons of pollock equals 32% of the 2002 commercial pollock harvest of 10,902 tons for the entire Kodiak Island management area, which encompasses virtually all of the island and Prince William Sound (NMFS 2002). If feeding aggregations of humpback whales are found throughout the Gulf of Alaska, removal of pollock biomass by these whales may actually exceed that of the fishery, though the whales and the fishery may be targeting different age classes of fish.

The likelihood that ecosystems are being affected by whale consumption increases when combined with commercial fishing and predation by other marine predators. One possible effect would be resource limitation. The degree to which prey limitation occurs is highly dependent on prey biomass and dietary overlap that exists between predators. Scat samples from Steller sea lion haul outs within the study area show the diets of these animals include arrowtooth flounder (*Atheresthes stomias)*, walleye pollock, Pacific sandlance (*Ammodytes hexapterus)*, capelin, and numerous other fish species (Wynne and Foy 2001). Commercial fisheries within Kodiak Island waters target some of these species as well. If humpback whales within the study are feeding on a diet like diet B hypothesized in this thesis, then prey overlap is occurring for certain species.

The composition of the humpback whale diet overlaps that of other predators, including other marine mammals and commercial fisheries. Humpback whales, and cetaceans in general, are unlikely to exhibit a high degree of direct prey overlap with commercial groundfish and salmon fisheries. Though humpback whales and fisheries may utilize fish of the same species, humpback whales generally feed on different age classes than are targeted by fishers (Perez and McAlister 1993; Kenney et al. 1997). In fact, the most significant prey overlap likely exists between whales and predatory fish (Livingston et al. 1993; Trites et al. 1997). Models suggest a 0.86 prey overlap between baleen whales and adult pollock (Trites et al. 1999). Adult pollock, Pacific halibut (*Hippoglossus stenolepis)*, and arrowtooth flounder consume many of the same species hypothesized to be eaten by humpback whales, including juvenile pollock, herring, capelin, and sandlance (Best and St. Pierre 1986; Yang 1995; Merrick 1997).

While prey overlap may be easily identified, determining if the overlap is causing competition or a limitation in resources is much more difficult. Two or more animals are in competition when they seek the same resource that is in short supply in relation to the numbers seeking it (Colinvaux 1973; Smith 1980). However, proof of competition can only come if vital parameters, such as abundance and productivity, of the species involved are negatively impacted (Lowry 1984). Thus, it can only be said that humpback whales near Kodiak Island may exhibit prey overlap with other marine predators and that this prey overlap may lead to competition for resources.

Historically, humpback whales were present in much higher numbers within the study area; as many as 343 whales may have been consuming over 19,000 tons of prey prior to 1926. Commercial whaling killed large numbers of humpback whales, reducing the population to an estimated low of 27 animals by 1938. The removal of so many large consumers likely had significant impacts on the surrounding ecosystem. Reducing historical consumption to that of current levels releases nearly 10,000 tons of prey with the study area alone in a single feeding season. Such a release could have invoked a trophic cascade effect, as smaller perturbations to ecosystems have been shown to have cascading effects (Bergquist and Carpenter 1986; Carpenter et al 1987).

Cetacean removals in the Southern Ocean have shown how trophic cascades can affect marine ecosystems (Laws 1985). It has been hypothesized that a similar situation to that in the Southern Ocean may have occurred in the Bering Sea and Gulf of Alaska, causing a reorganization of the marine community (Merrick 1997; Trites 1997). The decline in local whale abundance led to a reduced predation on certain fish, cephalopod, and zooplankton species. Consequently, the availability of these species to other predators would have increased. Trites (1997) hypothesized the freed prey was consumed by fishes, not by birds and other marine mammal species, as was the case in the Southern

Ocean. The increased abundance of prey sources may have provided opportunity for other predators, specifically groundfish species, to develop, and eventually, dominate the ecosystem (NRC 1996). The increase in groundfish abundance was likely aided by the 1977 regime shift that warmed ocean temperatures and favored groundfish recruitment (Merrick 1995, 1997; NRC 1996). It is further believed that declines in many pinniped species (harbor seals (*Phoca vitulina)*, Steller sea lions, and Northern fur seals (*Callorhinus ursinus)*) and marine bird species (common murres (*Uria aalge*), thick-billed murres (*U. lomvia*), and red-legged kittiwakes (*Rissa brevirostris*)) may have followed as a consequence of the dominant groundfish biomass limiting food resources (NRC 1996).

As an alternative to the above scenario, prey released by whale removals may have been consumed not only by fishes, but some marine mammal species as well. This increase in prey availability may have resulted in high productivity and abundance of Steller sea lions in the late 1950's as the carrying capacity of pinniped species increased into the 1960's. Thus, declines in Steller sea lion populations in the 1970's and 1980's may have represented normalization from inflated carrying capacities, as a reduction in available prey resources resulted from recovering whale stocks and regime shifts changing fish species composition. In either scenario, the reduction in humpback whale stocks due to commercial whaling and their subsequent resurgence may have played a role in fundamentally altering the Gulf of Alaska ecosystem from its historical state.

All effects of whaling on the ecosystem are not immediately noticeable. Time lags associated with large-scale changes to an ecosystem occur on scales of the generation times of the organisms involved (Kitchell et al. 1994). Thus, it is reasonable to assume that short-lived species, such as zooplankton and some forage fish, would experience immediate changes in abundance from cetacean removal, while the longer-lived marine mammal and bird species were likely not affected until years later (Mann and Lazier 1996). It follows that increased recruitment of groundfish following the 1977 regime shift could have been a partial factor in ecosystem changes, aided by commercial whaling some 40 years earlier. In fact, the Gulf of Alaska and Bering Sea ecosystems may still be seeing changes caused by baleen whale removals (NRC 1996). If the Kodiak Island study area was equally affected as the rest of the Gulf of Alaska by the trophic reorganization, estimating current consumption by humpback whales is essential in evaluating what role the recovery of the species is playing in ecosystem dynamics.

Had humpback whales not been removed from the study area and their numbers remained steady at 343 humpback whales, they could have been currently consuming as much as 7,700 tons of juvenile pollock, in addition to other species. That level of pollock removal equals nearly 72% of the total commercial fishery catch for the Kodiak Island management area in 2002. If the current level of consumption, when combined with predation by fisheries and other marine predators, were causing a limitation in resources, the extreme consumption by 343 whales would most certainly have much more devastating and far-reaching effects. That is, however, considering today's Kodiak Island ecosystem. Had commercial whaling not removed humpback whales from the study area, the ecosystem may look very different than it does today. Increased competition for resources by high numbers of whales could have brought about behavioral changes by other species, whales included, to avoid competition (Smith 1980). Behavioral changes could include exploitation of alternate prey sources or increased searching for available prey. It is not possible to determine how the ecosystem would look had whales not been removed, but it may be said that significant differences in species composition and biomass are likely.

The humpback whale represents only one of a myriad of species within the Kodiak Island ecosystem. Predictions of their effect cannot be made without sophisticated multi-species models and analysis of ecosystem interactions. The first step in creating these models is to increase knowledge of as many species represented within the ecosystem at hand, including both apex predators such as whales, human harvesters, Steller sea lions, and piscivorous fish species and their prey. This study has begun the process of understanding the foraging ecology and population dynamics of humpback whales in eastern Kodiak Island. Additional study will help to further clarify the humpback whale's role as an apex predator. Results presented here can be used in conjunction with other data sets to increase knowledge of the predator interactions and ecosystem dynamics in Kodiak Island waters.

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# APPENDIX A: Supporting information for Chapter 2.

## A.1. Equation details and definitions of the Schnabel maximum likelihood estimator.

$$1-\frac{r}{N}=\prod_{i=1}^{s}(1-\frac{n_i}{N})$$

where $N =$ abundance

$s =$ total number of samples

$n_i =$ the size of the ith sample

$r =$ the total number of marked animals at the end of the experiment.

Further let

$m_i =$ the number of marked animals in the ith sample

$u_i = n_i - m_i$

$M_i = \sum_{j=1}^{i-1} u_j$ or the number of marked animals just prior to the ith sample.

## A.2. Assumptions underlying the Schnabel maximum likelihood estimator.

1. The population is closed; there is no mortality, immigration, emigration, or recruitment during the study period.
2. All animals have the same probability of capture at each sample period.
3. Samples are simple random samples.
4. Marking does not affect the probability of capture.
5. All animals with marks are reported.
6. Recaptures are independent across all sample periods.

### A.3. Schnabel unconditional MLE model input and results of abundance estimate[*]. Schnabel MLE was applied to 2002 Kodiak Island humpback whale sighting only.

| i. | n | m | u | M |
|---|---|---|---|---|
| 1 | 3 | 0 | 3 | 0 |
| 2 | 6 | 1 | 5 | 3 |
| 3 | 11 | 2 | 9 | 8 |
| 4 | 10 | 2 | 8 | 17 |
| 5 | 28 | 2 | 26 | 25 |
| 6 | 1 | 0 | 1 | 51 |
| 7 | 5 | 3 | 2 | 52 |
| 8 | 7 | 3 | 4 | 54 |
| 9 | 0 | 0 | 0 | 58 |
| 10 | 0 | 0 | 0 | 58 |
| 11 | 2 | 2 | 0 | 58 |
| 12 | 4 | 1 | 3 | 58 |
| 13 | 2 | 0 | 2 | 61 |
| 14 | 11 | 3 | 8 | 63 |
| Sum | 90 | 19 | 71 | 71 |

| | |
|---|---|
| **s** | 14 |
| **r** | 71 |

| N | LHS | RHS | Difference |
|---|---|---|---|
| 157 | 0.548 | 0.548 | 7E-07 |

| N | SE | Upper CI | Lower CI | Bias | Variance | CV |
|---|---|---|---|---|---|---|
| 157 | 28.58 | 168.38 | 146.12 | 4.53 | 816.96 | 18.18% |

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[*] Model variables are defined in appendix A.1. The 95% confidence intervals (CI) shown here were calculated within the Schnabel MLE model and are not equal to the 95% confidence intervals calculated by the bootstrap method.

## A.4. Details of parametric bootstrap procedure to obtain 95% confidence intervals.

1. The bootstrap was based on the hypergeometric distribution.
2. Replications of the MLE equation (2.1) were made by generating successive values of $m_2$ through $m_i$ where each $m_i$ was a hypergeometric variable with parameters $N, M_i$, and $n_i$.
3. Bootstrap values for the cumulative number of marked were found from $M_i = M_{i-1} + n_{i-1} - m_{i-1}$.

**A.5. Delay difference historical population model input and abundance estimates.**

| Year | Catch ($C_t$) | Adjusted Catch ($C_t/4$) | Population Size when $C_t/4$ ($N_t$) | Net Recruitment ($r-M$) | Recruitment Rate ($r_t$) | Gross Recruitment ($R_t$) |
|---|---|---|---|---|---|---|
| 1920 | 0 | 0 | 343 | 0.040 | 0.000 | 0.000 |
| 1921 | 0 | 0 | 343 | 0.040 | 0.000 | 0.000 |
| 1922 | 0 | 0 | 343 | 0.040 | 0.000 | 0.000 |
| 1923 | 0 | 0 | 343 | 0.040 | 0.000 | 0.000 |
| 1924 | 0 | 0 | 343 | 0.040 | 0.000 | 0.000 |
| 1925 | 0 | 0 | 343 | 0.040 | 0.000 | 0.000 |
| 1926 | 236 | 59 | 329 | 0.040 | 0.040 | 13.725 |
| 1927 | 244 | 61 | 273 | 0.040 | 0.040 | 13.725 |
| 1928 | 178 | 45 | 218 | 0.040 | 0.040 | 13.725 |
| 1929 | 169 | 42 | 180 | 0.040 | 0.040 | 13.725 |
| 1930 | 178 | 45 | 146 | 0.040 | 0.040 | 13.725 |
| 1931 | 0 | 0 | 111 | 0.040 | 0.042 | 13.703 |
| 1932 | 128 | 32 | 120 | 0.040 | 0.048 | 13.157 |
| 1933 | 114 | 29 | 98 | 0.040 | 0.055 | 11.886 |
| 1934 | 139 | 35 | 78 | 0.040 | 0.059 | 10.617 |
| 1935 | 37 | 9 | 53 | 0.040 | 0.063 | 9.187 |
| 1936 | 107 | 27 | 51 | 0.040 | 0.067 | 7.443 |
| 1937 | 43 | 11 | 31 | 0.040 | 0.066 | 7.934 |
| 1938 | 0 | 0 | 27 | 0.040 | 0.069 | 6.713 |
| 1939 | 0 | 0 | 33 | 0.040 | 0.071 | 5.561 |
| 1940 | 0 | 0 | 37 | 0.040 | 0.074 | 3.886 |
| 1941 | 0 | 0 | 39 | 0.040 | 0.074 | 3.764 |
| 1942 | 0 | 0 | 41 | 0.040 | 0.076 | 2.334 |
| 1943 | 0 | 0 | 42 | 0.040 | 0.077 | 2.070 |
| 1944 | 0 | 0 | 42 | 0.040 | 0.076 | 2.482 |
| 1945 | 0 | 0 | 43 | 0.040 | 0.076 | 2.788 |
| 1946 | 0 | 0 | 44 | 0.040 | 0.075 | 2.960 |
| 1947 | 0 | 0 | 46 | 0.040 | 0.075 | 3.115 |
| 1948 | 0 | 0 | 47 | 0.040 | 0.075 | 3.162 |
| 1949 | 0 | 0 | 48 | 0.040 | 0.075 | 3.189 |
| 1950 | 0 | 0 | 49 | 0.040 | 0.075 | 3.244 |
| 1951 | 0 | 0 | 51 | 0.040 | 0.075 | 3.318 |
| 1952 | 0 | 0 | 52 | 0.040 | 0.075 | 3.400 |

A.5 continued

| | | | | | | |
|---|---|---|---|---|---|---|
| 1953 | 0 | 0 | 53 | 0.040 | 0.075 | 3.490 |
| 1954 | 0 | 0 | 55 | 0.040 | 0.074 | 3.579 |
| 1955 | 0 | 0 | 56 | 0.040 | 0.074 | 3.665 |
| 1956 | 0 | 0 | 57 | 0.040 | 0.074 | 3.752 |
| 1957 | 0 | 0 | 59 | 0.040 | 0.074 | 3.840 |
| 1958 | 0 | 0 | 60 | 0.040 | 0.074 | 3.930 |
| 1959 | 0 | 0 | 62 | 0.040 | 0.074 | 4.021 |
| 1960 | 0 | 0 | 63 | 0.040 | 0.073 | 4.115 |
| 1961 | 0 | 0 | 65 | 0.040 | 0.073 | 4.210 |
| 1962 | 0 | 0 | 67 | 0.040 | 0.073 | 4.307 |
| 1963 | 0 | 0 | 68 | 0.040 | 0.073 | 4.405 |
| 1964 | 0 | 0 | 70 | 0.040 | 0.073 | 4.504 |
| 1965 | 0 | 0 | 72 | 0.040 | 0.073 | 4.606 |
| 1966 | 0 | 0 | 73 | 0.040 | 0.072 | 4.708 |
| 1967 | 0 | 0 | 75 | 0.040 | 0.072 | 4.812 |
| 1968 | 0 | 0 | 77 | 0.040 | 0.072 | 4.918 |
| 1969 | 0 | 0 | 79 | 0.040 | 0.072 | 5.025 |
| 1970 | 0 | 0 | 81 | 0.040 | 0.072 | 5.133 |
| 1971 | 0 | 0 | 83 | 0.040 | 0.071 | 5.243 |
| 1972 | 0 | 0 | 85 | 0.040 | 0.071 | 5.354 |
| 1973 | 0 | 0 | 86 | 0.040 | 0.071 | 5.466 |
| 1974 | 0 | 0 | 88 | 0.040 | 0.071 | 5.580 |
| 1975 | 0 | 0 | 91 | 0.040 | 0.071 | 5.695 |
| 1976 | 0 | 0 | 93 | 0.040 | 0.070 | 5.811 |
| 1977 | 0 | 0 | 95 | 0.040 | 0.070 | 5.929 |
| 1978 | 0 | 0 | 97 | 0.040 | 0.070 | 6.047 |
| 1979 | 0 | 0 | 99 | 0.040 | 0.070 | 6.167 |
| 1980 | 0 | 0 | 101 | 0.040 | 0.069 | 6.288 |
| 1981 | 0 | 0 | 103 | 0.040 | 0.069 | 6.409 |
| 1982 | 0 | 0 | 106 | 0.040 | 0.069 | 6.532 |
| 1983 | 0 | 0 | 108 | 0.040 | 0.069 | 6.655 |
| 1984 | 0 | 0 | 110 | 0.040 | 0.068 | 6.779 |
| 1985 | 0 | 0 | 113 | 0.040 | 0.068 | 6.904 |
| 1986 | 0 | 0 | 115 | 0.040 | 0.068 | 7.030 |
| 1987 | 0 | 0 | 118 | 0.040 | 0.068 | 7.156 |
| 1988 | 0 | 0 | 120 | 0.040 | 0.067 | 7.283 |
| 1989 | 0 | 0 | 123 | 0.040 | 0.067 | 7.410 |

A.5 continued

| | | | | | | |
|---|---|---|---|---|---|---|
| 1990 | 0 | 0 | 125 | 0.040 | 0.067 | 7.538 |
| 1991 | 0 | 0 | 128 | 0.040 | 0.067 | 7.666 |
| 1992 | 0 | 0 | 130 | 0.040 | 0.066 | 7.794 |
| 1993 | 0 | 0 | 133 | 0.040 | 0.066 | 7.922 |
| 1994 | 0 | 0 | 135 | 0.040 | 0.066 | 8.051 |
| 1995 | 0 | 0 | 138 | 0.040 | 0.065 | 8.179 |
| 1996 | 0 | 0 | 141 | 0.040 | 0.065 | 8.307 |
| 1997 | 0 | 0 | 143 | 0.040 | 0.065 | 8.435 |
| 1998 | 0 | 0 | 146 | 0.040 | 0.065 | 8.563 |
| 1999 | 0 | 0 | 149 | 0.040 | 0.064 | 8.691 |
| 2000 | 0 | 0 | 151 | 0.040 | 0.064 | 8.818 |
| 2001 | 0 | 0 | 154 | 0.040 | 0.064 | 8.944 |
| 2002 | 0 | 0 | 157 | 0.040 | 0.063 | 9.070 |

| | | | LCI | UCI | CV |
|---|---|---|---|---|---|
| $C_t/4$ | Pristine | 343 | 331 | 376 | 3.24% |
| | 1938 | 27 | 14 | 61 | 42.21% |

## APPENDIX B: Supporting information for Chapter 3.

**B.1. Prey species composition from June 2002 prey availability surveys. Percent compositions were determined by methods outlined in chapter 3.**

| Month | Year | Subarea | Prey Species | Total Count* | Percent prey composition by subarea | Percent whale sightings by subarea | Percent prey composition X whale sightings |
|---|---|---|---|---|---|---|---|
| June | 2002 | 1 | Capelin | 20 | 0.94% | 4.13% | 0.04% |
| | | | Walleye pollock | 2035 | 95.85 | 4.13 | 3.96 |
| | | | Pacific sandfish | 2 | 0.09 | 4.13 | 0.004 |
| | | | Eulachon | 66 | 3.11 | 4.13 | 0.13 |
| June | 2002 | 2 | Walleye pollock | 362 | 44.47 | 11.98 | 5.33 |
| | | | Eulachon | 452 | 55.53 | 11.98 | 6.65 |
| June | 2002 | 3 | Capelin | 8 | 2.24 | 8.26 | 0.19 |
| | | | Walleye pollock | 349 | 97.76 | 8.26 | 8.07 |
| June | 2002 | 4 | Capelin | 3 | 2.05 | 0.00 | 0.00 |
| | | | Walleye pollock | 141 | 96.58 | 0.00 | 0.00 |
| | | | Eulachon | 2 | 1.37 | 0.00 | 0.00 |
| June | 2002 | Near Shore | Pacific sandlance | 100 | 100.00 | 2.07 | 2.07 |

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* Pollock numbers adjusted for percent juvenile pollock under 30 cm in mid-water trawls (2001 – 78.81%, 2002 – 59.01%).

**B.2. Species composition from July 2001 and 2002 prey availability surveys. Percent compositions were determined by methods outlined in chapter 3.**

| Month | Year | Subarea | Prey Species | Total Count* | Percent prey composition by subarea | Percent whale sightings by subarea | Percent prey composition X whale sightings |
|---|---|---|---|---|---|---|---|
| July | 2001 & 2002 | 1 | Capelin | 2000 | 4.24% | 2.89% | 0.12% |
| | | | Walleye pollock | 11336 | 24.03 | 2.89 | 0.69 |
| | | | Eulachon | 33818 | 71.70 | 2.89 | 2.07 |
| | | | Pacific sandfish | 13 | 0.03 | 2.89 | 0.001 |
| | | | Pacific herring | 1 | 0.002 | 2.89 | 0.0001 |
| July | 2002 | 2 | Capelin | 7097 | 85.95 | 36.78 | 31.61 |
| | | | Walleye pollock | 993 | 12.03 | 36.78 | 4.42 |
| | | | Eulachon | 167 | 2.02 | 36.78 | 0.74 |
| July | 2002 | 3 | Walleye pollock | 4145 | 100.00 | 3.31 | 3.31 |
| July | 2001 & 2002 | 4 | Capelin | 43 | 2.05 | 1.24 | 0.03 |
| | | | Walleye pollock | 1919 | 91.47 | 1.24 | 1.13 |
| | | | Pacific sandlance | 1 | 0.05 | 1.24 | 0.001 |
| | | | Eulachon | 135 | 6.43 | 1.24 | 0.08 |
| July | 2001 & 2002 | Near Shore | Pacific sandlance | 125 | 62.50 | 5.79 | 3.62 |
| | | | Capelin | 74 | 37.00 | 5.79 | 2.14 |
| | | | Pacific sandfish | 1 | 0.50 | 5.79 | 0.03 |

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[*] Pollock numbers adjusted for percent juvenile pollock under 30 cm in mid-water trawls (2001 – 78.81%, 2002 – 59.01%).

**B.3. Species composition from August 2001 and 2002 prey availability surveys. Percent compositions were determined by methods outlined in chapter 3.**

| Month | Year | Subarea | Common Name | Total Count* | Percent prey composition by subarea | Percent whale sightings by subarea | Percent prey composition X whale sightings |
|---|---|---|---|---|---|---|---|
| August | 2002 | 1 | Pacific herring | 7 | 0.75% | 4.13% | 0.03% |
| | | | Walleye pollock | 905 | 96.69 | 4.13 | 3.99 |
| | | | Pacific sandfish | 15 | 1.60 | 4.13 | 0.07 |
| | | | Capelin | 3 | 0.32 | 4.13 | 0.01 |
| | | | Eulachon | 6 | 0.64 | 4.13 | 0.03 |
| August | 2002 | 2 | Capelin | 1 | 0.27 | 9.09 | 0.02 |
| | | | Walleye pollock | 375 | 99.73 | 9.09 | 9.07 |
| August | 2002 | 3 | No Data | N/A | N/A | 0.00 | 0.00 |
| August | 2002 | 4 | Capelin | 1400 | 99.86 | 0.00 | 0.00 |
| | | | Walleye pollock | 1 | 0.07 | 0.00 | 0.00 |
| | | | Pacific sandfish | 1 | 0.07 | 0.00 | 0.00 |
| August | 2001 & 2002 | Near Shore | Pacific sandlance | 125 | 62.50 | 0.00 | 0.00 |
| | | | Capelin | 74 | 37.00 | 0.00 | 0.00 |
| | | | Pacific sandfish | 1 | 0.50 | 0.00 | 0.00 |

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* Pollock numbers adjusted for percent juvenile pollock under 30 cm in mid-water trawls (2001 – 78.81%, 2002 – 59.01%).

**B.4. Species composition from September 2001 and 2002 prey availability surveys. Percent compositions were determined by methods outlined in chapter 3.**

| Month | Year | Subarea | Common Name | Total Count* | Percent prey composition by subarea | Percent whale sightings by subarea | Percent prey composition X whale sightings |
|---|---|---|---|---|---|---|---|
| Sept | 2002 | 1 | Walleye pollock | 99 | 100.00% | 1.24% | 1.24% |
| Sept | 2002 | 2 | Pacific herring | 6 | 0.20 | 1.24 | 0.003 |
| | | | Capelin | 2 | 0.07 | 1.24 | 0.001 |
| | | | Walleye pollock | 2844 | 96.31 | 1.24 | 1.19 |
| | | | Eulachon | 101 | 3.42 | 1.24 | 0.04 |
| Supplement zone 3 with July data | | | Walleye pollock | 4145 | 100.00 | 4.96 | 4.96 |
| Supplement zone 4 with August data | | | Capelin | 1400 | 99.86 | 2.89 | 2.89 |
| | | | Walleye pollock | 1 | 0.07 | 2.89 | 0.002 |
| | | | Pacific sandfish | 1 | 0.07 | 2.89 | 0.002 |
| Sept | 2001 & 2002 | Near Shore | Pacific sandlance | 125 | 62.50 | 0.00 | 0.00 |
| | | | Capelin | 74 | 37.00 | 0.00% | 0.00 |
| | | | Pacific sandfish | 1 | 0.50 | 0.00% | 0.00 |

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* Pollock numbers adjusted for percent juvenile pollock under 30 cm in mid-water trawls (2001 – 78.81%, 2002 – 59.01%).

**B.5. Percent lipid composition and converted energy densities of prey species. Prey species were sampled during 2002 mid-water trawl surveys.**

| Lipid Conversion Factor | 9.4 | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Percent Lipid | | | | Energy (kcal/g) | | | |
| Species | June | July | August | Sept | June | July | August | Sept |
| Capelin | 0.0636 | 0.0751 | 0.0663 | 0.0930 | 0.5978 | 0.7059 | 0.6232 | 0.8742 |
| Pac. Sandlance | 0.0782[*] | 0.0782 | 0.0782 | 0.0782 | 0.7351 | 0.7351 | 0.7351 | 0.7351 |
| Pac. Sandfish | 0.0237 | 0.0634 | 0.0540 | 0.0540 | 0.2228 | 0.5960 | 0.5076 | 0.5076 |
| Eulachon | 0.1704 | 0.2089 | 0.2251 | 0.2277 | 1.6018 | 1.9637 | 2.1159 | 2.1404 |
| Herring | 0.1470 | 0.1470 | 0.1329 | 0.1534 | 1.3818 | 1.3818 | 1.2493 | 1.4420 |
| Juv. Pollock | 0.0419 | 0.0523 | 0.0573 | 0.0623 | 0.3939 | 0.4916 | 0.5386 | 0.5856 |
| Surf Smelt[**] | 0.0721 | | | | 0.6777 | | | |

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[*] Values in lighter colored font are assumed from another month's value.
[**] The value for surf smelt comes from Payne et al. (1999).

**B.6. Percent protein composition and converted energy densities of prey species. Prey species were sampled during 2002 mid-water trawl surveys.**

| Protein Conversion Factor | 4.3 | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Percent Protein | | | | Energy (kcal/g) | | | |
| Species | June | July | August | Sept | June | July | August | Sept |
| Capelin | 0.1234 | 0.1296 | 0.1331 | 0.1292 | 0.53062 | 0.55728 | 0.57233 | 0.55556 |
| Pac. Sandlance | 0.1588[*] | 0.1588 | 0.1588 | 0.1588 | 0.68284 | 0.68284 | 0.68284 | 0.68284 |
| Pac. Sandfish | 0.1496 | 0.1434 | 0.1416 | 0.1416 | 0.64328 | 0.61662 | 0.60888 | 0.60888 |
| Eulachon | 0.1294 | 0.1298 | 0.1302 | 0.14 | 0.55642 | 0.55814 | 0.55986 | 0.602 |
| Herring | 0.167 | 0.167 | 0.1619 | 0.1578 | 0.7181 | 0.7181 | 0.69617 | 0.67854 |
| Juv. Pollock | 0.1443 | 0.1335 | 0.1394 | 0.1536 | 0.62049 | 0.57405 | 0.59942 | 0.66048 |
| Surf Smelt[**] | 0.1842 | | | | 0.79206 | | | |

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[*] Values in lighter colored font are assumed from another month's value.

[**] The value for surf smelt comes from Payne et al. (1999).

**B.7. Total counts and percentages by month of prey species. Prey species were sampled during 2001 and 2002 mid-water trawl surveys used to calculate energy densities by methods described in chapter 3.**

| | Total counts by month | | | | | Percentage by month | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | June | July | August | Sept | Total | June | July | August | Sept | Total |
| Capelin | 31 | 9,214 | 1,478 | 1,452 | 12,175 | 0.25 | 75.68 | 12.14 | 11.93 | 100.00 |
| Pac. Sandlance | 100 | 126 | 125 | 125 | 476 | 21.01 | 26.47 | 26.26 | 26.26 | 100.00 |
| Pac. Sandfish | 2 | 14 | 17 | 2 | 35 | 5.71 | 40.00 | 48.57 | 5.71 | 100.00 |
| Eulachon | 520 | 34,120 | 6 | 101 | 34,747 | 1.50 | 98.20 | 0.02 | 0.29 | 100.00 |
| Herring | 0 | 0 | 7 | 6 | 13 | 0.00 | 0.00 | 53.85 | 46.15 | 100.00 |
| Juv. Pollock | 2,887 | 18,393 | 1,281 | 7,089 | 29,650 | 9.74 | 62.03 | 4.32 | 23.91 | 100.00 |