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Reprinted from the Alaska Fishery Research Bulletin
Vol. 12 No. 2, Winter 2007
The Alaska Fisheries Research Bulletin can be found on the World Wide Web at URL:
http://www.adfg.state.ak.us/pubs/afrb/afrbhome.php

Alaska Fishery Research Bulletin 12(2):187–196. 2007.

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ABSTRACT: A photo-identification, mark–recapture study was conducted on a feeding aggregation of humpback whales *Megaptera novaeangliae* in the waters of eastern Kodiak Island between June and September 2002. Historically, a portion of this population was targeted in a local commercial whale fishery. The fishery was conducted in eastern Kodiak Island out of Port Hobron, Alaska, between 1926 and 1937 and resulted in the removal of nearly 1,600 humpback whales. An estimated 157 (95% confidence interval: 114, 241) whales were in the study area in 2002 based on the Schnabel maximum likelihood estimator (MLE) for closed populations. The Schnabel MLE of abundance in 2002 and historic catch values were used to back-calculate the historical abundance trend in the study area between 1925 and 2002 using a delay-difference model with a density dependent recruitment function. Historical abundances were calculated both prior to commercial whaling in 1925 and immediately post-whaling in 1938. Estimated abundance within the study area just prior to commercial whaling was 343 (331, 376). Immediately following the cessation of whaling in 1938, estimated abundance within the study area was 27 (14, 61). Results from this study show the Port Hobron whale fishery likely had a significant impact on the local humpback whale population.

INTRODUCTION

Photo identification has been used for many years as a mark–recapture tool to estimate humpback whale populations and track their movements (Baker et al. 1986, 1992; Perry et al. 1990; Calambokidis et al. 1993; von Ziegesar 2001). Photo-identification studies have resulted in moderate understanding of humpback whale stocks in the North Pacific and have shown that, though they may converge on winter breeding grounds, during feeding seasons humpback whales are isolated into regional aggregations with very little exchange between them. Known feeding aggregations in the North Pacific are found along the California, Oregon, and Washington coasts, southeastern Alaska, and Prince Williams Sound, Alaska (Calambokidis et al. 1993; Straley 1994).

A group of feeding humpback whales *Megaptera novaeangliae* is found year-round in the Kodiak Archipelago in the western Gulf of Alaska, with a peak in sightings occurring between June and October (Figure 1; Waite et al. 1999; Denny Zwiefelhofer, Wildlife Biologist, U.S. Fish and Wildlife, Kodiak National Wildlife Refuge, personal communication). These whales are currently assigned to the Central North Pacific stock of humpback whales by the National Marine Fisheries Service (NMFS), though no directed research has been conducted on this population (Angliss et al. 2001). Previous research on humpback whales around Kodiak Island has occurred opportunistically during line transect surveys for killer whales *Orcinus orca* in the early 1990s (Waite et al. 1999). These surveys suggest that the Kodiak Island humpback whales may be a homogeneous feeding aggregation separate from the other known feeding aggregations in Alaskan waters, including southeastern Alaska and Prince William Sound. However, until directed research tests this hypothesis, our understanding of the stock structure of North Pacific humpback whales remains incomplete, making the need for directed research efforts in this region critical for effective management.

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Acknowledgments: The authors are indebted to a number of individuals whose assistance was essential to this project. Janice M. Straley, Dr. Robert J. Foy, and Dr. Brendan P. Kelly offered insight and guidance. Chris Gabriele of Glacier Bay National Park, Sally Mizroch of the National Marine Mammal Laboratory, and John Calambokidis of Cascadia Research shared their experience and suggestions and Lisa Baraff assisted in data collection. This manuscript was improved by the comments and suggestions of two anonymous reviewers. All research was conducted under provisions of NMFS Scientific Research Permit 473-1433.
Sponsorship: Financial support for this project was provided by the Rasmuson Fisheries Research Center and NOAA Grant number NA16FX1270 to University of Alaska Gulf Apex Predator-Prey Project.

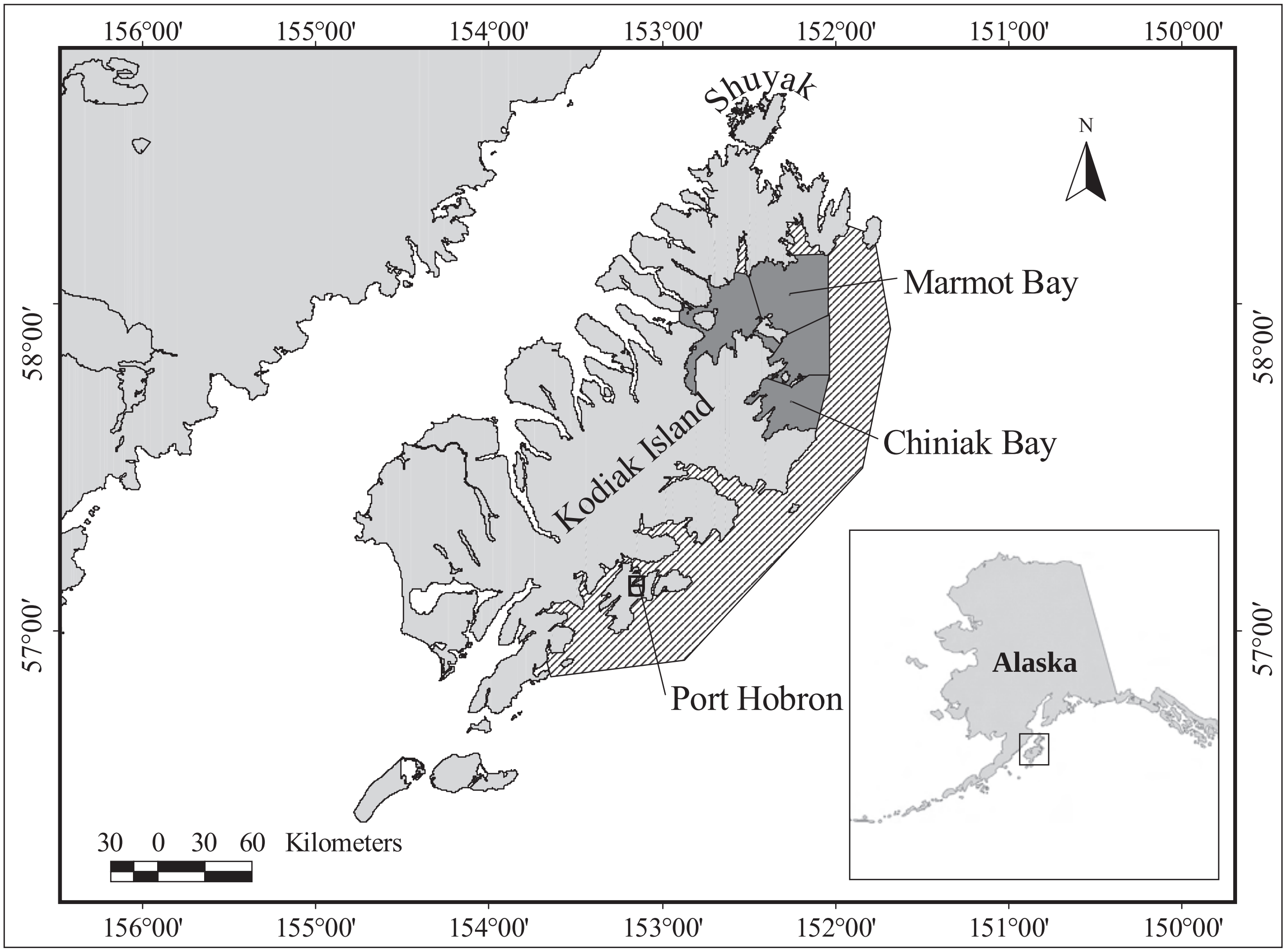

Figure 1. Map of the Kodiak archipelago showing Kodiak and Shuyak Islands. The study area is shown in shade. The location of the Port Hobron whaling station is also noted. The approximate coverage area of commercial whaling operations is shown in stripes.

The recovery rates of Kodiak Island area humpback whales as a population of marine predators is being monitored as part of the Gulf Apex Predator-Prey study (GAP). The GAP study was initiated in 1999 with the primary goal of documenting trophic relationships between apex predators, their prey, and potential competitors in waters near Kodiak Island. This commercial fishing area has seen declines in numerous marine species, including the endangered western Alaskan stock of Steller sea lions *Eumetopas jubatus.* Humpback whales comprise a significant component of the GAP study, not only because they are marine predators, but also because a large-scale commercial whale fishery operated around Kodiak Island between 1926 and 1937, significantly reducing the number of humpback whales in the area (William S. Lagen Collection, located at the University of Washington, Seattle, WA). The reduction in humpback population size caused by whaling likely affected the surrounding ecosystem. Modeling historical and current abundance for the Kodiak Island feeding aggregation of humpback whales can increase our understanding of their role as apex predators within the Kodiak marine ecosystem.

The purpose of this paper is to present the results of a study to assess humpback whale numbers in eastern Kodiak Island based on mark–recapture, photo-identification studies. Estimates of pre-whaling (1925) and immediate post-whaling (1938) populations within the study area are also constructed using a delay-difference population model (Quinn and Deriso 1999) to model the potential effects of historic commercial whaling on the local population of humpback whales.

METHODS

Study Area

For logistic reasons, the study area was limited to the waters of eastern Kodiak Island, including Chiniak and Marmot Bays (Figure 1). Kodiak Island is part of the Kodiak Archipelago and is located approximately 30 miles from the Alaskan mainland in the Gulf of Alaska. Due to the limited effort and data, 2001 efforts were used to assess study design and logistics. Data collected during that year were not used in analyses. Limitations of the 2001 study resulted in the expansion of the study area in 2002. Further, the study area was divided into 4 subareas of approximately equal size. The subareas were established in order to spread out sampling effort while ensuring thorough coverage within the study area.

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 (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. Photographs of calves were not used in the analysis, due to the tendency of the pattern on the flukes of some calves to change prior to maturity.

In addition to photographs, data collected at each sighting included the date, time, latitude and longitude, nearest headland, and general behavior of the whale. Information about the role (i.e. mother, calf, adult) of each whale was also documented for each encounter.

Study and Sample Periods

Vessel surveys were conducted between June and September 2002 from the R/V *Soundwave*, an 8.2 m bowpicker. In each year, the study period was divided into 7-day sample periods with the exception of the final sample periods in both years, which were shorter (Table 1). Effort consisted of 15 sample periods beginning June 4 and ending September 17. Surveys took place on 38 days for a total of about 224 hours (Table 1).

A survey of each subarea was attempted at least once during the sample period. Vessel surveys were often initiated in areas where whales were previously sighted. Inclement weather conditions such as fog and high winds limited survey effort in both years.

Table 1. Start dates, end dates, and effort for the 2002 sample periods for humpback whale photo-identification vessel surveys.

Sample Period	Period Start Date	Period End Date	No. of days Sampled	No. of hours Sampled
1	3-Jun	9-Jun	4	27.9
2	10-Jun	16-Jun	4	29.1
3	17-Jun	23-Jun	3	17.9
4	1-Jul	7-Jul	5	28.8
5	8-Jul	14-Jul	3	17.8
6	15-Jul	21-Jul	2	10.7
7	22-Jul	28-Jul	2	10.5
8	29-Jul	4-Aug	4	23.7
9	5-Aug	11-Aug	2	10.3
10	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
14	9-Sep	15-Sep	1	8.8
15	16-Sep	17-Sep	2	7.7
Total			38	224.1

Current Abundance Estimation

An estimate of current humpback whale abundance within the study area was made using the Schnabel MLE (Seber 1982). Two critical assumptions of the Schnabel MLE are that the population is closed and that all whales have equal capture probabilities at each sample period. The Schnabel MLE of $\hat{N}$ is the solution of the equation (see Table 2 for notation).

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

The Schnabel MLE was only applied to 14 sample periods in 2002 because no whales were seen in the shortened 15th sample period. A parametric bootstrap was performed with 1000 replicates to obtain a 95% confidence interval for estimated abundance $\hat{N}_{2002}$. In this procedure, marked recaptures for all sample periods were generated from the hypergeometric distribution. The 2.5 and 97.5 percentiles of the resultant abundance estimates across replications yield the lower and upper limits of the interval.

Alternatives to the Schnabel MLE with a common likelihood formulation were also explored through program MARK (White and Burnham 1999). Analyses conducted in MARK were Huggins-type models that incorporated time (t), behavior (b), and/or heterogeneity (h) (Huggins 1991). The most basic of the Huggins models (Mt) is equivalent to the Schnabel MLE which allowed for relative fits of all models to be compared

Table 2. Humpback whale sighting data for 2002. The Schnabel MLE was applied to 2002 Kodiak Island humpback whale sighting data only. n = the size of the i^{th} sample, m = the number of marked animals in the i^{th} sample, u = the number of unmarked animals in the i^{th} sample, M = the number of marked animals just prior to the i^{th} sample, and $r = \Sigma M$ or the total number of unique animals marked at the end of the experiment.

Sample Period	*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
Total	90	19	71	$r = 71$

with corrected Akaike information criterion (AICc) values generated by MARK.

The data were also pooled to 3 and 5 sample periods and run through Schnabel and MARK Huggins models. Pooling was performed by separating the study period into 3 or 5 sample periods, as opposed to the original 15, and analyzing sighting histories within those periods. The pooled sample periods were created to increase the number of mark–recaptures in each period and so an equal number of 7-day sample periods were represented in each of the pooled periods. As with previous analyses, AICc values were used to compare model fits.

Historical Abundance Estimation

Estimates of eastern Kodiak Island humpback whales within the study area were calculated for pre-commercial whaling 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:

$$N_{t+1} = (N_t - C_t)(1 - M) + R_t \qquad (2)$$

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
τ = lag time assumed for population response.

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

$$r_t = M = \left(1 - \frac{N_{t-\tau}}{N_0}\right)(r - M) \qquad (3)$$

where
r_t = recruitment rate in year t
N_0= initial population size (population size prior to commercial exploitation)
(r–M) = net recruitment rate.

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. 2004). 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 τ was set equal to 5 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 obtained 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 1). 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 4 times that of the study area (Figure 1). As a result, values of C_t were divided by 4 to account for the size difference between whaling grounds and the study area, assuming random harvest and uniform distribution of whales throughout the grounds.

Initial population size, $\hat{N}_0$, was estimated by first entering a trial value for $\hat{N}_0$ into equations (*2*) and (*3*) and projecting the population forward to 2002. The initial population size applies to the years 1920 through 1925 and is assumed to represent the abundance prior to commercial exploitation. Once a value of $\hat{N}_0$ was estimated, population size during any subsequent time period could be estimated. 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.

Sensitivity Study of Historical Estimation to Model Parameters

A sensitivity study of the *r* and *M* parameters in the delay-difference model determined which parameter was the most influential in the final estimation of historical population sizes. Changing the value of each of the parameters and rerunning 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. Both parameters were tested independently from one another. Values of *M* used came from the 95% confidence intervals of survival from Mizroch et al. 2004, 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).

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 (4 times the base run) as well as divided by 2 (2 times the base run) 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

Vessel surveys

Vessel surveys in 2002 resulted in 148 sightings of humpback whales (Table 2). A portion of the 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 in 2002.

Current Abundance Estimation

Data used in all model analyses are summarized in Table 2. The Schnabel MLE of abundance, N_{2002}, was 157 animals (CV 18%) with a 95% confidence interval (114, 241; Figure 2). Results from MARK suggest the basic Huggins model (equivalent to Schnabel) with no behavior and no heterogeneity (Mt) fitted the data best (AICc = 467.6; Table 3). Results from MARK analyses for data pooled to 5 periods suggest that the model incorporating both time and heterogeneity (Mth) fitted the data only slightly better than model Mt, with AICc values of 293.6 and 293.7 respectively. Abundance was estimated to be 268 (CV 32%) for model Mth and 181 (CV 23%) for Mt (Table 3). When data was pooled to 3 periods, the best fitting model was again Mt (AICc=189.4). The estimate of abundance for model Mt pooled to 3 periods was 158 (CV 23%; Table 3).

Estimated capture probabilities across the 14 periods were variable and imprecise (ranging from 0.00 to 0.18), but estimated whale abundance was more precise than from the pooled data analyses. Pooled data analyses tended to have more stable estimates of capture probabilities.

Historical Abundance Estimation

The delay-difference model estimated the pre-whaling humpback whale abundance at 343 (CV 3%) animals within the study area, given the value of $\hat{N}_{2002}$ equal to 157 (Figure 2). 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).

Sensitivity Study of Historical Estimation to Model Parameters

Pre-whaling abundance was estimated at 341 and 373 when *M* was equal to 0.02 and 0.06 respectively. $\hat{N}_{1938}$ equaled 5 and 72 under the same parameterization (Figure 3). Pre-whaling abundance was estimated at 392 and 371 when *r* was set equal to 0.06 and 0.10, respectively. $\hat{N}_{1938}$ was equal to 67 and 8 under the same parameterization. During the 1980 scenario pre-whaling abundance was estimated at 332 and $\hat{N}_{1938}$ was equal to 16 (Figure 3). 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, pre-whaling 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 3).

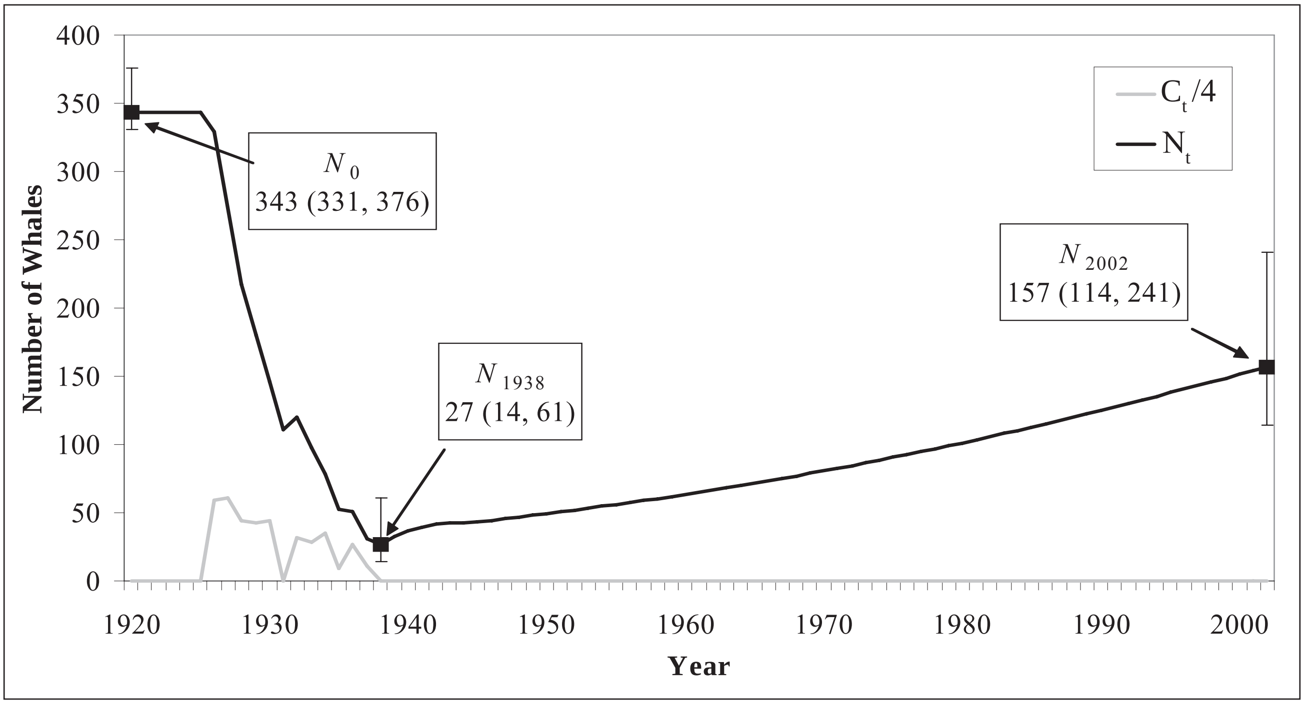

Figure 2. Comparison of adjusted commercial catch (C_t/4) and estimated abundance (N_t) between 1920 and 2002. Abundance estimates (± 95% confidence interval) from delay-difference model for N_0, N_{1938}, and N_{2002} are shown.

Table 3. Summary of model output from program MARK for all data and data pooled to 5 and 3 periods. Model outputs representing the Schnabel MLE are indicated by an asterisk, and model abbreviations are *t* = time, *h* = heterogeneity, and *b* = behavior (relative to capture probabilities). Abundance estimates and associated standard errors, coefficients of variance, and 95% confidence intervals are presented for the best fitting model for each set of data.

Model	Periods	AICc	Delta AICc	Parameters	Deviance	*N*	SE	CV	Lower CI	Upper CI
Mt*	14	467.6	0	14	560.0	157	28.7	18.2%	117	234
Mth	14	470.9	3.227	29	531.8					
Mtb	14	474.1	6.498	26	541.5					
Mtbh	14	483	15.33	41	518.1					
Mh	14	530.9	63.24	3	645.6					
Mth	5	293.6	119.9	11	481.8					
Mt*	5	293.7	120	5	494.5	181	40.7	22.5%	125	293
Mtb	5	296.5	122.8	8	491.1					
Mtbh	5	299	125.3	16	476.3					
Mh	5	309.3	135.6	3	514.2					
Mt*	3	189.4	0	3	475.6	158	36.2	22.9%	111	261
Mtbh	3	189.4	0.063	6	469.4					
Mtb	3	189.5	0.17	4	473.7					
Mth	3	191.6	2.201	7	469.4					
Mh	3	219.2	29.83	2	507.5					

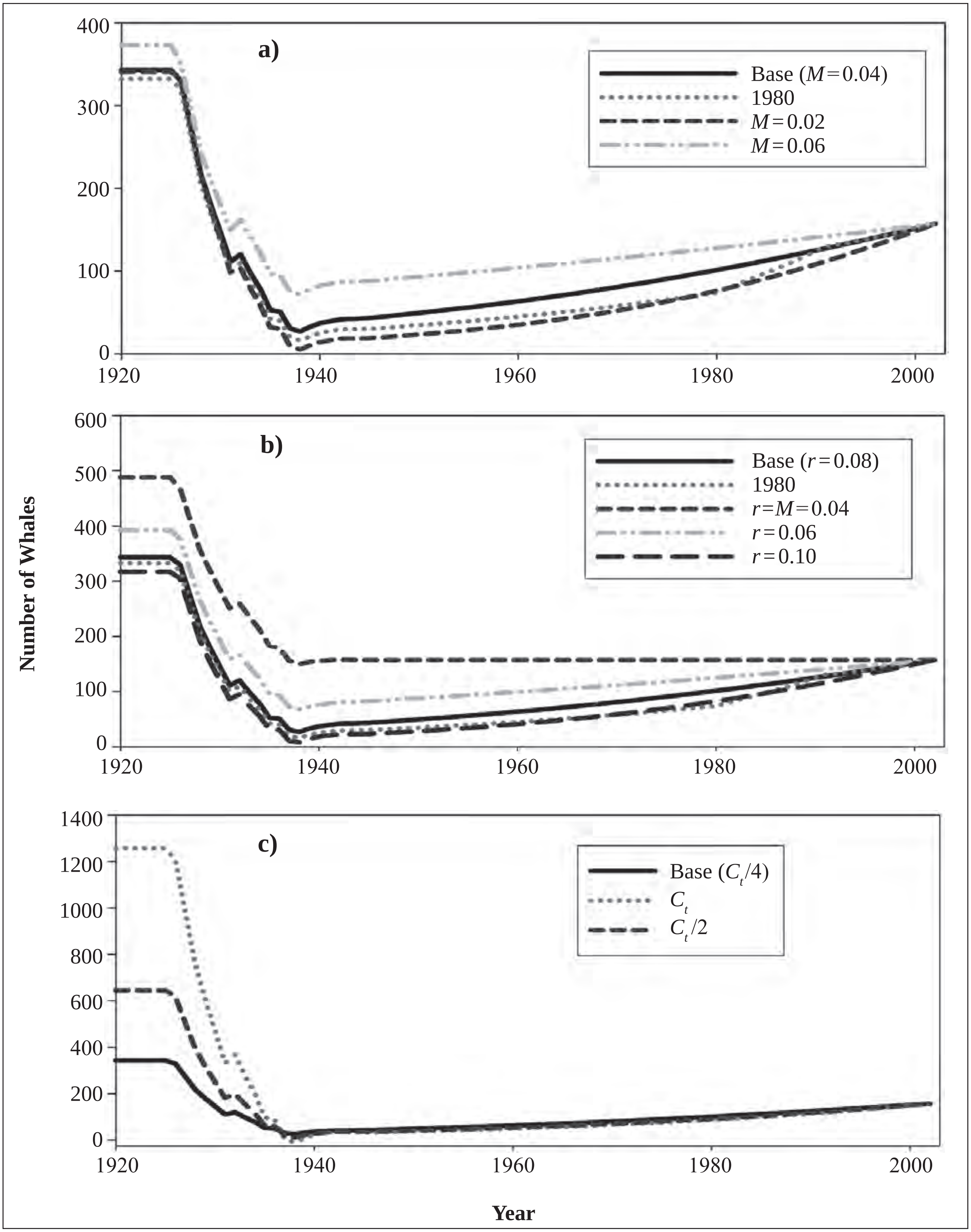

Figure 3. Comparison of estimated abundance showing sensitivity of the delay-difference model to a) the *M* parameter, b) the *r* parameter, and c) historic catch values (C_t). In the 1980 scenario, (*r*–*M*) was fixed at 0.10 between 1980 and 1990.

DISCUSSION

Current Abundance Estimation

The Schnabel MLE of 157 is the best estimate of inseason abundance for 2002. Alternate models which incorporated behavior and heterogeneity were analyzed through program MARK and were shown to have poorer fits than the Schnabel MLE. The Schnabel model also fit well when the data were pooled into 3 and 5 periods. However, both had higher CV values, indicating that the non-pooled data set produced a more precise estimate of abundance (Table 3). Though the Schnabel MLE produced the best estimates of abundance, the model may not have met at least 2 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 subpopulation of the whales that may be part of a much larger feeding aggregation. However, of the 31 whales sighted in 2001, 9 were resighted in 2002, which suggests a high rate of site fidelity to the study area—a characteristic of defined feeding aggregations. Still, whales may have migrated into and out of the study area throughout the study period; humpback whales have been previously observed throughout the Kodiak archipelago. The amount of movement that may have occurred 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, I sighted 67 individual whales outside of the study area—only two of which had been previously sighted in the study area within the study period.

These results suggest very limited movement between the whales within the study area and other feeding whales around the Kodiak archipelago, which could be indicative of an isolated population. In such a case, the Schnabel MLE may be an appropriate method of estimation for this population. It may also suggest a very large population is utilizing the entire island area, in which case the Schnabel MLE is evaluating only a subpopulation of humpback whales. If so, estimates provided by the Schnabel MLE still serve as important baseline data that can later be applied to more complex models for larger, open populations as additional data is collected in the coming years. However, if the closure assumption was violated to a high degree, abundance could 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 across time periods. Models that incorporated heterogeneity produced highly variable estimates of capture probabilities, which would indicate parameter instability and a poorer fit of the model. It is likely then that a high degree of heterogeneity was not present within the study period and area.

Potential problems with model assumptions may be rectified in the future as effort continues and sample size is increased. Additional research will validate the estimates with between-year captures, and 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

Estimation of the historical populations of humpback whales was dependent on the estimate of current abundance. Any biases associated with the current estimate would cause a cascading effect and be reflected in the historical estimates. Additionally, the estimated pre-whaling abundance was affected 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 percentage points 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 3).

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 variation in these parameters over time when, in reality, variation over a long time period, such as the one represented here, is likely to occur. Notably, the scenario that does allow for some variation in the parameters over time—the

1980 scenario—estimates abundances that are the most similar to the base model.

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.

Historical abundance here was estimated only within the study area, although humpback whale kills occurred throughout the east side of Kodiak Island. It is likely that historical abundance within the study area would be overestimated if catch had not been 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 (Figure 3). 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. The most conservative estimate of local abundance within the study area assumed that the study area comprises one quarter of the whaling grounds. Applying that same proportion to the historical catch numbers resulted in 343 (CV 3%) whales as the best estimate of historical abundance within the study area given the current level of data, and shows that Port Hobron whaling effort likely had a significant impact on the humpback whale population.

The total humpback whale population of the entire Kodiak area is clearly greater than that of the study area. Depending on their annual use of the study area, the whale population could range from 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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