

Seasonal Characteristics of Humpback Whales (*Megaptera novaeangliae*) in Southeastern Alaska

by

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Abstract

Humpback whales were studied in southeastern Alaska to assess seasonal distribution and numbers, migration patterns, length of stay, female reproductive histories, and calf survival. A mean annual estimate and 95% confidence interval of whales present in the study areas was 404 ± 54 individuals. The longest length of stay was nearly 7 months, and the shortest transit to the Hawaiian mating and calving grounds was 39 days. Generally, birth intervals did not vary from one calf every two or three years; individual variation ranged from one to five years. There were few resightings of whales first seen as calves. The recovery of North Pacific humpback whales will only occur through an increase in the survival of calves to become sexually mature and reproducing adults.

KEY WORDS: Endangered species, humpback whale, population estimates, seasonal distribution, migration, reproduction, survival.

Previous studies on humpback whales (*Megaptera novaeangliae*) in southeastern Alaska focused primarily on two areas, the Glacier Bay-Icy Strait and Frederick Sound areas, during the summer months. These studies made important contributions to the knowledge of this species, but humpback whales are present in large numbers in other areas and in other seasons. This fact complicates the present understanding of the natural history and biology of the

humpback whale in southeastern Alaska. The objectives of this study were to determine 1) seasonal distribution and numbers, 2) regional migration patterns and length of stay on the feeding grounds, and 3) reproductive histories of females, birth intervals, calf survival, and recruitment.

North Pacific humpback whales are seasonal migrants that feed on zooplankton and small schooling fishes in the cool, coastal waters of the western United States, western Canada,

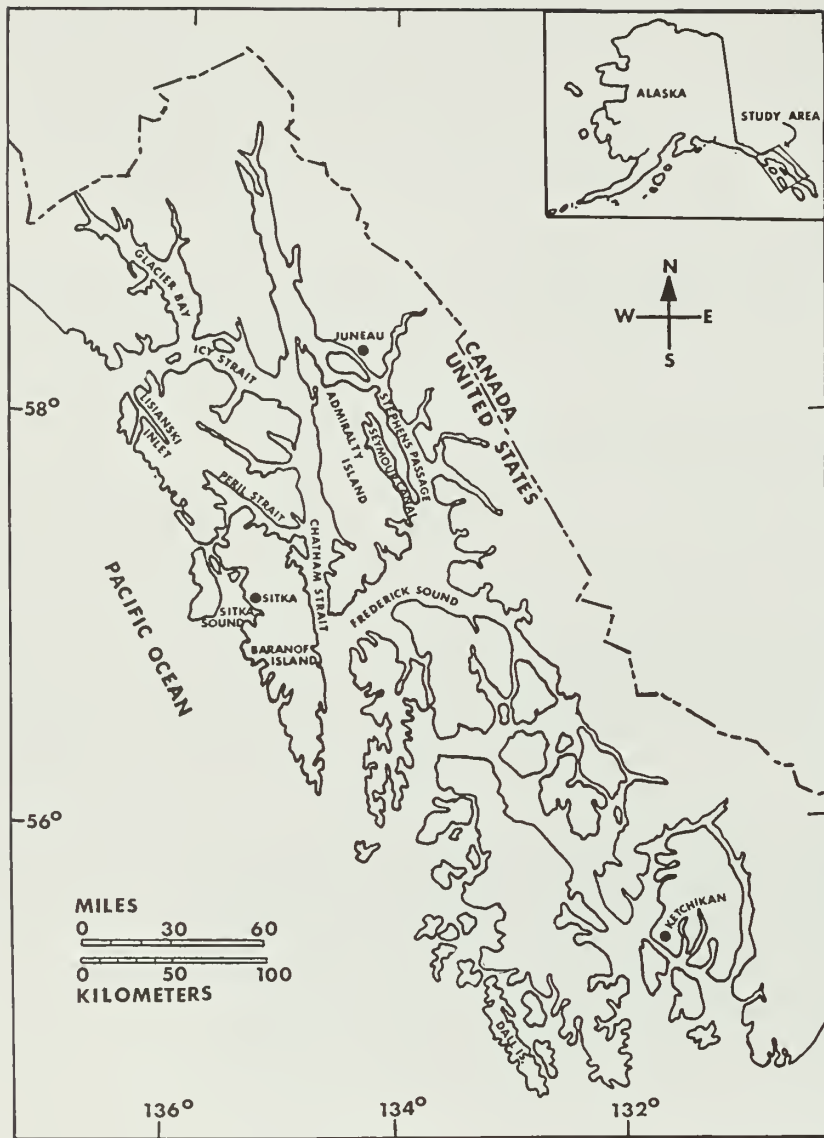


Fig. 1. Map of southeastern Alaska study areas.

and Russian Far East. The eastern North Pacific feeding area extends northward along the entire coast of California, Oregon, Washington, British Columbia, southeastern Alaska, Prince William Sound, the western Gulf of Alaska, and the Aleutian Islands, including the Bering Sea.

Humpback whales feed in discrete assemblages in areas that are geographically isolated. The largest number of humpback whales in Alaskan waters gather to feed in the southeastern part of the state. Humpback whales have been seen there in all months of the year (Straley, 1990); peak numbers occur during late summer (Baker et al., 1985). Individual humpback whales have been documented to

remain in southeastern Alaskan waters for more than 6 months (Baker et al., 1992).

Female humpback whales generally have a 2- or 3-year breeding cycle, with a 12 month pregnancy and a 10.5 month lactation period (Chittleborough, 1958). An average birth interval of 2.8 years was calculated for females in southeastern Alaska, during the years 1981-86 (Baker et al., 1992). Humpback whales studied in the North Atlantic from 1979 to 1987 resulted in a mean birth interval of 2.4 years (Clapham and Mayo, 1990). Reproductive rates will give some indication as to the recovery of this population but data collected on calf survival and eventual recruitment of these offspring into the population will ultimately determine the recovery status of humpback whales in the North Pacific.

Methods

The study was conducted in southeastern Alaska, which is an extensive archipelago with glacial fjords, sounds, inlets, bays, and straits (Figure 1).

The three primary study areas were 1) Glacier Bay-Icy Strait, 2) Frederick Sound-Seymour Canal-lower Stephens Passage, and 3) Sitka Sound. Other areas, including Lisianski Inlet, Chatham Strait, and Peril Strait were surveyed occasionally.

This study was conducted from 1980-1992, with a primary focus on data collected from 1985-1992. Skiffs were used as survey vessels, ranging in size from 3.9m to 6.9m, and powered by 25hp to 75hp outboard engines.

Individual humpback whales were identified from photographs of natural markings on the ventral surfaces of their flukes (Katona et al., 1979). A 35 mm SLR camera, equipped with a motordrive or winder, and a 70-200 mm or 300 mm lens, was used to take the photographs. High speed black and white film was used in the camera.

Photographic comparisons were made with photographic collections of whales from southeastern Alaska and Hawaii (University of Hawaii, Honolulu, HI).

A resighting of a whale was confirmed when two or more photographs showed that the same black and white pattern on the flukes, the same trailing edge, and other distinctive

markings were identical. Sightings of each whale during a given year were compiled and then added to the long-term sighting history of that whale or, if not sighted previously, a sighting history was initiated for that whale.

Photographs of the flukes were rated as "good," "fair," or "poor" quality, based on sharpness, contrast, and fluke angle. Poor quality photographs and photographs of the flukes of calves were excluded from analysis involving resighted individuals in estimates of population size.

A sighting matrix was developed from the sighting histories of individual whales for each of the primary study areas of Glacier Bay-Icy Strait, Frederick Sound, and Sitka Sound, as well as for the combined study areas in southeastern Alaska. These sighting matrixes summarized the numbers of adult humpback whales photo-identified each year, and this was the basis for the "capture-recapture" data analyses to estimate population size. The "recaptured" whales were those sighted and photographed in previous years, and the newly "captured" whales were those sighted and photographed for the first time in the given year. The sum of the resighted and newly sighted whales each year was equal to the total number of whales "captured" for that year. For each study area, the total number of newly sighted whales across all years was equal to the sum of individuals using the area.

The computer program JOLLY (available from James E. Hines, United States Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, MD 20708) was used to compute open estimates of population size for each year and probability of capture across all years, using the sighting matrixes developed for each primary study area (Pollock et al., 1990).

The models available from program JOLLY are dependent on the assumptions of an open population (Seber, 1982). An open population model allows for changes in the population over the time of the study. The population is subject to birth, death, immigration, and emigration. Emigration is considered permanent, meaning once an animal leaves the population it is treated as a "death", and is considered a "new" animal if it enters the population again.

The reproductive status of females was determined from the presence or absence of a calf during one or more observations. Calves (animals less than one year old) were identified from their size (estimated length 4-8 m) and their close, consistent affiliation with the same adult whale, presumed to be the mother. Juveniles were whales one to five years old, whose age was determined from previous documentation of their birth year. Adults were whales known to be more than five years old, which is the age at which the majority of females have reached sexual maturity (Chittleborough, 1959; Clapham, 1992).

The reproductive rate was measured by determining the birth interval, which was defined as the number of years between observations with a calf for each female. Only females that had been observed every year between the years sighted with calves were used for this calculation.

Results

Distribution and Numbers of Whales

Numbers of whales observed through photo-identification

The sighting matrix developed for each primary study area provided information on the numbers of adult humpback whales photo-identified each year (Tables 1-4).

There were 119 adult humpback whales individually identified ("captured") in the Glacier Bay-Icy Strait study area, 372 in the Frederick Sound study area, and 275 in the Sitka Sound study area from 1985 to 1992. In the other study areas, 15 whales were individually identified in Chatham Strait, 12 in Lisianski Inlet, and 3 in Peril Strait. A total of 648 whales were individually identified in all of the study areas of southeastern Alaska during this period; this number does not equal the sum of individuals identified in all areas, because some whales were sighted in more than one area.

The sum of the sightings of individual whales identified in all study areas during 1985 to 1992 was 796. Of these, 500 (62.8%) were seen in one area only, and 296 (37.2%) were seen in more than one study area at least once, in the same year or different years, during 1985 to 1992. The percentage of whales sighted in one or more of the other areas ranged from 100% for Peril Strait to 28.5% for the Frederick Sound area (Table 5). This demonstrates that there is some fidelity to specific areas, although the extent of this fidelity is difficult to quantify due to unequal sampling effort across seasons and years in the study areas.

Numbers of whales estimated through capture-recapture methods

The yearly estimates of population size, standard errors, confidence intervals, and probability of capture, computed from program JOLLY, for the study areas of southeastern Alaska are presented in Table 6.

Seasonal Movements and Migration

Movement within southeastern Alaska

During 1985 to 1992, there were 92 whales that made 99 transits between study areas in southeastern Alaska, within

Table 1. Humpback whale sighting matrix for the Glacier Bay-Icy Strait study area in southeastern Alaska, 1985-1992.

| TIME OF LAST CAPTURE | TIME OF RECAPTURE: | | | | | | | | TOTAL # WHALES (Σ NEWLY CAPTURED) |
|----------------------|--------------------|------|------|------|------|------|------|------|--|
| | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | |
| 1985 | 0 | 24 | 5 | 1 | 0 | 0 | 0 | 1 | |
| 1986 | 0 | 0 | 31 | 4 | 0 | 0 | 0 | 0 | |
| 1987 | 0 | 0 | 0 | 30 | 3 | 4 | 2 | 1 | |
| 1988 | 0 | 0 | 0 | 0 | 27 | 7 | 1 | 0 | |
| 1989 | 0 | 0 | 0 | 0 | 0 | 25 | 7 | 1 | |
| 1990 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | 4 | |
| 1991 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 36 | |
| RECAPTURED | 0 | 24 | 36 | 35 | 30 | 36 | 40 | 43 | 119 |
| NEWLY CAPTURED | 38 | 15 | 20 | 13 | 8 | 9 | 8 | 8 | |
| TOTAL CAPTURED | 38 | 39 | 56 | 48 | 38 | 45 | 48 | 51 | |

Table 2. Humpback whale sighting matrix for the Frederick Sound study area in southeastern Alaska, 1985-1992.

| TIME OF LAST CAPTURE | TIME OF RECAPTURE: | | | | | | | | TOTAL # WHALES (Σ NEWLY CAPTURED) |
|----------------------|--------------------|------|------|------|------|------|------|------|--|
| | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | |
| 1985 | 0 | 59 | 6 | 1 | 3 | 3 | 2 | 6 | |
| 1986 | 0 | 0 | 21 | 11 | 29 | 4 | 3 | 7 | |
| 1987 | 0 | 0 | 0 | 4 | 5 | 2 | 3 | 1 | |
| 1988 | 0 | 0 | 0 | 0 | 3 | 1 | 6 | 3 | |
| 1989 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 10 | |
| 1990 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 3 | |
| 1991 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | |
| 1992 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| RECAPTURED | 0 | 59 | 27 | 16 | 40 | 12 | 17 | 33 | 372 |
| NEWLY CAPTURED | 139 | 103 | 36 | 10 | 32 | 6 | 12 | 34 | |
| TOTAL CAPTURED | 139 | 162 | 63 | 26 | 72 | 18 | 29 | 67 | |

Table 3. Humpback whale sighting matrix for the Sitka Sound study area in southeastern Alaska, 1985-1992.

| TIME OF LAST CAPTURE | TIME OF RECAPTURE: | | | | | | | | TOTAL # WHALES (Σ NEWLY CAPTURED) |
|----------------------|--------------------|------|------|------|------|------|------|------|--|
| | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | |
| 1985 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | |
| 1986 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 1 | |
| 1987 | 0 | 0 | 0 | 15 | 2 | 2 | 4 | 0 | |
| 1988 | 0 | 0 | 0 | 0 | 15 | 2 | 17 | 2 | |
| 1989 | 0 | 0 | 0 | 0 | 0 | 5 | 15 | 1 | |
| 1990 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 4 | |
| 1991 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 68 | |
| RECAPTURED | 0 | 1 | 5 | 18 | 17 | 9 | 44 | 76 | 275 |
| NEWLY CAPTURED | 3 | 11 | 42 | 37 | 14 | 6 | 114 | 48 | |
| TOTAL CAPTURED | 3 | 12 | 47 | 55 | 31 | 15 | 158 | 124 | |

Table 4. Humpback whale sighting matrix for all study areas in southeastern Alaska, 1985-1992.

| TIME OF LAST CAPTURE | TIME OF RECAPTURE: | | | | | | | | TOTAL # WHALES (Σ NEWLY CAPTURED) |
|----------------------|--------------------|------|------|------|------|------|------|------|--|
| | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | |
| 1985 | 0 | 89 | 14 | 4 | 6 | 3 | 8 | 7 | |
| 1986 | 0 | 0 | 69 | 20 | 26 | 5 | 11 | 11 | |
| 1987 | 0 | 0 | 0 | 51 | 18 | 7 | 18 | 2 | |
| 1988 | 0 | 0 | 0 | 0 | 47 | 9 | 32 | 7 | |
| 1989 | 0 | 0 | 0 | 0 | 0 | 37 | 30 | 13 | |
| 1990 | 0 | 0 | 0 | 0 | 0 | 0 | 44 | 13 | |
| 1991 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 120 | |
| RECAPTURED | 0 | 89 | 83 | 75 | 97 | 61 | 143 | 173 | 648 |
| NEWLY CAPTURED | 182 | 122 | 72 | 50 | 41 | 21 | 98 | 62 | |
| TOTAL CAPTURED | 182 | 211 | 155 | 125 | 138 | 82 | 241 | 235 | |

Table 5. Number of humpback whales individually identified in each study area in southeastern Alaska, 1985-1992. Shown also are the number of whales seen in more than one area and the number seen only in one area during this period.

| AREA | # PHOTO-IDENTIFIED | SEEN IN MORE THAN ONE AREA | SEEN IN ONLY ONE AREA |
|-----------------|--------------------|----------------------------|-----------------------|
| GLACIER BAY | 119 | 71 (59.7%) | 48 (40.3%) |
| FREDERICK SOUND | 372 | 106 (28.5%) | 266 (71.5%) |
| SITKA SOUND | 275 | 95 (34.5%) | 180 (65.5%) |
| CHATHAM STRAIT | 15 | 10 (66.7%) | 5 (33.3%) |
| LISIANSKI INLET | 12 | 11 (91.7%) | 1 (8.3%) |
| PERIL STRAIT | 3 | 3 (100%) | 0 (0%) |
| TOTAL | 796 | 296 (37.2%) | 500 (62.8%) |

Table 6. Estimated annual population size for humpback whales in all southeastern Alaskan study areas, 1985-1992. Mean estimates of population size (N), standard error (SE), confidence interval (CI), and probability of capture (ρ), are shown from the appropriate Jolly-Seber capture-recapture model.

| AREA | N | SE | CI | ρ (SE) |
|------------------------|-----|-------|---------|-------------|
| GLACIER BAY-ICY STRAIT | 64 | 4.72 | 55-73 | 0.73 (0.03) |
| FREDERICK SOUND | 379 | 55.99 | 270-489 | 0.18 (0.02) |
| SITKA SOUND | 133 | 24.46 | 85-181 | 0.42 (0.13) |
| SOUTHEASTERN ALASKA | 404 | 27.60 | 350-458 | 0.42 (0.03) |

the same year. These 92 whales were included in the 296 whales observed in one or more study areas during 1985 to 1992 (Table 5), and comprise the subset that was observed in different study areas within the same year. This subset is used here to demonstrate seasonal movements within southeastern Alaska. Of these 92 whales, 86 made at least one transit, 4 whales made at least two, and one whale made at least three transits between study areas within the same year.

In general, there was a seasonal movement to the Frederick Sound area during late spring-early summer and mid-summer-fall. The seasonal movement in the fall and early winter was mainly to the Sitka Sound area and Lisianski Inlet.

Other observations showed the presence of the same whales across seasons in the same study areas. In 1985 and 1986 there were 21 whales that were sighted in the Frederick Sound study area during the summer and sighted later in the same study area in fall of the same year.

Length of stay on the feeding grounds

Between 1985 and 1992, one whale (#1073) remained on the feeding grounds 206 days. Whale #1073 was first sighted in 1991 in Icy Strait on June 3, next sighted in Sitka Sound on December 15, and last observed in Lisianski Inlet on December 26.

Migration time to the Hawaiian mating and calving grounds

The shortest known migration time from the southeastern Alaskan feeding grounds to the Hawaiian breeding grounds was 39 days. Whale #339 was last seen in Sitka Sound on January 3, 1988 and was resighted by University of Hawaii researchers near the island of Hawaii on February 11, 1988. No other same year matches were found and whale #339 has not been sighted in southeastern Alaska since 1988. The migrational speed from Alaska to Hawaii, a distance of 4500 km, was about 4.8 km/hour and is 2 km/hour faster than any previously reported transit (Baker et al., 1985). The actual transit time probably was less because the whale probably was not photographed on the last day in Alaskan waters or on the first day in Hawaii.

Reproduction and Calf Survival

Birth intervals

From 1980 to 1992, a total of 136 of the photo-identified humpback whales in southeastern Alaska were identified as female. In that same period, these females were sighted with

222 calves. No female was seen with more than one calf per year.

To determine a birth interval, an individual female humpback whale must be seen in at least two different years with a calf. To remove ambiguity from the determination of birth intervals, the whale also must be seen every year between the years when sighted with calves. Of the 136 individual females, only 23 met that criterion.

For the 23 females with complete sighting records, 46 birth intervals were measured. These ranged in length from one to five years. The most frequent birth interval was 2 years (n=23), followed by 3 years (n=11), 1 year (n=8), 4 years (n=3), and 5 years (n=1).

Nine females with sufficiently long sighting records showed variation in birth intervals; three females were more consistent, and the rest were indeterminate. The most extreme case of variation was in whale #193, with two 4-year birth intervals, followed by two 1-year intervals.

For the 23 females with one or more completely documented birth intervals, the mean interval was 2.26 ± 0.71 SE years (n=46). That is, the adult females sighted in southeastern Alaska were accompanied by a new calf on an average of once every 2.26 years. Because these were calves that had survived their first oceanic migration from tropical or subtropical waters to southeastern Alaska, this is a conservative estimate.

Calf survival, recruitment, and return

Of the 222 calves observed from 1980 to 1992 in southeastern Alaska, 85 were successfully photographed for identification purposes from 1980 to 1991.

Of these 85 calves, 21 were resighted in southeastern Alaska as juveniles and adults. Because the maximum age at first resighting was 8 years, only the resightings of calves born in 1980 to 1984 qualified for calculation of the mean age at first resighting, and this was 4.0 years (SE=0.76, n=7).

Of the 21 calves that were resighted, 8 were observed when at least 5 years old, the presumed average age at sexual maturity but only two of them (#353 and #967), have been observed with calves. These were at ages of 8 and 12 years, respectively. Whale #353 was first resighted at age 3, and has been seen every year since then in Icy Strait. She bore her first calf at 8 years. Whale #967 was seen with a calf for the first time at the age of 12 years. Because the sighting record of this whale as an adult is not complete, her age at first birth is unknown.

The return of known-age whales to the feeding ground in southeastern Alaska, where they were first sighted as calves with their mothers, has been documented previously for three humpback whales (Baker et al., 1987). The return of 19

additional whales that were first sighted as calves is reported here for the first time. Two of these whales returned with their own calves.

Of the 21 calves that were observed to return to the southeastern Alaskan feeding ground, 11 were seen feeding as juveniles and adults near, but not with, their mothers. These observations were in areas where they were initially observed with their mothers as calves. This further corroborates the return of the same whales to the same subregion within a North Pacific feeding ground, as previously reported by Jurasz and Palmer (1981) and Baker et al. (1987).

Discussion

Distribution and Numbers of Whales

A considerable degree of fidelity to feeding areas has been demonstrated by this study. Nonetheless, for each of the three primary study areas, the total number of individual whales identified from 1985 to 1992 was nearly double the number observed in any given year. The difference between the 8-year total and the annual numbers could be due to 1) whales being missed, 2) whales failing to return every year, or 3) death. Death could not have been a major cause, as most of the whales did eventually reappear. We think fewer whales were missed in Glacier Bay-Icy Strait than elsewhere because of the comprehensive survey coverage, hence most of the "missed" whales simply did not return every year. This conclusion is supported by the fact that over half of the whales observed at least once in the Glacier Bay-Icy Strait area were seen also in the other study areas. This area may not be able to accommodate more than 60-70 whales per year, due to habitat limitations. These limitations could be due to prey availability, space, and competition with human or other marine mammal sources. In the Frederick Sound study area, where sampling effort was irregular, and the numbers of whales sighted per year fluctuated widely, we think a higher proportion of whales could have been missed during the sampling effort. The Sitka Sound study area had the most extreme annual variation in the number of whales and a marked increase in the number in 1991 and 1992. This was likely due to an influx of whales coming from other areas. Also some whales were missed because this area is difficult to study in the fall and early winter, when whale numbers are highest, because of inclement weather and limited daylight.

With any capture-recapture method used to estimate population size, it is important to consider the assumptions of the model and the effects of violations those assumptions. Equal probability of capture was the underlying assumption of these models that probably was violated. All whales did

not behave in the same way when showing their flukes, hence were not equally identifiable. Furthermore, the distribution of whales was non-random, and the sampling effort was heterogeneous. Non-random distribution of whales was a problem in all study areas because some whales had a tendency to stay in one area and others moved around. There was not total mixing of the population between sampling periods. Heterogeneous sampling effort was a problem in the Sitka Sound and Frederick Sound study areas because Sitka Sound surveys were often prevented by inclement weather and rough seas, and the Frederick Sound area surveys were limited by irregular sampling effort among years. Not surprisingly, both these areas had somewhat low capture probabilities (<50%).

Violating the assumption of equal capture probability results in a negative bias and an underestimate of the population size. The magnitude of the bias is a function of sample size and the probability of capture. The higher the average probability of capture (over 50%), the less influence unequal capture probabilities have upon the estimate of population size (Carothers, 1973; Gilbert, 1973). The samples from the Glacier Bay-Icy Strait study area had the highest capture probabilities and most uniform sampling effort, hence population estimates for that area are probably less negatively biased than were those for the other study areas.

Seasonal Movements and Migration

The movements of whales in the Glacier Bay-Icy Strait area to the Frederick Sound area by late summer was strongly confirmed with 39 transits observed, only nine of which had been previously reported (Baker et al., 1992). A similar seasonal shift from other areas to Frederick Sound established that whales travel the inside waters of southeastern Alaska, rather than the more direct route, south of Baranof Island.

The seasonal movement from the summer to fall and early winter to the Sitka Sound area and Lisianski Inlet is a seasonal response to herring schools, which move in from open passages to overwinter in the deep, sheltered bays and sounds of southeastern Alaska. Sitka Sound and Lisianski Inlet are both areas where herring congregate in the fall and early winter (Larson et al. 1991). Half of the whales identified in Lisianski Inlet in the winter of 1991 had been observed earlier that year in at least one of the other study areas. One whale moved from the Glacier Bay-Icy Strait area, south to the Sitka Sound area, and back north to Lisianski Inlet. These fall and early winter movements into areas where herring overwinter have a major influence on the length of time spent on the feeding grounds by humpback whales. It is now apparent that many of the

whales present during the spring and summer stay through late fall or early winter to capitalize on this energy-rich prey source, before their southward departure for the mating and calving grounds.

Earlier, Straley (1990) speculated that the whales present in southeastern Alaska during the fall and winter were late migrants--part of a staggered or irregular migration pattern, in which the whales that arrived early departed early, and these fall-winter animals reached southeastern Alaska later and returned later to the mating and calving grounds. With the shortest transit to Hawaii from southeastern Alaska being 39 days, and the longest length of stay in Alaska being nearly 7 months, a longer stay on the feeding grounds is possible than was thought previously. The duration on the feeding grounds may be especially long in years when food resources are abundant during the fall and winter. Humpback whales could stay on the feeding grounds for 8 to 9 months, leave in January, and still reach Hawaii in time for peak mating activities in February and March. This would still allow enough time to return to southeastern Alaska for the next summer's feeding season. The 7-month stay documented here is longer than any reported before, and the prospect of whales staying on the feeding grounds for up to two-thirds of the year is not unlikely.

Reproduction and Calf Survival

The average birth intervals for female humpback whales in this study did not differ from the previous estimate of one calf every 2 or 3 years. The data used to calculate birth intervals were all from females that had complete sighting records between births; that is, they had been observed every year during the intervals. Hence, there was no ambiguity in determining the number of calves between females for these females. Because many whales were not observed every year, however, a bias towards documenting the shorter, rather than the longer, birth intervals exists. This bias would lower the mean birth interval, or births would appear to be more frequent than they actually were. Another bias is introduced by the fact that what was recorded were the surviving calves that make it through the migration and to the feeding grounds, and not the actual birth interval observed on the mating and calving grounds. This bias would make the recorded birth intervals in this study more conservative than what they actually were.

There was considerable variation per individual female in the length of the birth intervals; some whales had regular and some had irregular intervals. Presumably, the minimal interval is one year, and all longer intervals are a function of the female's physical condition (Mizroch, 1983). That is, to maintain a pregnancy and nurse a calf, sufficient food must be found for at least one feeding season prior to conception

and all through the pregnancy and lactation. In years when food is abundant, females can maximize their reproduction; in years when food is scarce, whales may move around more, searching for better food sources. Essentially, whale reproductive rates will vary as an adaptation or in response, to changes in their environment (i.e., fluctuations in food availability). The females with the longest intervals between births may have had difficulty in finding adequate food and did not have sufficient energy reserves to ovulate, conceive, or nurse a calf until they rebuilt their energy reserves (Lockyer, 1986). The reasons for not building sufficient energy reserves could have been due to inexperience in finding food in lean years, or to a smaller body size; a larger body size gives a larger capacity to store more fat. The whales with less variable birth intervals may have been larger, older, and more experienced at finding food. Because humpback whales are long-lived animals, the need for producing offspring at frequent intervals is not as great as it is for other species with shorter life spans. Humpback whales have many years to produce calves, and they may not begin or complete a reproductive cycle until food availability is sufficient to allow them to store enough energy for reproduction. Ultimately, the success of different reproductive strategies for these females will be determined through documenting the survival of their offspring as juveniles and adults.

The return of whales whose ages were known, because they were first sighted as calves, continues to document maternally-directed fidelity to the feeding grounds in the North Pacific. In the North Atlantic, fidelity to the Massachusetts Bay feeding ground also has been documented (Clapham and Mayo, 1990). The return rate to Massachusetts Bay (37/46), however, was significantly greater than that to southeastern Alaska (21/85) (G-test, $G=39.36$, $n=131$, $p=0.00$; Zar, 1984). While this difference could be due to higher mortality, it could be attributed to more thorough sampling in Massachusetts Bay, compared with southeastern Alaska.

The average age at first birth has yet to be determined for North Pacific humpback whales. Given that the average age at sexual maturity elsewhere is 5 years the earliest average age at first birth would be 6 years, because a pregnancy lasts 12 months. Eleven of the whales in this study were 6 years old or older in 1992, and at least two of them were females. Only one of those females returned with a calf when the age at first birth could be determined, and she was 8 years old. Sexual maturity at 5 years may be the average age for North Pacific humpback whales, but whether any of them successfully conceive and maintain a pregnancy at this age is unknown.

The recovery of humpback whales in the North Pacific will only occur though an increase in the population.

Currently, we do not know the North Pacific population size of humpback whales in the North Pacific, the rate of calf survival, the age at first birth, or many other biological parameters for this endangered species. To assess whether the population of North Pacific humpback whales is increasing and recovering from exploitation, one of the foremost thrusts of future research should be to gather information on the life histories for whales of known age, especially females and their offspring, to document survival and reproductive rates. In southeastern Alaska, there have been few resightings of whales first seen as calves and later as juveniles and adults. How many of these calves are surviving and how many are recruited into the sexually mature population of reproducing adults is not yet known. This information will be of crucial importance for monitoring the recovery of humpback whales in the North Pacific.

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